AN ECOLOGICAL STUDY OF *PARANEPHROPS PLANIFRONS* WHITE (DECAPODA : PARASTACIDAE) IN LAKE ROTOITI, NORTH ISLAND

A thesis

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Frontispiece. A rare individual. *Paranephrops planifrons* is typically heavily pigmented and occurs in a range of colours including off black, dark greens, blues, browns and mottled browns. The photograph was taken in L. Tarawera at 15 m depth.

Frontispiece
A rare individual

In dedication to Eileen and Leo who have given me so much in so many ways.

"Mollusks are far more interesting - bugs sweeter - while the dinner crayfish hath no parallel for intense and absorbing interest in the three kingdoms of nature"

Thomas Huxley 1876

ABSTRACT

The *Paranephrops planifrons* population in mesotrophic L. Rotoiti consists of 2 bathymetrically and temporally separate breeding groups. Late autumn breeders comprise about 80% of the population, occupy depths mainly above 30 m and at night feed in the littoral zone, where food is 80% more concentrated than elsewhere. Early summer breeders exist mainly below 30 m depth. Utilisation of the whole lake bottom and seasonal changes in food available to the early summer breeders are tentatively given as explanations of this pattern.

Crayfish show increased sensitivity to light intensities greater than 150-205 lux and consequently occupy shelters above around 12 m depth. Shelters include any recesses subjected to intensities below this range. This zone accomodates almost the entire juvenile population and ca 10-20% Of the adult population. This response to light intensity is believed to be an adaptation promoting avoidance of their main predator, the shag. Nocturnalism is another adaptation reducing losses to predators, including trout. Crayfish at greater depths lie unprotected and inactive by day and ca 70-80% of these adults form a high density band around the lake at a mean annual depth of 19.2±2.8 m. The band has a mean annual vertical depth range of 11.4±2.1 m and densities up to 50 crayfish m^{-2}.

At dusk activity begins in the deepest waters first and crayfish forming the band migrate shorewards, while those above emerge from shelters. Within the hour feeding

on detritus mainly, commences amongst the weed beds which extend to 6 m depth. At dawn a downward migration preceeds reformation of the high density band. These dual diel migrations apply almost solely to late autumn breeders and are part of a circadian rhythm, the timing of which is modified by light. Locomotion associated with migratory activity appears to be effected mainly through leg proprioceptors responsive to gravity. Directional orientation at this time and also generally, is inversely related to bottom slope angle.

The diel distribution pattern varies seasonally. In summer and autumn the high density band is displaced shorewards by a vertical distance of 3.3 m, to a mean depth of 18.3 m and there is a 4 fold increase in crayfish inhabiting shallow water shelters. This closer association with the main feeding ground is probably an adaptation to meet coincident increases in energy needs. It applies especially to late autumn breeding females, whose period of ovarian development occurs between December and April. Energy requirements appear to be met through food consumed rather than from food stored. Female feeding activity is directly related to temperature but not in males, and prewinter storage is apparently of little importance in both sexes.

Hypolimnetic deoxygenation affects early summer breeders mainly and induces a mass migration from the deeper regions to above the 30 m contour by February. Complete recolonisation of these parts follows lake turnover in May. Crayfish occur on all substrate types in approximately equal numbers except very soft muds, which support densities of <0.001 crayfish m^{-2}.

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SYMBOLS

The following symbols and abbreviations have been used throughout the thesis:

ns	=	no significant difference
*	=	$p < 0.05$
**	=	$p < 0.01$
***	=	$p < 0.001$
n	=	number of observations
N	=	number of crayfish
r	=	value of the correlation coefficient
t	=	student's t
SD	=	standard deviation
CV	=	coefficient of variation
D	=	statistic of the Kolmogorov-Smirnov goodness of fit test
χ^2	=	Chi - square
CL	=	cephalothoracic length
EI	=	egg index

INTRODUCTION

Two allopatric species of the endemic genus *Paranephrops* (family Parastacidae) inhabit fresh waters of New Zealand (Hopkins 1970). *Paranephrops planifrons*, or koura, occurs throughout the North Island and in the West Coast, Nelson and Marlborough districts of the South Island. *Paranephrops zealandicus* is found on the eastern side of the Southern Alps, from North Canterbury southwards to Stewart Island. Their geographical history has been reviewed by Carpenter (1977) who believed that the two species probably separated in the early Pliocene and became isolated by the Pleistocene, when the Main Dividing Range reached its present-day configuration.

P. planifrons was first named and described by White (1842). *P. zealandicus* was originally called *Astacus zealandicus* (White 1847), then later changed to its present-day nomenclature by Miers (1874). There was early confusion as to the actual number of species in New Zealand. A third South Island species, *Paranephrops setosus*, was named by Hutton (1873) and accepted by various authors including Faxon (1898) and Archey (1915) but has since been synonymised with *P. zealandicus* (Hopkins 1970). Chilton (1889a) proposed the merger of *P. setosus* with *P. zealandicus* under the new name *P. neo-zealandiae* but withdrew this suggestion in a later paper (Chilton 1900). Undoubtedly the confusion arose from certain morphological differences that exist between individuals from different localities (Chilton 1889a).

Morphologically distinct populations of *P. planifrons* also occur and form a cline from Northland to the South Island, with the more southern populations resembling *P. zealandicus* (Archey 1915). The systematics of both species have been reviewed by Hopkins (1970).

Both species occur between sea level and altitudes approaching 2500 m (Carpenter 1977). They occupy similar habitats including stony and muddy substrates within waters ranging from small creeks to large rivers and from ponds to lakes (Hopkins 1970), as well as swamps (Archey 1915, Eldon 1968). Largest sizes are attained in lakes. Riek (1972) classifies *Paranephrops* as a moderate burrower and Hopkins (1970) mentions that both species commonly form burrows where substrates are suitable. They feed mainly at night and are omnivorous bottom feeders, consuming a wide variety of autochthonous and allochthonous material as detritus mainly but also in a less decomposed form, as well as live aquatic macrophytes (Archey 1915, Devcich 1974).

In a general review, Chapman and Lewis (1976) comment that although many New Zealanders are familiar with *Paranephrops*, surprisingly little is known of its biology. This is especially true of crayfish inhabiting lakes, for apart from a preliminary study on the ecology of *P. planifrons* in L. Rotoiti (Devcich 1974), a physiological study on respiration (Whittle 1973) and a biochemical analysis of wax esters (Robinson 1975) in the same species, information is lacking. A little more is known of crayfish in streams. Hopkins (1966; 1967a; b) studied aspects of the breeding biology and growth in

populations of *P. planifrons* in streams within the Wellington and Wairarapa districts. Physiological studies have included that by Quilter (1975) on circadian activity rhythms of *P. zealandicus* from streams in the Dunedin area and work on the osmoregulation of both species in streams throughout the country (Wong and Freeman 1976a; b). From a commercial viewpoint the highly palatable nature of *Paranephrops* has recently prompted feasibility studies into the farming of both species (Shaddick 1976; Dr B. Jones, Fisheries Research Division, Ministry of Agriculture and Fisheries, Wellington, unpub. data).

This study is based on the ecology of *P. planifrons* inhabiting lakes within the Volcanic Plateau region and was specifically designed to enable a detailed answer to the question "why are crayfish where they are?" An account is given of diel and seasonal spatial distribution patterns of the population in L. Rotoiti and analysed in terms of the controlling effects of specific environmental factors on these patterns. These environmental factors included light, temperature, oxygen, bottom slope, substrate, shelter and food. As well, seasonal biological cycles are presented and related to seasonal changes in the diel distribution pattern. The importance of predators in determining this pattern is also considered.

THE STUDY AREA

The study area included Lakes Rotoiti, Okataina, Rotoma, Tikitapu, Tarawera and Rerewhakaaitu, all of which occur within a 30 km radius between northeast and southeast of Rotorua city, and L. Taupo, some 75 km further south (figure 1). The study lakes lie in the Taupo Volcanic Zone, and are volcanic in origin. They were formed over the past 50,000 years by way of 3 main processes acting either singly or in combination (Healy 1975a). These processes were firstly, eruptions that produced craters by explosion (Lakes Rotoma, Tikitapu and the Awaatua Basin in L. Rerewhakaaitu), secondly, subsidence that produced crater-like depressions or calderas (Lakes Tarawera and Taupo) and thirdly, eruptions of lava and other ejecta that caused the damming of valleys (Lakes Rotoma, Rotoiti, Tikitapu and Okataina) (Grange 1937, Healy 1963; 1975a).

Catchment soils are derived from series of ash showers which mantled the region between 131 AD and very recent times (New Zealand Soil Bureau 1968). Briefly, rhyolitic Taupo ashes erupted in 131 AD and form the soils around L. Taupo. Kaharoa ashes are also rhyolitic and erupted from Mt. Tarawera about 1150 AD to produce the soils at the northwestern end of L. Rotoiti. Collectively, they comprise the yellow brown pumice soils which are typically very friable and although highly prone to leaching, respond well to fertilisers to produce pastures for farming sheep and cattle mainly. Overlying the Kaharoa ash beds are basaltic Tarawera ash and rhyolitic Rotomahana mud, erupted in 1886. Tarawera ash is also

Figure 1. Map of the Rotorua district showing the location of its major lakes including Lakes Rotoiti, Rotoma, Tikitapu, Okataina, Tarawera and Rerewhakaaitu. Lake Taupo is shown in the insert at right. Sampling sites are marked S. The map at left indicates the position of both study areas in relation to the rest of the North Island of New Zealand.

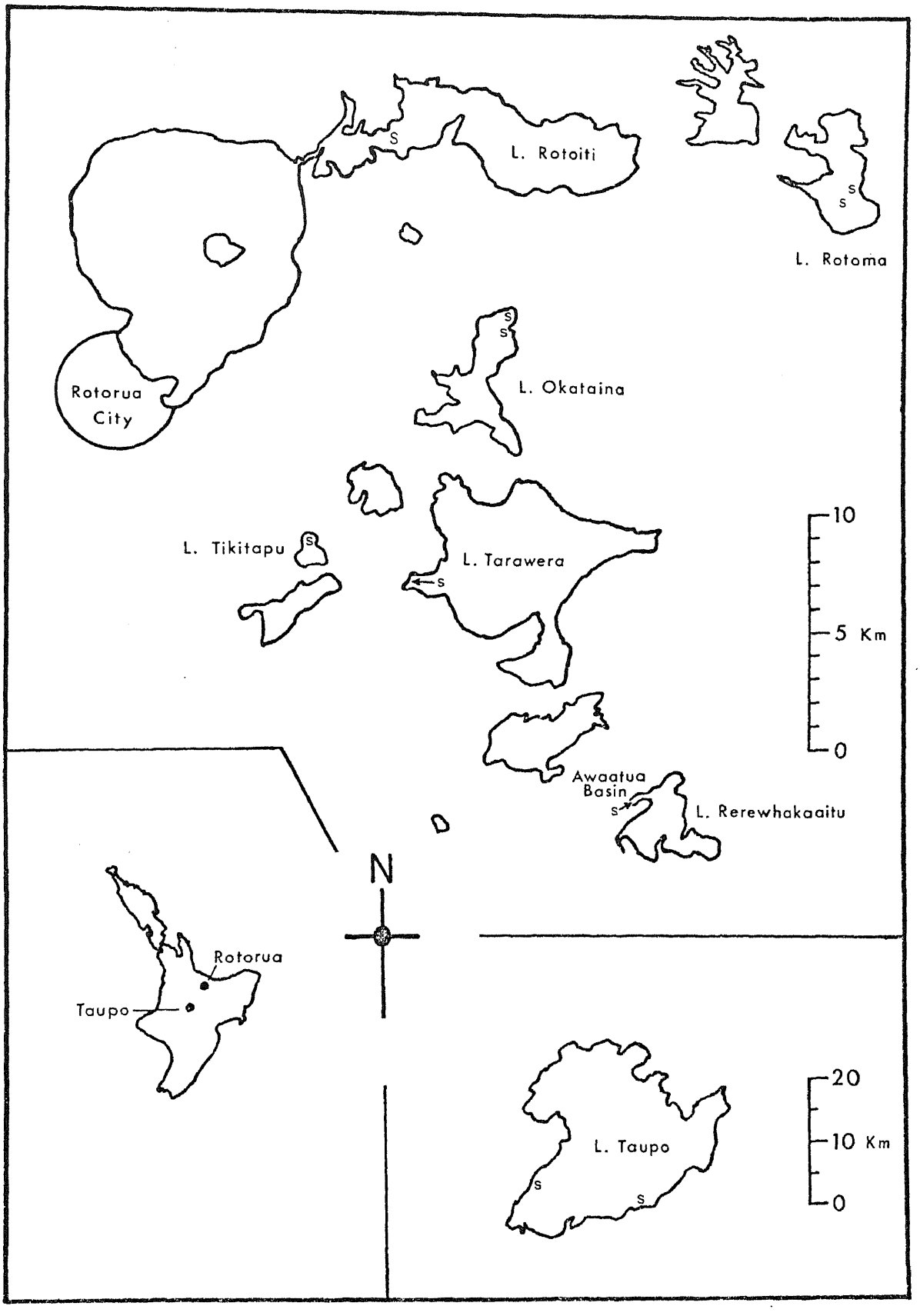

Figure 1
Map of the Rotorua District ...
Between pp 4,5

from Mt. Tarawera and covers the catchments of Lakes Rotoma and Okataina and most of Lakes Rotoiti and Tarawera. The resultant soils are gravelly sands and tend to be low in moisture and nutrients. Rotomahana mud was ejected from L. Rotomahana and spread over Lakes Rerewhakaaitu and Tikitapu northwards to the western arm of L. Rotoiti. It has given rise to sandy loams which tend to be richer in nutrients than Tarawera soils, owing mainly to hydrothermal weathering of minerals before eruption.

Some features of the 7 lakes and their catchments are given in Table 1. Typically the sides of the lake basins are fairly steep, resulting in relatively narrow littoral zones and extensive deep water basins that flatten out towards the centre. The larger lakes possess a number of basins, some of which are modified by small, deep explosion craters and near vertical subsurface volcanic plugs, giving a somewhat irregular bottom contour. Bottom substrates are generally of coarse materials (rocks, pumice, sand) in the shallows, giving way to increasingly fine muds as depth increases. A few islands and islets occur scattered mainly around the periphery of the larger lakes. All of the lakes are prone to fluctuations in water level, especially those without surface outflows. For example, Maori villages which existed about 200 years ago now lie ca 10 m and 6.7 m below the present levels of Lakes Rotoma and Okataina respectively (Healy 1975b).

The water chemistry of a lake affects its limnology. The study lakes are typically neutral and soft, with bicarbonate or chloride as the dominant anions and a high

TABLE 1. Characteristics of the lakes studied and their catchments. Data compiled from Jolly (1968), McColl (1972; 1974; 1975), Healy (1975a), Burstall (pers. comm.) and myself. *Awaatu Basin only.

Lake	Alt. above s.l. (m)	Max. length (km)	Max. breadth (km)	Peri-meter (km)	Max. depth (m)	Surface area (km^2)	Total volume ($x10^6 m^3$)	Strat-ifies	Apprec. hypolim. deox.	Trophic status	Surface outflow	Inflow	Catch-ment area (km^2)	Catch-ment usage
Rotoiti	278	17.3	3.6	72.6	93.5	36.8	1068.1	Yes	Yes	Meso.	Kaituna River	L. Rotorua streams, hot & cold springs	67.0	Agric. & forest
Rotoma	315	5.5	3.5	28.7	80.0	10.9	458.9	Yes	No	Oligo.	None	Streams & hot spring water from streams	16.0	Agric. & forest
Okataina	307	5.7	3.9	31.4	80.0	10.0	477.3	Yes	No	Oligo.	None	Streams & probably springs	55.4	Some agric. & forest
* Rerewha-kaaitu	438	0.6	0.3	1.7	31.0	0.1	-	Yes	Yes	Meso.	Joins main lake	Small streams	-	Agric. & scrub
Tikitapu	415	1.6	1.3	5.0	26.0	1.5	27.7	Yes	Seldom	Oligo.	None	Small streams	4.3	Native forest
Tarawera	298	10.4	10.4	65.3	87.5	44.2	-	Yes	No	Oligo/ Meso.	Tarawera River	L. Rotomahana, streams & hot springs	194.0	Some agric. & forest
Taupo	369	40.2	27.3	181.3	164.6	616.0	-	Yes	No	Oligo.	Waikato River	Tongariri River, many streams, hot & cold springs	3238.0	Agric., forest, industry

ratio of monovalent (K^+ and Na^+) to divalent (Ca^{++} and Mg^{++}) cations (McColl 1975). As a result they are broadly similar biologically, although L. Rerewhakaaitu lacks the beds of exotic macrophytes which exist in the other lakes (Fish 1978). Crayfish probably have a minimum calcium requirement and it is interesting to note that McColl found lakes with hot-spring inflows to be considerably higher in calcium than those without known hot-springs. Calcium levels ranged from 0.7 - 6.3 mg l^{-1} in the 7 lakes.

Apart from L. Okataina which was stocked with *P. planifrons* from L. Taupo in the 1940's (Devcich 1974), it is not known how or when crayfish became established in the Rotorua lakes. Crayfish could have naturally invaded Lakes Rotoiti, Tarawera and Taupo through their river outflows, while lakes without surface outflows were possibly stocked by man. There is an alternative explanation for the presence of crayfish in lakes with surface outflows. Past volcanic activity has caused the union of some lakes, for example Lakes Rotoiti, Rotoma, Rotorua and Rotoehu (Fish 1975), during which colonisation may have occurred through their common surface outflow. Subsequent downcutting at the outflow lowered the water level and the lakes became isolated, each with its population of *P. planifrons*.

The study area was restricted mainly to L. Rotoiti (38° 02' S, 176° 24' E) (plates 1 and 2). L. Rotoiti is unusually long and sinuous compared to other lakes in the Rotorua district. Its geological history has been

Plate 1. Aerial view of L. Rotoiti. The view is from west to east and includes L. Rotorua (foreground), Ohau Channel (between the lakes) and the location of the Kaituna River outlet (end of foremost lake extension at left). The main area of research is shown by an X.

Plate 2. View from Te Puhoe Bay, L. Rotoiti, overlooking the main area of research.

Plate 1
Aerial view of L.Rotoiti
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Plate 2
View from Te Puhoe Bay
Between pp 7,8

outlined by Grange (1937). Briefly, the eastern half is deep and originated as the northern corner of the huge Haroharo Caldera which formed during the late Pleistocene. The steep cliffs running along the northern shores are actually part of the caldera's rim. Rhyolitic lava flows within the caldera then formed the southern shoreline. Volcanic quiescence followed, the lake waters rose and eroded a passage westward to finally form the Kaituna River. As a result the western arm of L. Rotoiti is shallower and has a highly irregular shoreline with many embayments.

L. Rotoiti is mesotrophic and may be classified as a monomictic, second-class lake (Hutchinson 1957) since it shows an alternation of stable summer stratification and winter mixing (Fish 1975). During periods of stratification, internal seiches commonly occur and have been documented by Green, Norrie and Chapman (1968), Fish and Chapman (1969) and Fish (1975). This lake is particularly susceptible to seiche formation from prevailing westerly winds, for it is elongated east to west and usually remains stratified for about 6 months of the year.

At the far western end lies the Western Basin, where both the main inflow from L. Rotorua and the Kaituna River outflow are situated. This basin is small and biologically distinct from the rest of the lake (Fish and Chapman 1969). Possible causative factors are its general shallowness (maximum depth of 10 m) and that it receives the more eutrophic L. Rotorua waters, which incidentally may also explain generally lower Seechi readings within Rotoiti's

western arm compared to the eastern end.

An interesting feature of the lake is the recent discovery of large heat flows through isolated parts of its bottom sediments (Evison and Calhaem 1972). Fish (unpub. data) found that the associated heat input slightly raised water temperatures of the hypolimnion and, as a result, induced a comparatively short period of summer thermal stabilisation, as well as marked increases in phosphate accumulation and oxygen depletion rates within the hypolimnion during that period. The lake bottom is also occasionally subjected to minor bursts of volcanic activity in the vicinity of these 'hot spots'. A recent disturbance occurred on 3 June 1979 at the eastern end of the lake and resulted in water discolouration and the death of aquatic life, including *P. planifrons*.

Vegetation in the catchment comprises exotic forest to the south of the western arm, native bush mainly at the eastern end, pastureland which occupies the northern and northwestern boundaries (constituting about 33% of the catchment area), and scattered scrub. As indicated in Table 1, the human population is fairly dense and is concentrated around the northwestern and southeastern shorelines. There is an undesirably high nutrient input into the lake, the main contributing factors being superphosphate, which is applied liberally to the low fertility soils, stock effluent, sewage, hot-springs and the L. Rotorua discharge. As a result the lake's present condition has given some cause for concern, though McColl (1974) considers the lake would probably respond well to

control of nutrient inputs. Burnet and Wallace (1973) assessed P_{max} (maximum carbon assimilation rate) values as an estimate of the productivity of L. Rotoiti and found that its waters gave a relatively low mean value of 16.5 µg C assimilated l^{-1} hr^{-1}.

A list of the principal plant and animal species within the lake is presented in Table 2. In addition, the more commonly found aquatic birds include 3 species of shag (*Phalacrocorax* spp.), duck (*Anas* spp.), scaup (*Aythya novaeseelandiae*), dabchick (*Podiceps rufopectus*), black swan (*Cygnus atratus*), and inland gulls (*Larus dominicanus, L. novaehollandiae scopulinus*). Also, cattle and sheep drink from the lake and man uses it for domestic and recreational purposes. Brown and rainbow trout were first introduced in 1889 and 1898 respectively. These trout actually came from consignments of fingerlings released in L. Rotorua, having entered L. Rotoiti via the Ohau Channel. The subsequent restocking of L. Rotoiti with trout has varied considerably over the years and since 1971 a rate of 12,500 yearlings per annum has been maintained (Burstall pers. comm.).

A bathymetrical map of L. Rotoiti compiled in 1966 from echosounding traverses (Irwin 1969) is presented in Figure 2. A more detailed map (figure 3) (taken from Irwin and Main 1979) shows the bathymetry of the main research area located in the western arm of the lake. Also included in Figure 3 is a bottom profile taken from the shoreline of Te Puhoe Bay to the 50 m contour.

Table 2: Principal species in L. Rotoiti.

Classification	Species	Reference
Algae	*Melosira granulata*	Cassie 1974
	M. distans	"
	M. granulata var. *angustissima*	"
	Asterionella formosa	"
	Mougeotia sp.	"
	Actinotaenium pyramidatum	"
	Dinobryon cylindricum var. *alpinum*	"
	D. sertularia	"
	Closterium aciculare	"
	C. acutum var. *variabile*	"
	C. setaceum	"
	Actinastrum hantzschii	"
	Ankistrodesmus falcatus	"
	Staurastrum floriferum	"
	Peridinium sp.	Fish & Chapman 1969
	Volvox sp.	"
	Nitella hookeri	Chapman et al 1971
	N. gracilis	"
	Enteromorpha nana var. *rivularis*	"
	Ulothrux subtilis	"
	Spirogyra sp.	"
	Anacystis cyanea	"
Lycopsida	*Isoetes kirkii*	"
Angiospermae	*Glossostigma elatinoides*	"
	G. submersum	"
	Elodea canadensis	"
	Lagarosiphon major	"

Cont. over

Classification	Species	References
Angiospermae		
	Limosella lineata	Chapman et al 1971
	Ludwigia palustris	"
	Lilaeopsis lacustris	"
	Myriophyllum elatinoides	"
	M. propinquum	"
	Potamogeton cheesemanii	"
	P. cripus	"
	P. ochreatus	"
	Utricularia protrusa	"
Copepoda		
	Calamoecia lucasi	Chapman 1973
	Macrocyclops albidus	"
Cladocera		
	Ceriodaphnia dubia	"
	Bosmina meridonalis	"
Rotifera		
	Asplanchna priodonta	Jolly & Chapman 1977
	Keratella cochlearis	"
	K. sancta	"
	Trichocerca longiseta	"
Coelenterata		
	Craspedacusta sowerbyi	Fish 1971
Diptera		
	Chironomous spp.	Forsyth 1975
Gastropoda		
	Potamopyrgus antipodarum	pers. obs.
Bivalvia		
	Hyridella menziesi	"
Decapoda		
	Paranephrops planifrons	Devcich 1974
Pisces		
	Gobiomorphus cotidianus	McDowall 1975
	Retropinna lacustris	Jolly 1967
	Galaxias brevipinnis	McDowall, Hopkins & Flain 1975
	Salmo trutta	Smith 1959
	S. gairdnerii	"

Figure 2. Bathymetric map of L. Rotoiti. Contours are at 20 m intervals. The location of the main research area is indicated by the arrow.

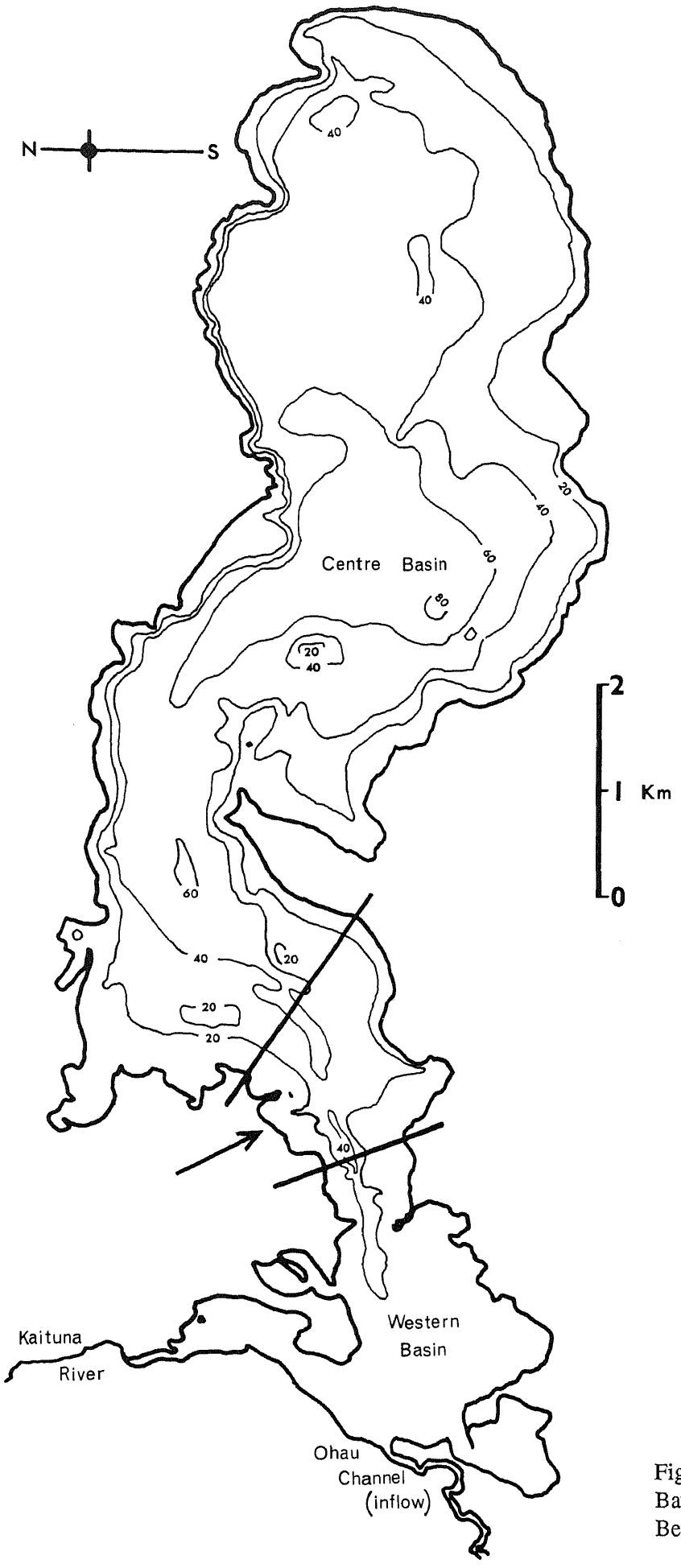

Figure 2
Bathymetric map of L.Rotoiti
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Figure 3. Detailed bathymetry of the main study area indicated in Figure 2. Contours are at 10 m intervals. The traverse giving the bottom profile below is indicated by the heavy line extending from Te Puhoe Bay. The location of dive transects (numbered 1-3) is also given.

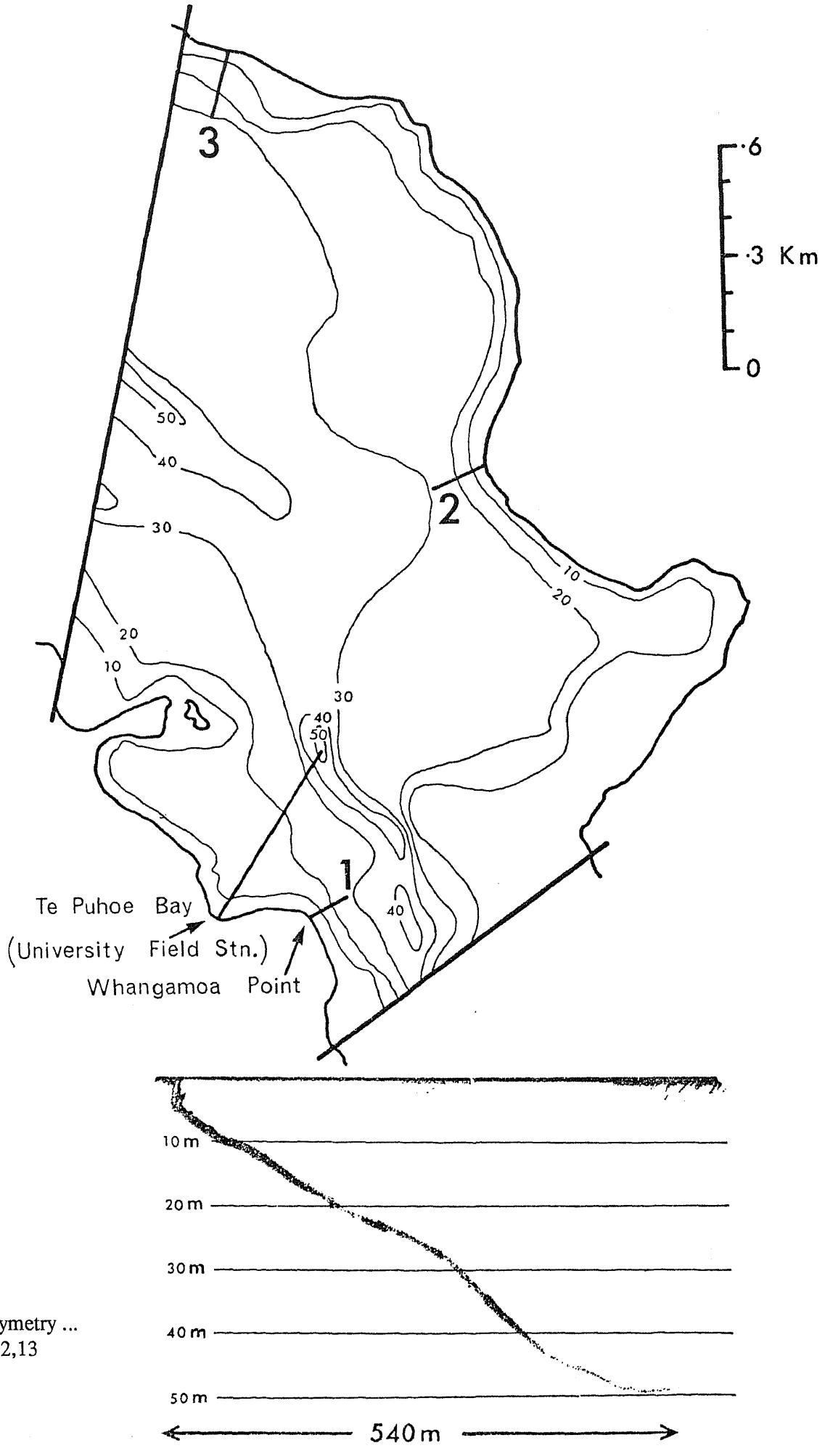


Figure 3
Detailed bathymetry ...
Between pp 12,13

METHODS

1. Crayfish Collection

Crayfish were sampled mainly by trapping but also by various means using SCUBA. The traps were used at night to depths of 50 m whereas SCUBA was generally used during the day and at depths less than 40 m, although a few night dives were made to complement trapping results. Additional collections were by snorkeling to 5 m during the day and by handnetting to 1 m around the shore at night.

2. Determining Distribution by SCUBA

By swimming down a bottom slope of relatively constant gradient the vertical distribution of crayfish was determined. A 3 m pole with a depth gauge attached was held by its midpoint and at right angles to the direction of slope. For every 2 m of vertical fall between the 6 and 30 m contours all the crayfish within the 3 m strip were counted. Numbers were recorded on an underwater pad. A relatively smooth substrate was chosen so that all crayfish present were visible. Single runs, along 3 transects (indicated in figure 3), were made within the same day and the average number of crayfish seen was calculated for each depth range. A single night run was made with the aid of an underwater torch. Sampling was conducted in March 1978 when no crayfish existed below 30 m depth.

3. Underwater Photography

Underwater photography was used to show in situ behaviour induced by environmental stimuli. Photographs were taken with a Nikonos III camera and either a 35 mm, 80 mm, or close-up lens. Lighting was provided by a Sunpak 28 flash unit and the films used were rated at 125 ASA and 400 ASA. The comparatively high loading of particles in suspension within L. Rotoiti induced light scatter, which consequently made it difficult to obtain prints that were clear in definition and contrast. Best results were obtained in the clearer Lakes Taupo, Okataina, Rotoma and Tarawera.

4. Trapping

a) Traps

Traps were simple in design, being cylindrical and funnelled at both ends (plate 3). They were made from a framework of 6.8 mm gauge steel rod, covered with galvanised wire mesh (1.2 x 1.6 mm mesh diameter) and one end was detachable to allow baiting and removal of crayfish. Each trap was baited with ca 100 g of fresh beef liver, by attaching it with wire to a supporting central rod.

Moriarty (1971) compared the effectiveness of 9 bait types for *Astacus pallipes*: dead crayfish, herring, fresh and stale pike, perch, stale mackerel, red meat (beef or mutton), canned sardine and beef liver, of which the last mentioned was the most successful.

Plate 3. Type of trap used throughout the sampling programme.

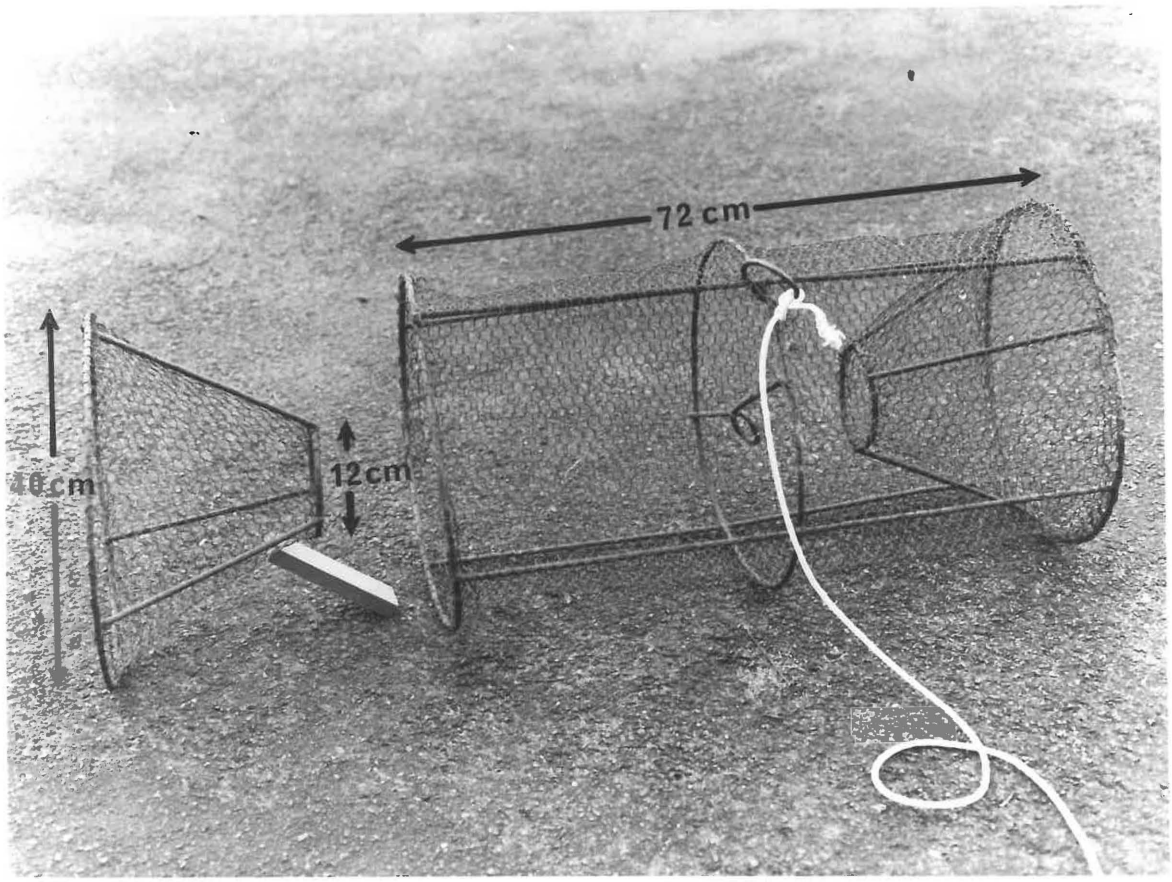


Plate 3
Type of trap used throughout
the sampling programme
Between pp 14,15

Since size of the mesh used in traps can affect catch rate, minimum size retention and ease of their handling through the water column, the effect of mesh size on these parameters was examined. 3 traps were constructed with different mesh sizes: 0.2 x 0.2 cm 'fine', 1.2 x 1.6 cm 'medium' and 2.1 x 2.7 cm 'coarse'. On 4 occasions they were set at night, 1 m apart, in a weed bed containing approximately 10 crayfish m^{-2}. Traps were raised each following morning and the number caught per trap and the CL of the smallest crayfish were noted. Results are given in Table 3. The medium mesh size gave the most acceptable compromise since, although more and smaller crayfish were retained by the trap made of fine mesh, it tore easily and was very heavy to raise by hand.

b) Procedure

Trapping was conducted at midmonthly intervals over a 2 year period, from January 1975 to December 1976. 4 traps, each separated by at least 20 metres were set at 1, 10, 20, 30 and 50 m depths and connected to a buoy and graduated line. Traps were lowered and raised by hand. For the last 3 months of 1976 a Marlin DIR-60 depth recorder was used to determine sampling depths. Traps were set in the late afternoon or evening and raised during the following morning. Setting and raising times were noted to allow total trapping time per depth to be

Table 3: Number captured and minimum size retained in traps of different mesh size.

Trial number	Mesh size		
	fine	medium	coarse
1	27	19	9
2	25	27	8
3	28	14	17
4	5	9	5
Total:	85	69	39
Min. Size (mm CL)	26.9	29.4	41.0

calculated.

5. Field Analysis

The total numbers and those of males and females captured at each depth were recorded. The CL, taken from the tip of the rostrum to the mid-dorsal posterior border of the cephalothorax of each animal was measured with Vernier calipers (accurate to 0.1 mm). Males were checked for sperm extrusion from the paired gonopores and presence of spermatophores. Females were examined for the presence of spermatophores and egg shells attached to pleopods. The number of gravid females was recorded and a simple egg indexing system, similar to that used by Pandian (1967; 1970) for *Crangon crangon* and *Homarus gammarus* respectively, was devised to allow quick assessment of degree of egg maturation while in the field (table 4). The index was based on yolk colour and associated embryonic development and consisted of 5 stages of unequal duration. A x10 magnification hand lens was used to aid in distinguishing those eggs difficult to categorise. Also shown in Table 4 are details of mean egg length, the relative duration and percentage water content at each stage.

All trapped crayfish were examined for external foreign growths. The occasional large adult carried a single encrusting sponge [Spongillidae sp. (Penney and Racek 1968)] up to 1 cm in diameter on its cephalothorax. No specimens of *Temnocephala novae-zealandiae* were found in any of the 7 crayfish populations. This is an epizoite

Table 4: Egg index with criteria for each stage.

Stage	Yolk colour	Approx. embryonic development (%)	Relative duration (%) N = 27	Mean egg length (mm) N = 20	Water content (%)
1	light brown turning darker	none	28.2	2.06±0.21	49.9
2	dark brown	≤25	23.1	2.15±0.14	55.5
3	dark brown or plum red	25-50	16.8	2.21±0.10	59.5
4	dark brown or plum red	50-75	8.6	2.31±0.16	62.1
5	brown and yellow	75-100 (hatched larvae)	23.3		69.3

common in *P. zealandicus* (Fyfe 1942) but apparently confined to only a few populations of *P. planifrons* (Chilton 1889b).

6. Moult Cycle

Numbers of recently-moulted crayfish obtained during trapping were used as an indicator of moulting activity in the adult population. Water content of the exoskeleton varies during the moult cycle (Drach 1939, in Passano 1960a) affecting carapace rigidity, which can thus be used as an indicator of moulting cycles. Such changes in carapace pliancy were used by Abrahamsson (1972) to determine stages in the moulting cycle of *Astacus astacus*.

An instrument was designed to assess carapace rigidity in the field (plate 4). It consisted of a flexible copper strip with a projecting metal lip, resting against a rotatable cam with indicator needle, and mounted on a board. A crayfish was securely positioned by hand with its carapace abutting the metal lip and the cam was turned causing the copper strip to exert pressure on the carapace.

Very recently-moulted crayfish were not caught in traps since they did not commence feeding until about 36 hours after moulting (Whittle pers. comm.), however, since exoskeleton hardening continues for a variable time (6-10 weeks) after moulting, the instrument was calibrated using laboratory-kept animals to approximately distinguish those crayfish which had moulted within the

Plate 4. The carapace rigidity testing device. The device has been calibrated such that if indentation occurs while the needle lies within the white sector of the disc, which is being turned in the direction noted by the arrow, then the exoskeleton is recorded as soft. Conversely, if indentation does not occur inside the white sector the exoskeleton is noted as hard. (see text for further explanation.)

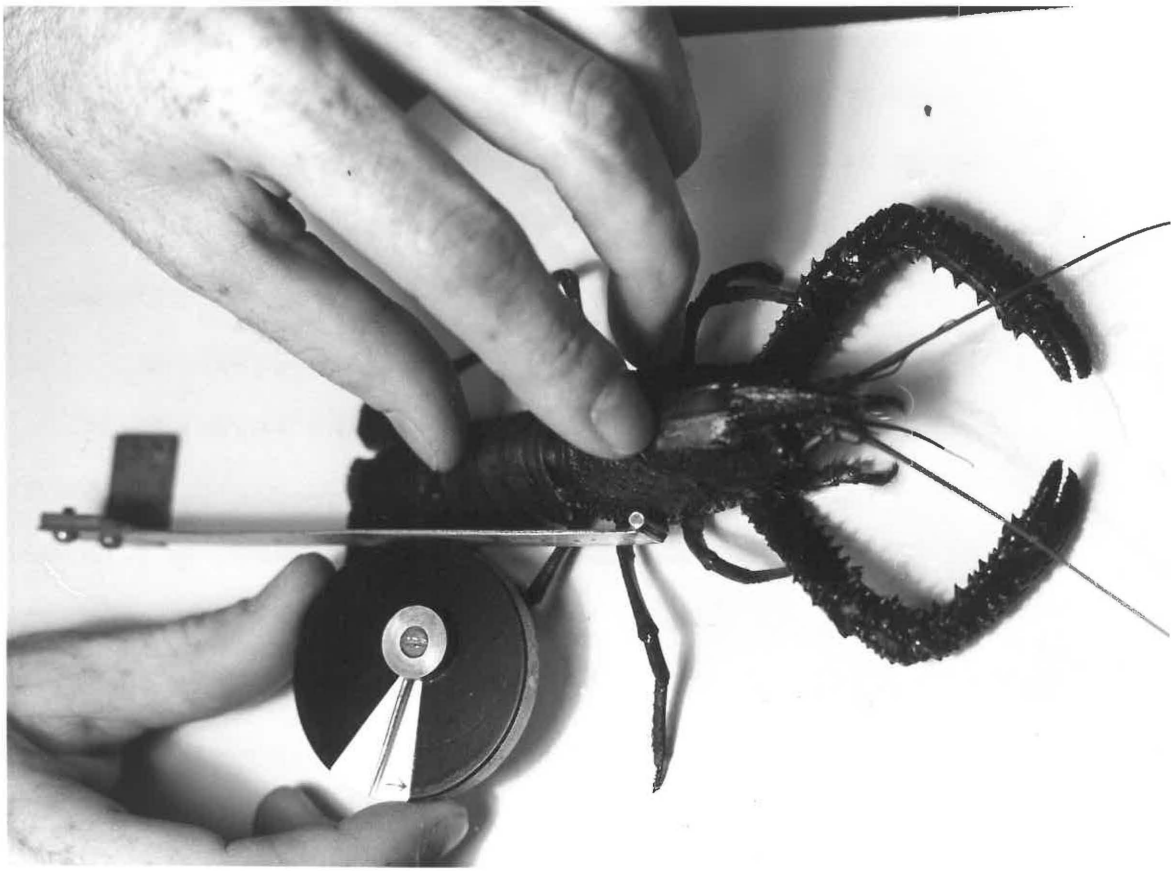


Plate 4
The Carapace rigidity testing device
Between pp 19,20

previous month. The carapaces of 20 such crayfish were tested to determine the amount of pressure required before indentation occurred. Results ranged from almost zero in the most recently moulted animals, to 28 g. This latter figure was taken as the critical value and was marked by a line (at tip of arrow) on the cam. The corresponding carapace water content was found to be 57.7±3.1%. If carapace flexion occurred up to the calibration line, the crayfish was classified as having moulted in the previous month.

It was possible that not all carapaces fully hardened between moults, so the above method may have incorrectly included some of these individuals as having recently moulted. Field evidence indicated these crayfish comprised less than 6% of the male population (as indicated by June and July readings in figure 37, following p. 155), while the female population was unaffected. As the actual moult could have occurred 3-30 days before the animals were captured, the results were backdated by 14 days to give a truer indication of actual moulting times.

7. Collection of Surface Sediment

In order for sediment food value to be assessed, surface samples of the bottom sediments were collected from depths of 1, 10, 20, 30 and 50 m during the monthly trappings in 1975. Winter samples and those from 30 and 50 m were taken with an Ekman grab. In addition, a few samples from shallower depths were obtained in this manner at other times of the year. It was found that extreme care

in raising the grab was essential to minimise the loss of surface sediment in escaping water. When successfully raised, a sample (ca 150 g) of the uppermost 2 mm of sediment was taken with a broad bladed knife and placed in a container with ca 5 ml of 4% buffered formalin (Na_2HPO_4 and $NaH_2PO_4.H_2O$ in a 1.6:1 ratio) to preserve the organic fraction. Hargrave (1972) states that a 2% formalin solution is sufficient to stop biological uptake of oxygen by microorganisms in surface sediments.

During spring, summer and autumn, samples were taken directly from depths of 1, 10 and 20 m using SCUBA. Initially a 2 mm layer 20-80 cm long was skimmed off the sediment surface with an 8 cm diameter open screw top container. For the last 6 months a special surface sediment sampler was constructed (plate 5) which enabled more consistent sampling and gave a larger sample size. It consisted of a 37 x 60 cm plastic bag, the open end of which was attached to a rectangular aluminium frame, 27 cm in length and 10 cm in height. A 1 mm gauge, 2 cm wide tin plate attached to the opening acted as a scoop and directed sediment into the bag. The collected sediment was transferred to a labelled screw-top container and preserved with buffered formalin.

8. Temperature, Oxygen and Light

Measurements of temperature, dissolved oxygen and light intensity were made at approximately midmonthly intervals throughout 1975 and 1976. Measurements between January and May of 1975 were made with a YSI Model 54

Plate 5. Surface sediment sampler being used in L. Okataina at 16 m depth.

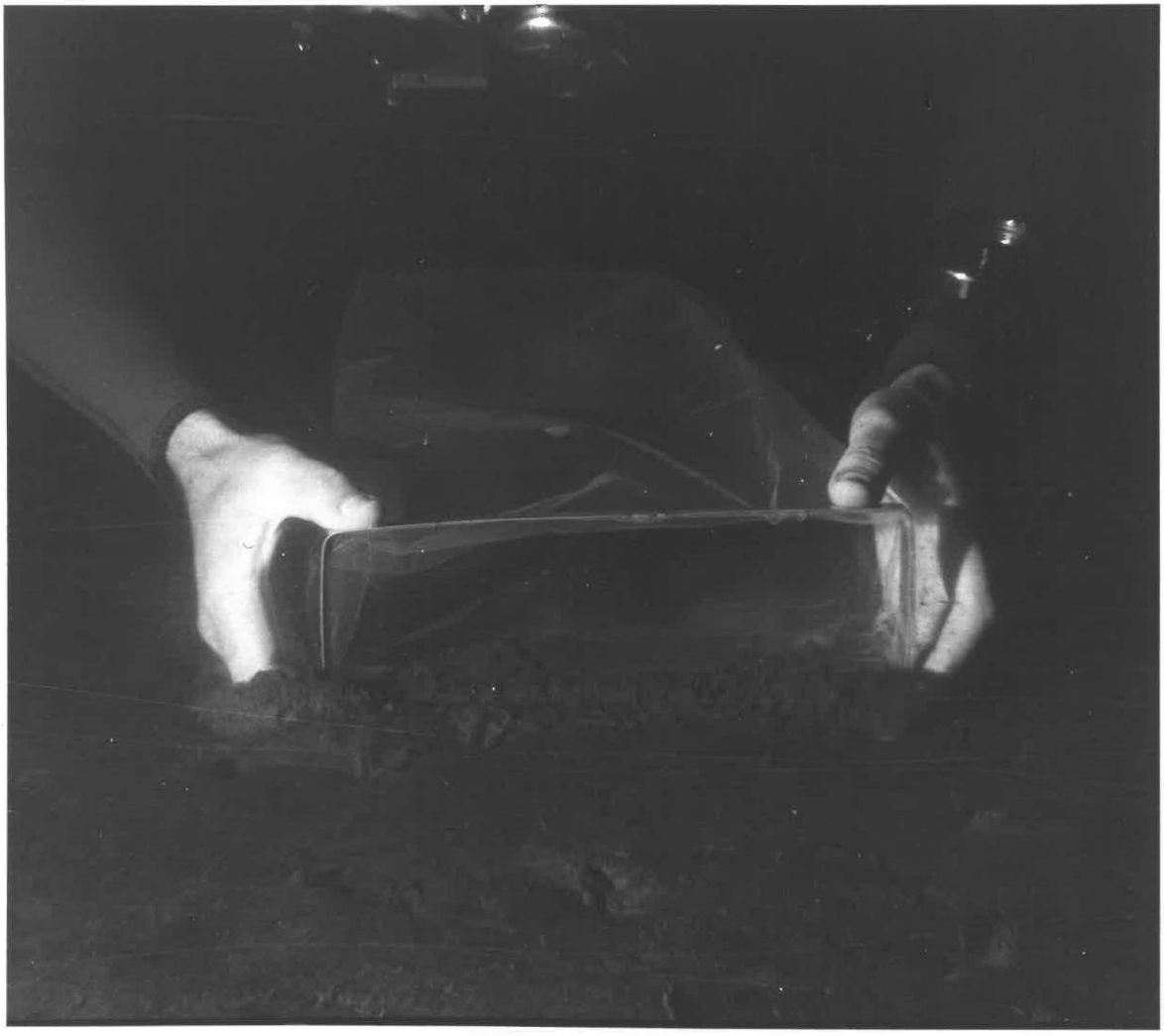


Plate 5
Surface sediment sampler ...
Between pp 21,22

oxygen/temperature meter and a photometer (Bell 1966). Temperature and dissolved oxygen were recorded at 1 m intervals from the surface to a depth of 50 m and light intensity at 1 m intervals from the surface to a depth of 30 m. But after this, data supplied by Dr. G. Fish of the Fisheries Research Division, Ministry of Agriculture and Fisheries, Rotorua, were used. These data were obtained with a YSI Model 5419 oxygen meter and temperature recorded with a thermistor thermometer capable of reading to 0.1°C. Readings of light intensity were made to depths of around 30 m. This meter used a red filter with a percentage transmission quoted at 22.5% and dominant wavelength of 617.2 Å. Spectral curves for the two light meters are given in Figure 4.

9. Laboratory Analysis of 1975 Collections

a) Sediments

The sediment calorific content was determined by wet acid dichromate oxidation using the semi-micro method of Maciolek (1962). This method was used in preference to bomb calorimetry because of the relatively low energy content of the sediment. Since Devcich (1974) found that gut contents of *P. planifrons* ranged down to 125 µm in diameter, collected sediments were sieved to remove all material of smaller size. Samples were then dried for 3 days at 60°C and ground in a mortar. Determinations were made in duplicate and values obtained were corrected by 10% as only about 90% of the organic

Figure 4. Spectral response curves of the 2 light meters used throughout the study. One used a Phillips ROY 2322 600 9400 LDR (solid line), the other a Schott RG 2 filter (broken line).

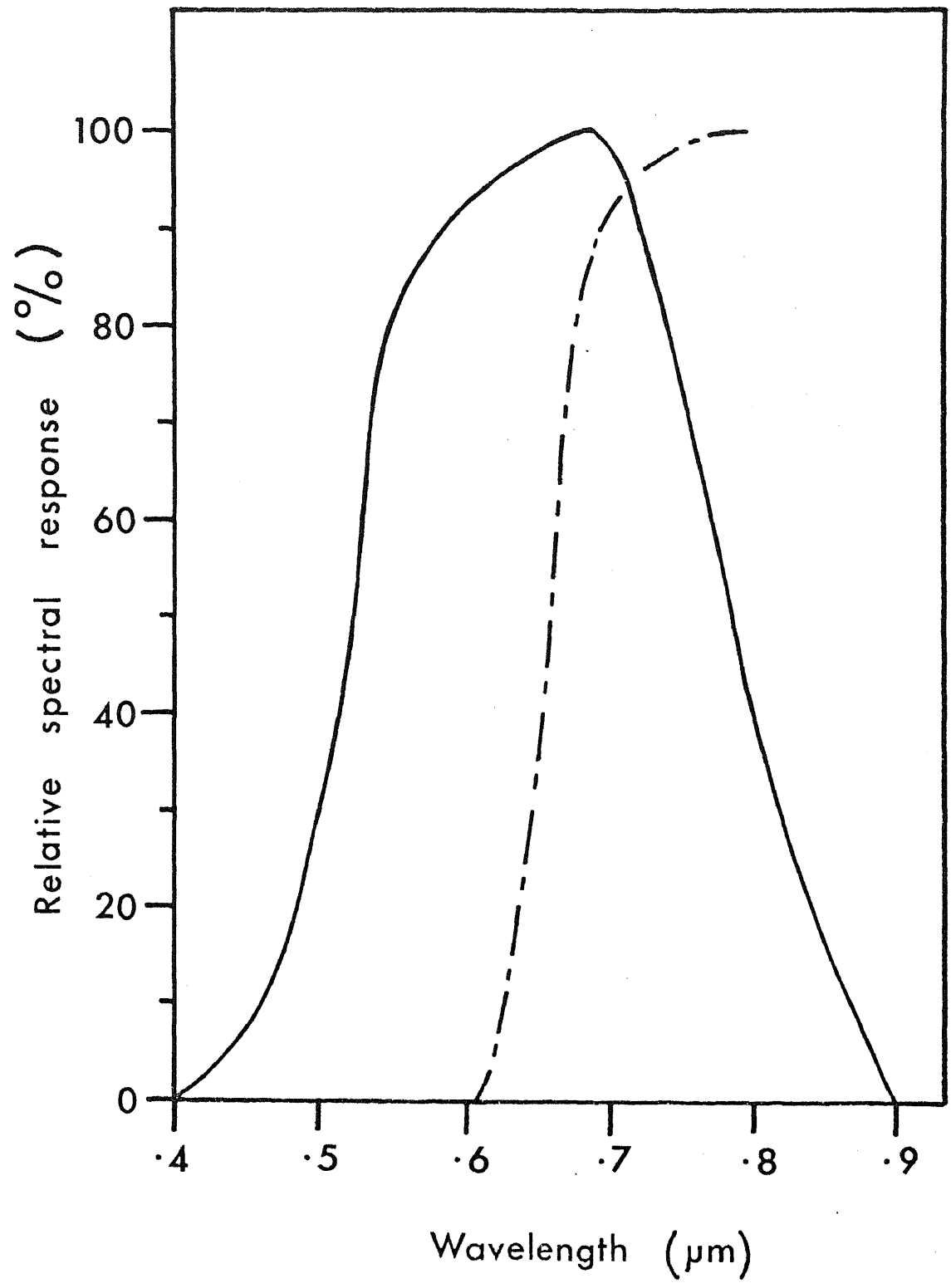


Figure 4
Spectral response curves ...
Between pp 22,23

matter present is oxidised by this method (Winberg 1971).

To check the comparability of the Ekman grab and the surface sediment sampler, 5 paired samples were collected by each method. Each pair was taken from within a 40 cm diameter plot. Table 5 compares calorific contents obtained from the two methods. An average difference of 63.7% existed between the methods, so all results obtained from Ekman grab samples were corrected by this amount.

b) Selection of crayfish for chemical analysis

Most laboratory analyses were of crayfish captured during the monthly trappings of 1975. In 1976 crayfish trapped at 1 and 10 m depth and at 30 and 50 m depth were combined into shallow and deep water groups respectively. Males and females from each group were separated and stored in labelled plastic bags at -15°C.

For each month of 1975 the 3 largest males and females trapped from 1-10 m depth and 30-50 m depth, representing 6 shallow and 6 deep water crayfish respectively, were selected for tissue energy, lipid, percentage water and dry weight analyses. Large animals were chosen to ensure that enough tissue was available for biochemical analyses. Altogether 70 females, from 41.2 - 64.4 mm CL (mean CL = 49.6 mm) and 72 males, from 37.1 - 59.9 mm CL (mean CL = 51.6 mm) were collected for this purpose. Only 1 deep water

Table 5: Comparison of sediment sampling techniques.

Sample number	Surface sediment sampler (cal g^{-1} dry wt sed)	Ekman grab	% difference	Substrate location and composition
1	1413	795	43.7	mud in weed bed
2	3765	772	79.5	detritus on sand
3	595	399	32.9	mud below weed bed
4	535	360	37.7	within dense *Hyridella menziesi* bed
5	1309	440	66.4	open mud bottom
Mean:	1523	553	63.7	

female from January was analysed. As insufficient large crayfish were obtained from the deeper waters during March, April and May, the remainder were acquired from 20 m depth trappings.

c) Use of formalin

Each crayfish was rapidly killed and preserved by injecting it with 1-2 ml of 4% buffered formalin through the arthrodial membrane immediately posterior to the sternum between the last pair of pereiopods. Then deep and shallow water crayfish were stored separately in 2% buffered formalin.

Formalin is generally regarded as a universal preservative of animal tissue (Humason 1967). However, it can alter the biochemical composition of some tissues. For example, Lovegrove (1966), Fudge (1968) and Omori (1970) reported variations between fresh samples and tissues treated with formalin. It seems that the extent of such variations depends on formalin concentration and the duration of tissue immersion. Increasing the concentration and/or immersion time tends to effect larger deviations. For comparative purposes and also to negate the need for corrections, it is preferable to have tissue as little affected as possible. Buffered or neutralised formalin is better than nonbuffered formalin for this purpose; it produces quicker penetration and a slower rate of hardening in the tissue. Therefore, in this study only 2% buffered

formalin was used, and preservation did not exceed 2 weeks before analyses were begun. Longer delay periods would probably have been acceptable however, for Russell-Hunter et al (1968) state there should be no significant biochemical breakdown of tissues treated with neutralised formalin.

To test the effect of formalin on tissue composition a large, fresh sample of hepatopancreas, gonad and abdominal muscle was firstly assessed for dry weight, water and lipid content and then similarly reassessed at infrequent intervals following treatment with 2% formalin. Carapace was similarly assessed for changes in water content only. Duplicate samples were taken on each occasion and the results were averaged. The results are expressed in Table 6 and show overall increases in dry weight and lipid concentration and a decrease in water content with time. However, the generally low values of CV imply that these changes were probably not significant over the 8 week experimental period.

d) Tissue dry weight and percentage water content

All injected crayfish were washed with tap water to remove excess formalin and dissected. The hepatopancreas, abdominal muscle, gonads and posterior half of the carapace were retained for analyses. These organs were similarly washed in water, touch dried with blotting paper and weighed in separate aluminium 'boats' using a Mettler $H10_W$

Table 6: Effect of formalin on tissue conposition.

		Fresh.	Days in 2% neutralised formalin. 7	21	56	Mean.	SD	CV(%)
Water content (%)	hepatopancreas	85.8	84.5	84.2	82.8	84.3	1.2	1.5
	ovary	50.6	49.0	48.5	48.0	49.0	1.1	2.3
	testes	77.7	76.5	74.0	-	76.1	1.9	2.5
	muscle	84.4	82.0	82.0	81.0	82.4	1.5	1.8
	carapace	61.4	61.0	59.5	58.4	60.1	1.4	2.3
Dry weight (%)	hepatopancreas	26.2	27.4	27.7	28.4	27.4	0.9	3.4
	ovary	49.4	50.0	50.0	51.1	50.1	0.7	1.4
	testes	22.6	25.0	22.8	-	23.5	1.3	5.7
	muscle	19.8	19.6	20.0	20.8	20.1	0.5	2.6
Lipid (mg g^{-1} dry wt)	hepatopancreas	450	450	460	472	458.0	10.5	2.3
	ovary	428	440	430	445	435.8	8.1	1.9
	testes	126	130	136	-	130.7	5.0	3.8
	muscle	90	87	90	101	92.0	6.2	6.7

balance. Organs were dried at 60°C for dry weight and percentage water content assessment.

Typically, tissues are temperature equilibrated in a desiccator before weighing. This method is satisfactory for a small number of samples but when many samples require weighing, moisture uptake by tissues may produce a discrepancy between samples. The extent of this effect was examined by reweighing dried crayfish organs maintained in a desiccator at irregular intervals during a 3 hour period. Results shown in Figure 5 indicated that moisture uptake occurred in all tissues and was greatest for carapace.

So that no discrepance of this kind occurred between samples, all samples were exposed to weighing room conditions (yearly temperature and relative humidity ranges were 21-22.5°C and 38-44% respectively) for 4 hours before weighing. Although values obtained were not actual dry weights, this method probably gave less variation between values than if samples had been desiccated before weighing.

e) Lipid extraction

Lipids were extracted from the hepatopancreas, muscle and gonads of 70 females and 72 males selected from L. Rotoiti at monthly intervals throughout 1975 with 2:1 chloroform methanol solution. This method, according to Giese (1967), is superior to Soxhlet extraction which uses ethyl ether, as it removes both structural and storage

Figure 5. Changes in tissue dry weight during weighings, as a result of moisture uptake from the atmosphere. Tissues were reweighed every 10 minutes for the first 1-1½ hours and then 3 hours after the initial weighing. Curves have been fitted to the data points. Control samples were subjected to weighing room conditions and showed variations in percentage dry weight as follows: hepatopancreas (0.01), muscle (0.02), carapace (0.03), ovaries (0.02) and testes (0.05).

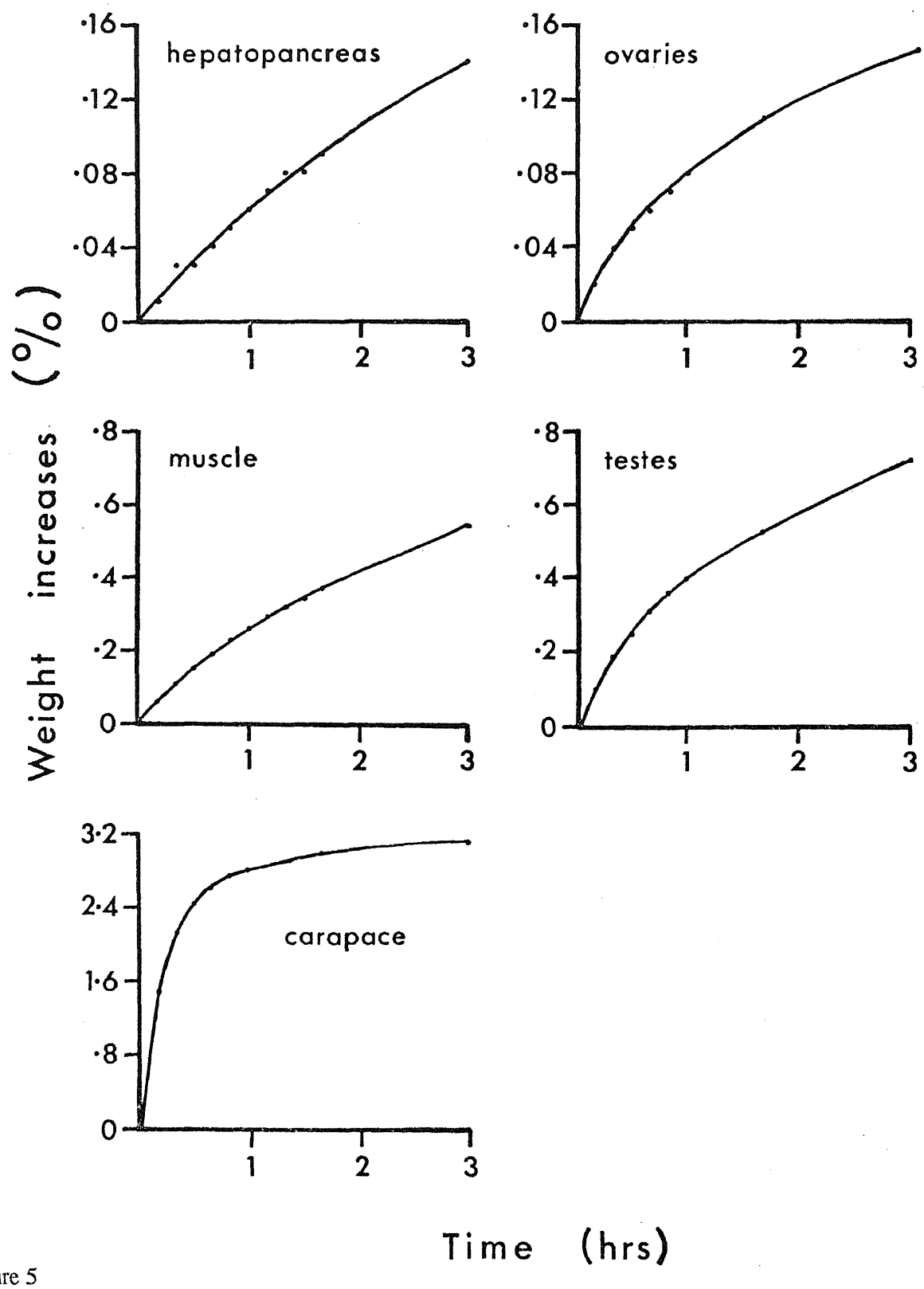


Figure 5
Changes in tissue dry weight ...
Between pp 28,29

lipids, while the Soxhlet removes only the latter. A similar drip method using petroleum ether was adopted by Armitage et al (1972) to extract lipids from the hepatopancreas, muscle and gonads of *Orconectes nais*.

An apparatus capable of extracting lipids from 24 samples simultaneously was developed (plate 6). A 2 litre glass reservoir, fitted with an outlet glass tube and tap, regulated the solvent flow. The tube angled downwards to an inverted Y section, the arms of which were angled at 100° from the vertical. A glass manifold with 12 outlets was fitted to each arm and the outlet holes were plugged with glass wool to purify the solvent. To each outlet was connected a short length of clear surgical tubing provided with a metal clamp to regulate solvent flow. The tissue samples were contained in 5 cm plastic pipette tips inserted into the tubing. Plastic tips were used because their weight to tissue weight ratio was low. Also, treatment with the solvent caused no alteration to the weight of the pipette tip. Solvent collection was in a stainless steel tray with high sides and a false bottom tapering towards the centre, and a centrally located opening leading to a 2 litre collecting bottle. This design served to reduce solvent loss through evaporation.

Tissue preparation and extraction procedure was as follows: Dried tissue was ground to a fine

Plate 6. Apparatus used for extracting lipid from tissues

a – reservoir with solvent mixture

b – tap

c – clamp

d – pipette tip containing tissue sample

e – collecting tray

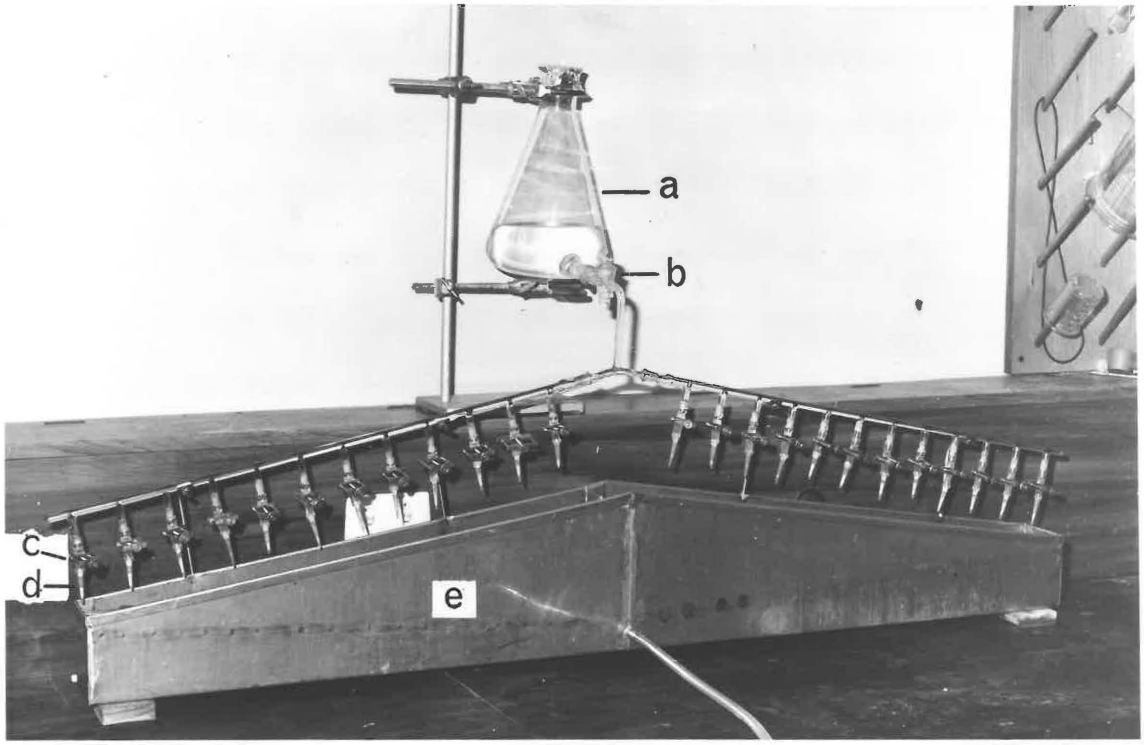


Plate 6
Apparatus used for extracting
lipid from tissues
Between pp 29,30

consistency then loosely packed in preweighed pipette tips, the exits of which were plugged with glass wool to prevent sample loss. Tissues of the range 5.5 - 73.4 mg for hepatopancreas, 11.2 - 117.6 mg for muscle, 2.9 - 80.8 mg for ovary and 4.5 - 52.4 mg for testes, were extracted. Pipette tips plus tissue were dried to constant weight at 60°C and weighed on a Mettler M5SA balance to within 0.00001 g. Clamps on the surgical tubing were closed and the apparatus flooded with solvent. Each pipette tip was held to seal its outlet and filled with methanol. A small cotton wool plug, presoaked in methanol, was then inserted to prevent tissue loss. Each sample was fitted onto the apparatus and its appropriate clamp opened. By squeezing the tubing below each clamp, entrapped air was released allowing a continuous flow of solvent. Clamps were adjusted to achieve flow rates of approximately 1 drip second^{-1}. Extractions were run for a minimum of 3 hours, after which the cotton wool plugs were removed and the drying and weighing process repeated. Lipid weights were determined by difference and results expressed as mg g^{-1} dry weight lipid.

As a large number of samples were extracted (ca 1800), running duplicates was considered impractical. However, tests of replicate samples from a number of animals were made to determine the coefficients of variation for the ranges of lipid

concentration of each organ (table 7). Tissues with high lipid content gave low coefficients of variation but values were high for tissues low in lipid.

f) Calorimetry

The total energy content of the hepatopancreas, abdominal muscle and gonads of the 70 females and 72 males collected each month in 1975 was measured with a Phillipson oxygen microbomb calorimeter (Phillipson 1964), coupled to a Honeywell Electronik 196 chart recorder. Samples of between 4.31 - 15.84 mg for hepatopancreas, 4.19 - 26.71 mg for muscle, 2.88 - 20.93 mg for ovaries and 3.80 - 14.49 mg for testes were bombed. Values were expressed in calories g^{-1} ash free dry weight.

A piece of tissue was removed from the whole organ, dried to constant weight at 60°C and weighed in a preweighed platinum pan on a Beckman LM - 500 microbalance and then bombed. Sample weight was calculated by difference and bombed samples were reweighed to assess the ash content. Owing to the time required (each sample took a minimum of 30 minutes) and the large number of bombings performed (ca 900), duplicates were not run.

The bombed samples came from whole nonhomogenised organs, so the obtained values could have differed significantly from the organ mean caloric content. To check for this, a number of replicate samples

Table 7: Lipid extracted from replicate samples of hepatopancreas, abdominal muscle, ovaries and testes.

	Organ number	Replicates	Lipid (mg g^{-1} dry wt)	SD	CV (%)
HEPATO-PANCREAS	1	1	332	12.7	3.8
		2	350		
		3	324		
	2	1	624	16.3	2.7
		2	601		
		3	614		
	3	1	696	10.3	1.5
		2	703		
		3	709		
		4	689		
	4	1	706	7.0	1.0
		2	695		
		3	693		
		4	692		
OVARY	1	1	427	12.0	2.9
		2	410		
		3	399		
	2	1	369	0.7	0.2
		2	370		
		3	365		
	3	1	417	7.0	1.7
		2	409		
		3	423		
		4	425		
	4	1	366	5.5	1.5
		2	372		
		3	377		
		4	376		

Cont. over

	Organ number	Replicates	Lipid (mg g^{-1} dry wt)	SD	CV (%)
TESTES	1	1	94	8.5	9.1
		2	82		
		3	103		
	2	1	67	17.7	22.4
		2	78		
		3	92		
	3	1	173	21.2	13.6
		2	143		
		3	151		
	4	1	67	17.0	10.1
		2	59		
		3	43		
MUSCLE	1	1	111	2.1	1.9
		2	108		
		3	114		
	2	1	72	14.0	20.5
		2	86		
		3	58		
		4	57		
	3	1	57	6.8	10.7
		2	60		
		3	72		
		4	67		
		5	61		
	4	1	93	5.7	6.7
		2	92		
		3	85		
		4	81		
		5	73		

from each of the 4 organ types was bombed (see table 8). The low coefficients of variation indicated a high degree of constancy between replicate samples.

Caloric content of stomach contents of crayfish obtained at the 1, 10, 20, 30 and 50 m depth intervals during the monthly trappings of 1975 was also assessed by microbomb calorimetry. After capture, crayfish were immediately killed in formalin and their stomach contents dissected out. Stomachs containing fragments of bait were discarded. The contents of 5-8 stomachs collected at each depth were combined and preserved in formalin. Samples were washed with distilled water, dried then ground in a mortar. A pill of each sample was made, then dried to constant weight at 60°C, weighed on the microbalance and bombed. Pills ranged from 5.46 - 19.28 mg.

Parry (1960) states that in aquatic invertebrates the main end product of nitrogen metabolism is ammonia. In oxygen bomb calorimetry nitrogen is oxidised further, the effect being that overestimations of tissue caloric content may occur (Kersting 1972). Kersting showed that overestimates by as much as 10% can exist if nitrogen corrections are ignored. Such corrections are obviously important whenever actual caloric values are required. However, in this study the obtained values were used to express seasonal trends in organ energy content and so there was less need for such accuracy. For this reason

Table 8: Coefficients of variation for replicate samples bombed from a single organ.

Organ	Replicates	Cals g^{-1} ash free dry wt	Mean	SD	CV(%)
Hepatopancreas	1	7009	7013	116.7	1.7
	2	6892			
	3	6979			
	4	7171			
Ovary	1	6544	6514	108.0	1.7
	2	6410			
	3	6449			
	4	6652			
Testes	1	5446	5446	54.3	1.0
	2	5514			
	3	5381			
	4	5444			
Muscle	1	5327	5348	61.7	1.2
	2	5270			
	3	5404			
	4	5390			

nitrogen corrections were not determined.

TRAPPING AND SCUBA AS METHODS

1. Trapping

Trapping is a versatile method often used for crayfish sampling. Workers including Svärdson (1949), Camougis and Hichar (1959), Aiken (1965), Abrahamsson (1966; 1971), Momot (1967a), Abrahamsson and Goldman (1970), Moshiri et al (1970), Momot and Gall (1971), Moriarty (1971), Momot and Gowing (1972; 1975), Fast and Momot (1973), Devcich (1974), Gowing and Momot (1974) and Flint (1975; 1977) have trapped crayfish to obtain information on certain aspects of population ecology. However, the main drawback of this method is that traps serve to provide information only on that part of the population which enters them (Hazlett, Rittschoff and Rubenstein 1974) and so give only approximate indications of population events. Also, since trapping using baits is an indirect means of assessing events other than feeding activity, correction values are often required to improve accuracy.

When trapping is used as a method for assessing distribution patterns there are probably two principal factors which introduce errors: crayfish behaviour and trap design.

In order to collect the widest population size range possible, traps should be designed so that entry effort by the crayfish is miminal but retention or carrying capacity maximal.

Movement and feeding are the two main behaviours

influencing trapping results, so any factor affecting these activities also affects catch numbers. For instance, in response to inhibitory light levels, entrapped crayfish in shallow waters prolong their movements after dawn. Inhibitory light levels penetrated to around the 12 m contour in L. Rotoiti (see later), therefore higher efflux rates would have been expected from traps set at depths of 1 and 10 m compared with those set deeper (table 9). To allow for this difference in trap efficiency with depth, all traps needed to be raised by dawn.

Light also affects feeding behaviour in a number of ways. Although a nocturnal animal, *Paranephrops planifrons* feeds continually when below 20 m but above this depth feeding occurs only at night (Devcich 1974). Under high natural light conditions foraging activity is almost totally suppressed, implying that the effective trapping times at 20, 30 and 50 m depths differed from that at 1 and 10 m depths. Also, as a consequence of falling light levels associated with dusk, feeding at 10 m depth begins one half hour before its initiation at 1 m depth (see later).

Food abundance has a profound effect on the numbers of crayfish entering traps. Crayfish must choose between trap bait and environmental food sources, so the level of natural food abundance affects the numbers trapped. To estimate the extent of this effect, 23 crayfish were placed in each of 2 troughs of equal area (ca 3.5 m^2), 1 of which (trough 1) was low and the other (trough 2) high in food concentration. The energy content of the

Table 9: Crayfish efflux rates from traps at 1-2 m depths and 20 m depth during daylight. Traps were set at 5 am with 10 crayfish each and raised at 10 am. Meshed tubes were positioned at trap entrances to prevent crayfish entering but not leaving.

Trap number	Depth (m)	
	1-2	20
	Numbers retained	
1	6	10
2	8	10
3	7	8
4	10	9
5	4	10
Total	35	47
Efflux rate (crayfish $trap^{-1}$ hr^{-1})	0.60	0.12

sediment in trough 1 closely approximated lake mean food levels at 10, 20, 30 and 50 m depths, while that in trough 2 closely resembled food levels at 1 m depth (see later). A freshly baited trap was placed in each trough on 10 successive evenings. Traps were raised before dawn and the crayfish caught were counted (table 10). Since there was a 227% higher catch rate in the lower food environment, a corresponding correction was made to the 1 m depth trapping results.

Food abundance probably affects foraging distances, hence a greater distance is covered where food levels are low, for example below 10 m, than in the rich feeding grounds of the shallows. This means that crayfish at 10, 20, 30, and 50 m depths have a greater chance of coming into contact with traps than crayfish at 1 m depth. However, it must be remembered that an individual's state of hunger determines the amount of time it spends foraging and for this reason a hungry crayfish is more likely to approach a baited trap than one less hungry. Since crayfish in deep water are free to satiate their appetites by day, it may be assumed that these individuals would be less hungry than those in shallow water at night and so would be less readily trapped, even though surrounding food levels are lower.

Bait quality decreases with time. Devcich (loc. cit.) found that fresh beef liver was effective for 15 hours, after which bait decay caused an appreciable reduction in catch numbers. Water temperature would affect the duration of effectiveness, with higher temperatures causing more

Table 10: Effect of food abundance on numbers of crayfish trapped.

	Trough 1	Trough 2
Sediment food value (cal g^{-1} dry wt sed)	650	3250
Equivalent lake depth (m)	7-50+	1-6

Day	Number of crayfish in trap	
1	3	3
2	5	1
3	2	0
4	4	2
5	3	1
6	2	1
7	1	1
8	2	1
9	2	0
10	1	1
Total:	25	11
% trapped	10.9	4.8

rapid decay.

Catch rate can be regulated by temperature, for Momot and Gowing (1972) noted that greater numbers of *Orconectes virilis* were trapped in summer than in autumn and that below 10°C locomotor activity decreased rapidly. A comparison between summer and winter catch numbers in the present study revealed no significant difference ($t = 0.516$, $p = ns$, $n = 11$), which suggested that the annual temperature range in L. Rotoiti did not effect changes in movement of *P. planifrons*. However, further examination revealed relatively high correlations ($r = 0.79$, $r = 0.81$) between numbers of adult females trapped at 1 m and temperature, throughout the monthly trappings of 1975 and 1976 respectively (see later).

Drach (1939) found that feeding does not occur at the time of moulting in crustaceans. Consequently, trapping becomes ineffective during this period. Using the classification of Baumberger and Olmstead (1928) for the moult cycle of brachyurans, suppression of feeding occurs from the latter stages of proecdysis, through the actual moult process, until the early paper shell stage. Whittle (pers. comm.) has observed that *P. planifrons* ceases feeding for a period of 3 days at the time of a moult. Locomotion is affected too, for Roberts (1944) noted that normal locomotion did not occur in *Cambarus virilis* until the second or third day after ecdysis.

Quilter (1975; 1976) found that the microsporozoan *Thelohania contejeani*, which infects the musculature of *P. zealandicus*, promotes a decrease in locomotor activity

and may eventually cause the death of heavily infected individuals. An as yet unidentified species of *Thelohania* also occurs in *P. planifrons* inhabiting lakes within the study area (Jones in prep.). It was found that the abdominal muscles of heavily infected L. Rotoiti crayfish appear an opaque white colour, whereas the muscles of noninfected or only slightly infected individuals appear more translucent. A significant proportion of the L. Rotoiti population is likely to be adversely affected by *Thelohania* sp., for of 50 adults collected at random, all were found to be infected to varying extents.

Tack (1941) comments that females of *Cambarus immunis* are less active when gravid. Abrahamsson (1966) noted a similar phenomenon in breeding *Astacus astacus* females but when they lost their eggs and attached young, activity increased and catch numbers increased concomitantly. To check whether the stage of the breeding cycle affected the catch rate of female *P. planifrons*, 20 gravid and 20 nongravid females were placed in a trough 1.8 x 2.6 m long by 0.8 m deep, and trapped over 5 consecutive nights. Results are given in Table 11 and show no significant difference between the two groups ($t = 0$, $p = ns$, $n = 10$). It seems that feeding activity is not markedly suppressed in gravid females, for Momot (1967a) states that breeding females of *Orconectes virilis* continue feeding and dissection of laboratory maintained breeding *P. planifrons* females revealed full stomachs in every case. However, it is more likely that movement is reduced in consequence of maternal behaviour associated with egg and young care and

Table 11: Effect of stage of breeding cycle on number of females trapped. Traps were set before sunset and raised before sunrise, from 5-9 September 1977.

Day	Number trapped each night	
	Gravid	Nongravid
1	1	2
2	3	1
3	0	3
4	2	0
5	2	2
Total:	8	8

protection (Mason 1970a), so it is conceivable that relatively fewer gravid females were trapped in this study.

Aspects of social behaviour can lead to incorrect interpretations of data. Bovbjerg (1953; 1956) states that males of *O. virilis* and *Procambarus alleni* tend to be the dominant sex. Abrahamsson (1966) comments that large males of *A. astacus* are powerful competitors for food and space, as shown by their agression toward females and smaller males. Furthermore, these entrapped males restrict more subordinate crayfish from entering traps. However, this behaviour was not observed in entrapped large *Paranephrops planifrons* males. This species appears to display similar traits in dominance to that of *Cambarellus shufeldtii*, in which Lowe (1956) observed a relationship with size but not sex.

The lunar cycle may affect catch numbers. Kubo and Ishiwata (1964) noted that a preponderance of the Japanese spiny lobster was trapped during the new moon compared to the full moon period. Their evidence suggested that the higher light intensities associated with the full moon caused the reduction in catch numbers. Similarly, Flint (1977) found that even a small amount of moonlight caused a reduction in the activity period of *Pacifastacus leniusculus*. It is uncertain whether the lunar cycle affected catch numbers of *Paranephrops planifrons* because the often prevailing cloud cover interrupted moonlight intensities during the trapping programme. However, it is likely that 1 m traps on a clear night during the full moon

yielded less crayfish than for any other period in the moon's cycle or degree of cloud cover.

Lastly, adverse weather conditions can have an effect on catch rates, especially in shallow water. The 1 m traps usually caught fewer crayfish on a stormy night with onshore winds. Also, numbers were unusually low when the shallows became strongly discoloured as a result of catchment runoff from heavy rains.

Although a good means of obtaining crayfish, traps are restrictive as regards their application to certain aspects of population research. As indicated above, trapping is subject to many influences, each of varying impact, so the validity of results is often questionable. Results can be adjusted or complemented through the use of alternative methods. One such method is SCUBA.

2. SCUBA

SCUBA is another highly versatile method with the advantage that the diver is in direct contact with his subject. Because of this, results can be obtained directly which obviates the need to make corrections. Jones (1971) gives a good outline of the virtues and vices of diving as a method.

Diving, however, was not without its problems. Of all the lakes surveyed in this work, Rotoiti had the lowest lateral visibility, ranging from 3-5 m near the surface to 0-1 m at a depth of 30 m. Below about 25 m depth the reduced light, in combination with suspended particles, sometimes produced unpleasant conditions to the extent

that crayfish and the bottom could not be seen clearly. This effect was most pronounced in late autumn and throughout winter.

Movements of divers often disturbed bottom sediments for up to 45 minutes, markedly reducing visibility. However, reduced and slowed movements minimised bottom disturbances, allowing prolonged examinations even in confined areas.

The cold became a problem in winter and below the thermocline in summer and autumn. Here temperatures were ca 10°C, which reduced immersion times to about 30 minutes. Full-length wetsuits, made of 5 mm thick neoprene and occasionally undervests, were worn to reduce the loss of body heat.

RESULTS

PART 1. SPATIAL DISTRIBUTION

1. Introduction

Many crayfish species are nocturnal in nature and migrate from deeper waters to forage in the shallows at night (Huxley 1884, Crocker and Barr 1968); consequently cosiderable shifts in position are likely to occur during a 24 hour period. Crayfish in lakes have also been shown to undergo vertical seasonal migrations (Momot 1967a, Momot and Gowing 1972, Fast and Momot 1973, Capelli and Magnuson 1975, Flint 1977), as well as migrations on a more horizontal plane (Camougis and Hichar 1959, Kossakowski 1965, Abrahamsson 1966). As a group therefore, crayfish display a high degree of mobility and *P. planifrons* proved to be no exception.

In a preliminary study (Devcich 1974), *P. planifrons* was found to undergo seasonal vertical migrations in L. Rotoiti. It was suggested that the movement patterns may have been the result of hypolimnetic deoxygenation and environmental factors affecting reproductive behaviour.

In this study the spatial distribution pattern of *P. planifrons* has been more accurately defined and a more detailed examination made of the factors affecting it. The location of adult crayfish within a 24 hour period was closely monitored, together with the timing of the major changes within that period. In an attempt to determine what factors were controlling the distribution

patterns, experimental observations were made of crayfish both in situ and the laboratory.

2. Juvenile Distribution Pattern

It is difficult to quantitatively sample the juvenile crayfish populations of lakes in the Rotorua district. During the day individuals are out of sight, hiding within shelters, many of which are inaccessible. Even crayfish under movable objects can not often be counted because of the clouds of sediment which rise when these are uplifted. Sampling is easier at night when the animals emerge from shelters, although obtaining an accurate count is still difficult, due to restricted vision in the weed beds and the camouflaging nature of the bottom elsewhere. For these reasons, only a general assessment was made of the distribution of juveniles within L. Rotoiti. This was achieved by casual observation of the population while diving and from the depth distribution of females at the final stage of their breeding cycle.

These females had attached young which were in the EI = 5 stage of development (see p. 18). This stage lasts approximately 3 weeks (in table 4, p. 18) and therefore the distribution pattern of these mothers might show depths at which offspring are released in the lake. The distribution of females with young in this stage of development was assessed from animals caught during the 1975 and 1976 trapping programme. Results are presented in Figure 6 and show that over 82% of these females were

Figure 6. Depth distribution of females carrying hatchlings (EI = 5 stage) in L. Rotoiti. The number of females is given.

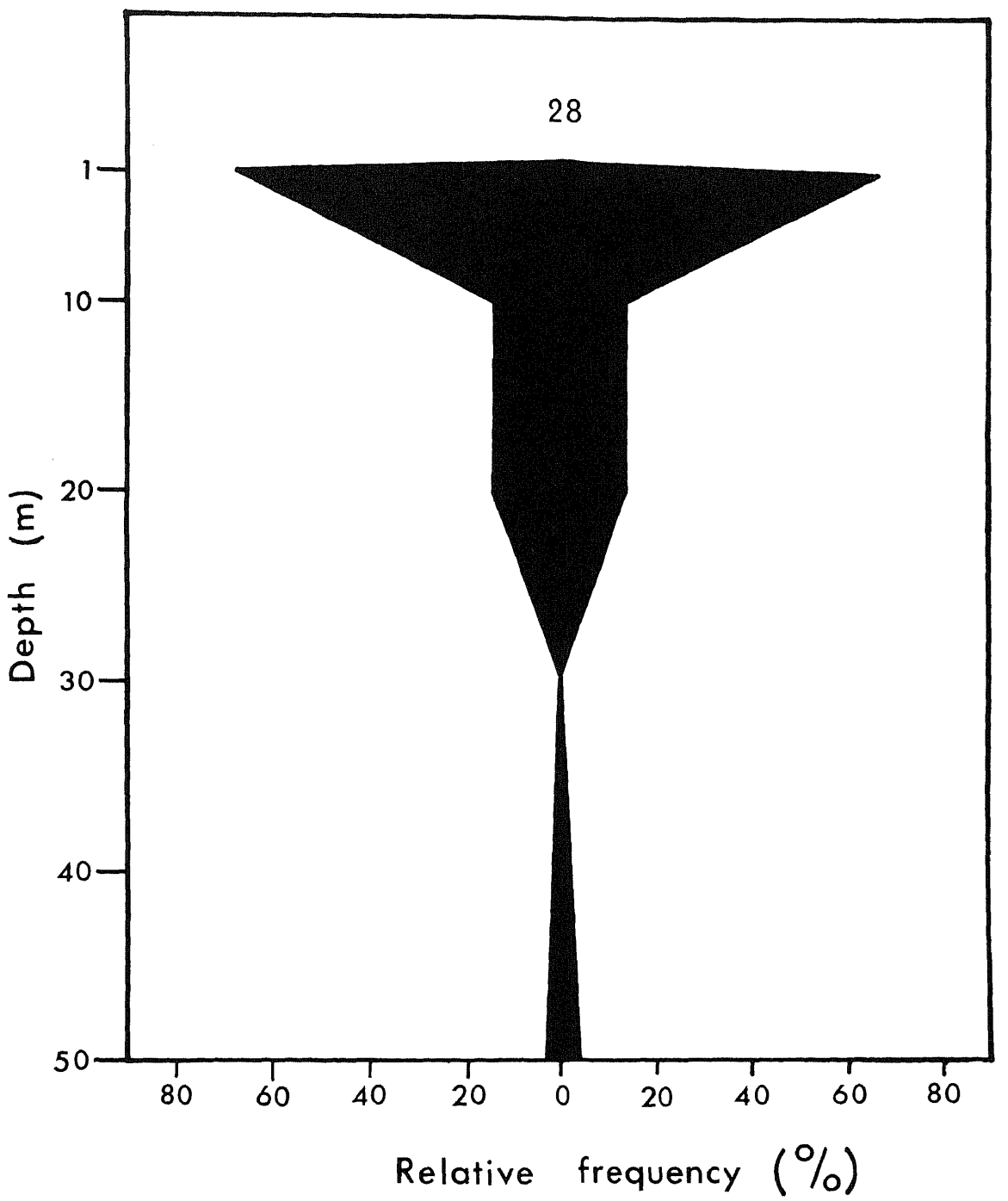


Figure 6
Depth distribution ...
Between pp 49,50

trapped within the upper 10 m.

Daytime dives extending down to 30 m revealed the majority of juveniles to also inhabit the top 10 m, although a few larger juveniles were found below this depth. A similar pattern was observed in Lakes Rotoma and Okataina on 3 March 1976 and 11 March 1978 respectively. At night there was little change from the daytime distribution pattern. Activity began at about the same time as that of adults (see later) and foraging was mainly within, or in the general vicinity of the weed beds.

A. THE ADULT DIEL PATTERN

Sampling was confined to late summer, when the total population lay above the 30 m contour. The day and night spatial distribution patterns were assessed by SCUBA, using the procedure outlined on page 13, and results are shown in Figures 7 and 8 respectively. To substantiate night-time results the combined trapping results from 1975, between the 1 and 30 m contours, have been included (figure 9).

Daytime results showed that there were few crayfish in shallow water and that the great majority were between the 15 and 27 m contours. Spot dives in other parts of L. Rotoiti revealed similar numbers within this zone, which implied the existence of a high density band of crayfish around the entire lake. Similar high density bands also occurred in Lakes Okataina, Rotoma, Tarawera, Tikitapu and Taupo but not in Rerewhakaaitu. In L. Rotoiti, crayfish shallower than 12 m were confined mainly to rocky areas, while those below this depth showed no preference for any particular substrate type (see later). Crayfish in the daytime were generally inactive but some activity did occur, predominantly within the top part of the band.

During the night there was a disruption of the daytime pattern. All crayfish became active and those of the high density band appeared to have dispersed upward into the weed bed zone. Thus, it appeared that a large proportion of the population had undergone a vertical migration of about 18 m.

Figures 7 & 8. The late summer distribution pattern by day (figure 7) and night (figure 8) of *P. planifrons* in L. Rotoiti in 1978. The broken outline indicates depth zones where counts were regarded as unreliable because by day crayfish above 12 m depth were hidden from view and densities here varied markedly around the lake, whilst at night vision within the weed beds was restricted.

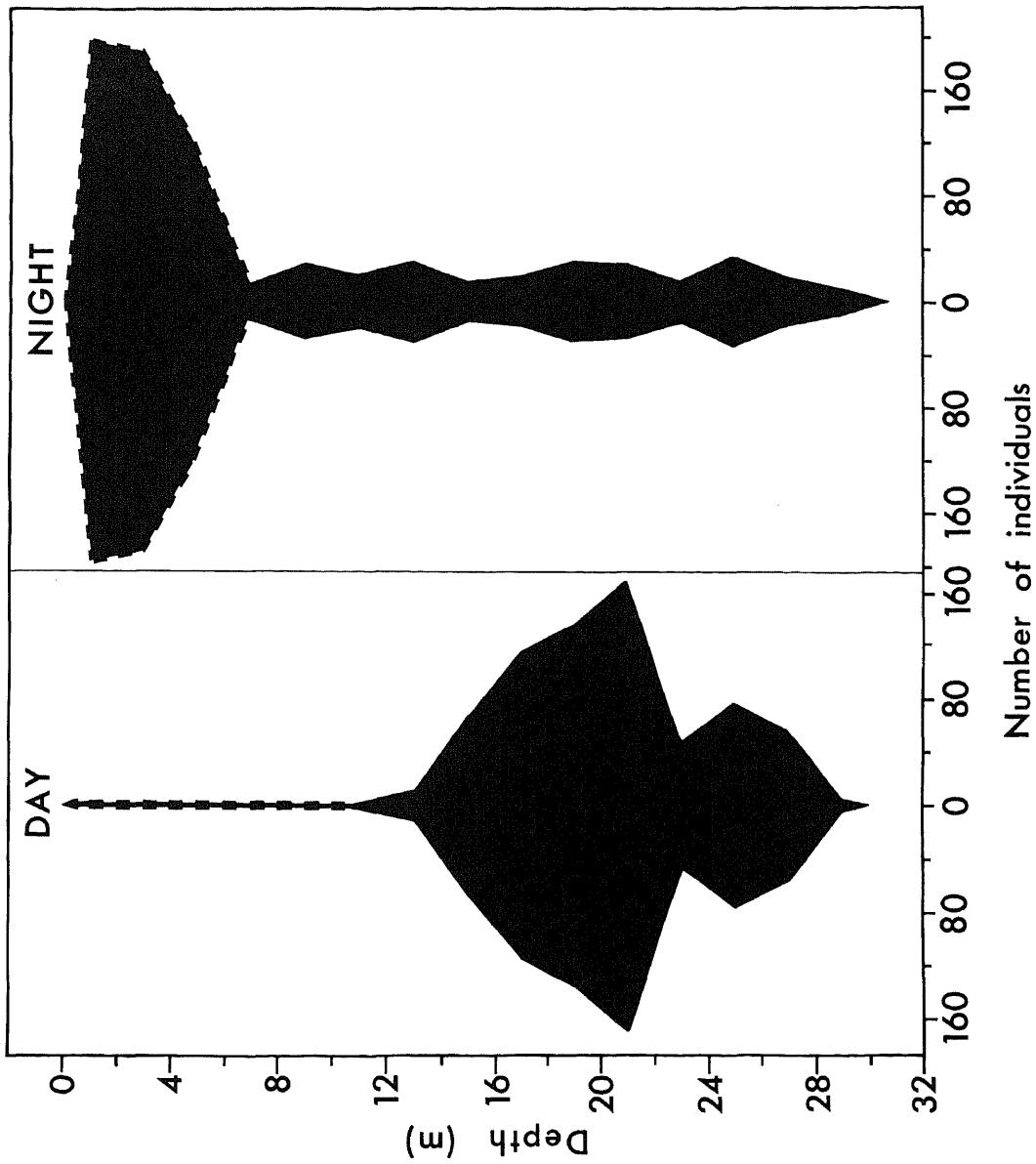


Figure 7 & 8
The late summer distribution ...
Between pp 51,52

Figure 9. Adult distribution pattern at night, assessed as the means of combined numbers trapped each month at 1, 10, 20, and 30 m depths respectively during 1975. The 227% correction has been applied to 1 m numbers. The total trapped is given.

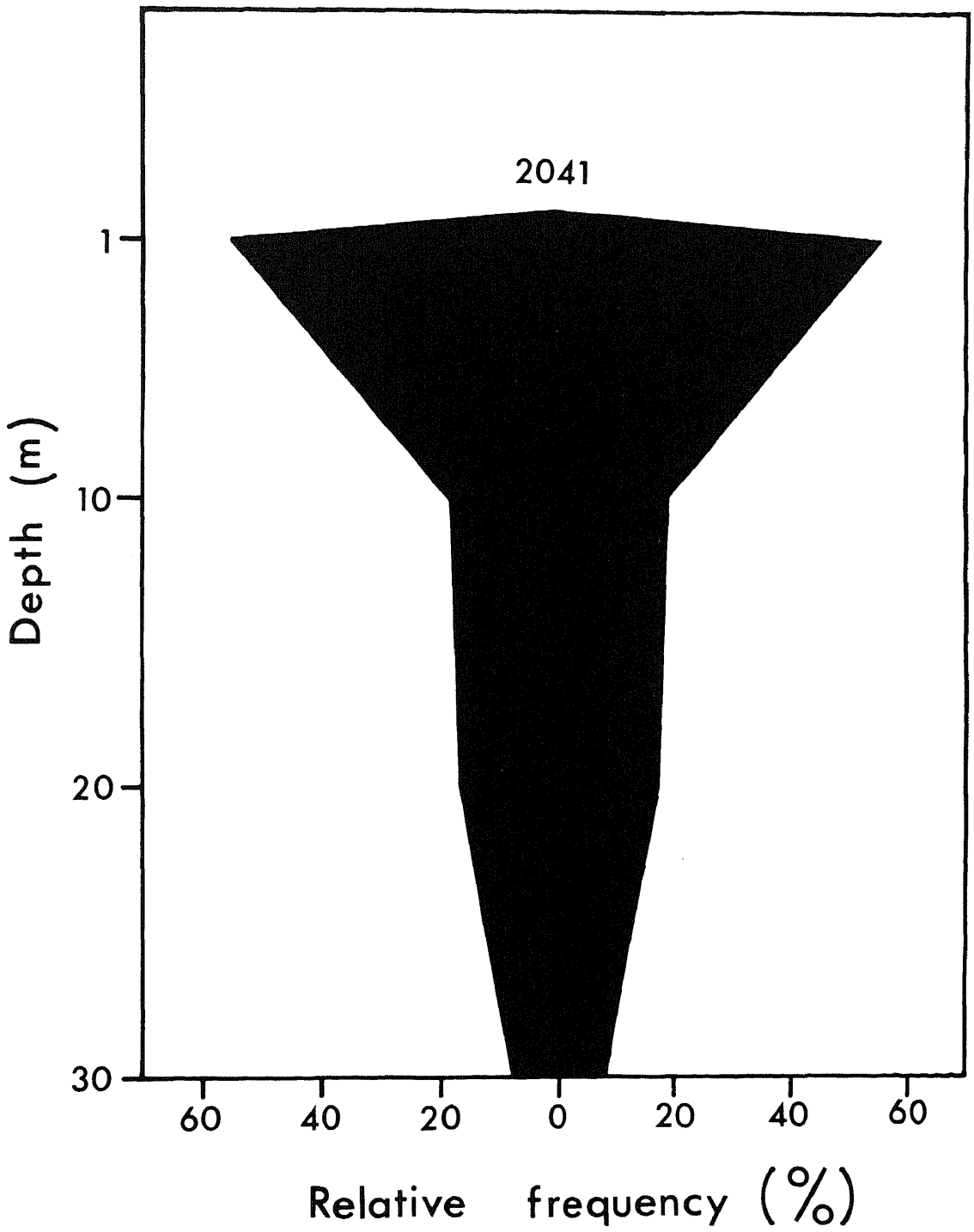


Figure 9
Adult distribution pattern at night ...
Between pp 51,52

To check this, a series of dives were made in April 1977 at 15 minute intervals to ascertain the depths occupied by crayfish from sunset onwards (figure 10). Increased activity at the 12 m contour began 3-15 minutes after sunset. Within 30 minutes crayfish had reached the lower weed bed fringe at 6 m depth, having traversed a measured distance of 48 metres. During this period most crayfish at depths of 6-12 m were seen to be oriented shoreward and to be moving up the slope. Crayfish did not appear at the 1 m contour until 1 hour after sunset, by which time the shallow water residents had emerged and commenced foraging. Actual feeding in the weed beds was not seen to occur until 1 hour after sunset (an observation also supported from trappings) and continued until 1 hour before sunrise. Between these hours, extensive foraging also occurred below the weed beds down to 30 m.

Check dives to 28 m depth at 2200 hrs, 0130 hrs and at 0430 hrs, revealed that this distribution pattern remained basically unchanged. However, by sunrise (0629 hrs) no active crayfish were seen in the shallows and the daytime pattern was re-established. Subsequent diving revealed that *P. planifrons* had moved downwards. From these dives it was also apparent that migrations continued throughout the night.

To clarify the timing of the dawn migration, a dive was made before dawn to note the time when the last crayfish was seen to leave the 1, 5 and 10 m contours and when activity ceased at 15 m. Results shown in Table 12

Figure 10. Movement pattern of crayfish (shown by heavy line) at dusk in L. Rotoiti on 12 April 1977. Sunset at 1758 hours.

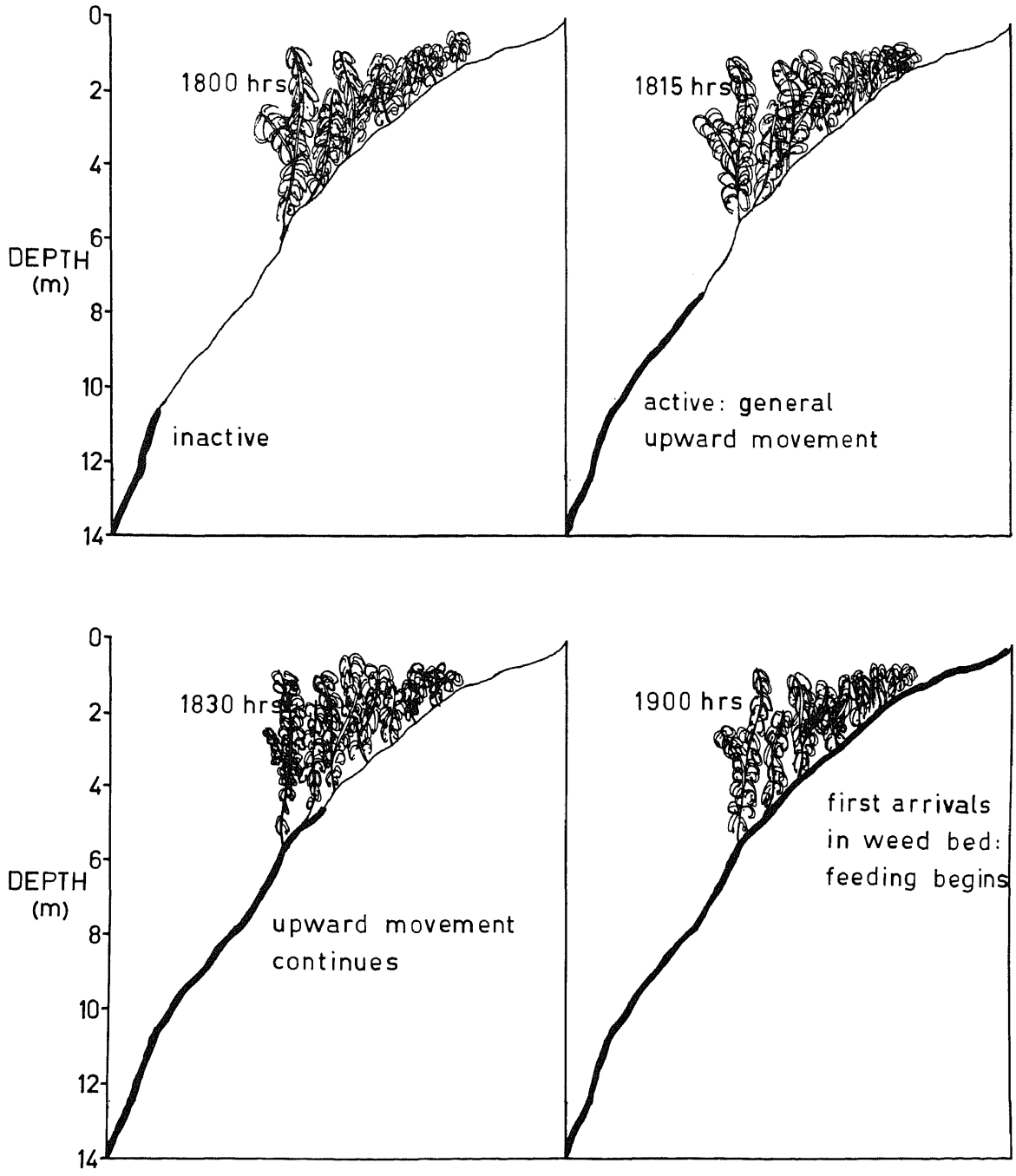


Figure 10
Movement pattern of crayfish ...
Between pp 52,53

Table 12: Departure times of the last observed crayfish from specific depths during the dawn migration.

Depth (m)	Departure time (00 hrs)
1	0530
5	0600
10	0645
15	† 0700

26 March 1978
Sunrise at 0629 hrs.

† high density band re-established.

suggested that all migrating crayfish had left the shallows within 1 hour of sunrise; within 1¼ hours all were below 10 m. Half an hour after sunrise the daytime pattern was fully re-established.

To summarise, a large difference in bathymetric distribution of the adult population occurred between night and day. These pattern changes involved two major vertical migrations during the hours of twilight. Lesser migratory movement probably continued throughout the night.

A model depicting these events is presented in Figure 11. It describes the generalised behaviour of the population, to which individuals may conform to varying extents every diel period. The differences in individual behaviour are undoubtedly due to differences in physiological states, but the net effect is such that about 80% of the population conforms to the overall pattern. It is in this way that the diel pattern appears stable fromm day to day.

In winter and spring crayfish also inhabited deeper waters (see later), so these individuals could have either covered greater vertical distances than the model indicates, or alternatively did not conform to it but rather remained below 30 m depth. Later evidence illustrates the presence of a small subgroup of the population, which was confined mainly to the deeper waters and whose individuals did not fit the model.

The various environmental factors likely to be involved in influencing the distribution patterns were considered in terms of the model. Those regarded as

Figure 11. Model depicting basic trends in the depth distribution, movement patterns and their timing in the adult population during each 24 hour period. The circles represent 24 hour clocks and associated blackened areas indicate crayfish relative abundance with depth. Orientation of sketched crayfish denotes direction of migration. Actual timing of the migrations alters every diel cycle, in accordance with sunset and sunrise times.

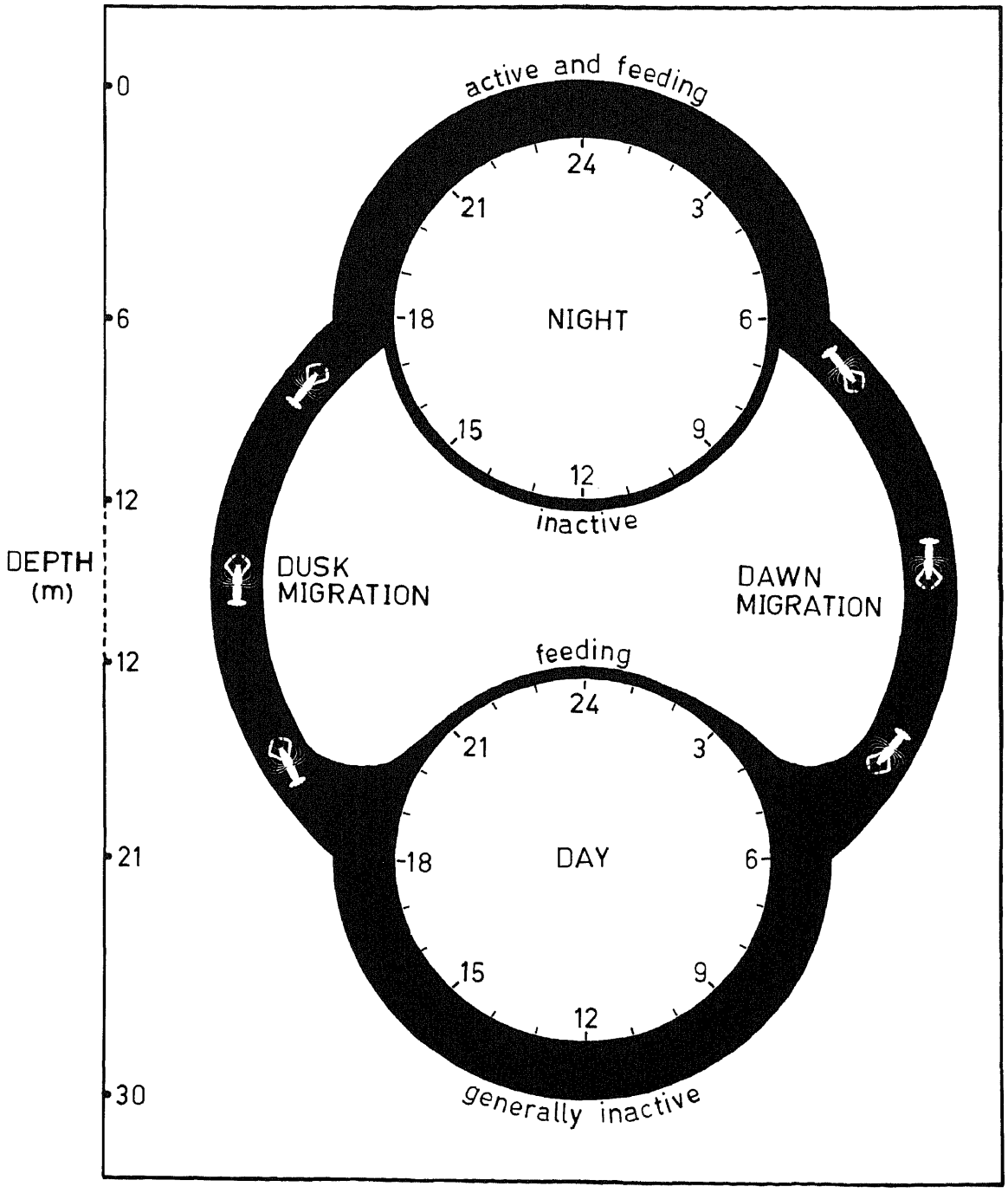


Figure 11
Model depicting basic trends ...
Between pp 54,55

important included light intensity, substrate type, food distribution and bottom slope. Each was considered separately so that its effect could be clearly defined. From a behavioural study of the affects of environmental stimuli on various receptor organs, an understanding of the mechanism associated with movement and postural control during the migrations was achieved.

Since the diel pattern remained basically unchanged seasonally (see later), it was reasoned that temperature was probably of little significance in maintaining the general pattern and was thus not considered here. Its possible significance is examined in a later section.

FACTORS AFFECTING THE ADULT DIEL PATTERN

1. The Daytime Pattern

a) Light

Like most crayfish species *P. planifrons* is negatively phototactic, so it may be assumed that daytime location is restricted to areas where low, noninhibitory light levels prevail. Since light intensity in lakes decreases as water depth increases (James and Birge 1938, Hutchinson 1957), one such area naturally occurs in the deeper waters. Another embraces shallow water recesses. Crayfish in shallow water were never found in direct light in the open but deeper down, in lower light intensities, they were (plates 7 and 8 respectively). This suggests that above a certain intensity light is inhibitory to *P. planifrons*, which implies that light intensity is likely to play a critical role in regulating their distribution. To define the limiting effect of light on crayfish location, the maximum tolerable light intensity in these two areas was assessed.

At irregular intervals throughout the study, dives were performed from the shoreline at Whangamoa Point (figure 3 follows p. 12) down the bottom slope until the first fully exposed crayfish was sighted. The light intensity at this depth was recorded on each occasion. Results are shown in Table 13. Although a distinct seasonal variation in depth of the first sighting occurred (this aspect is considered later), the light intensity was confined to a relatively narrow range (150-205 lux). This range defines the depth of transition below which

Plate 8. Adult crayfish on a mud substrate and comprising part of the high density band at 26 m depth in L. Rotoiti. Totally unprotected, these crayfish are displaying the typical behavioural response to light below the "boundary zones" (see following text) of all the lakes studied. Raised chelae is a defensive posture induced by the presence of a diver. The field of view covers about 0.6 m^2.

Plate 7. Adult crayfish within a shelter (broken beer bottle) at 9 m depth in L. Rotoiti. Crayfish in shallower waters were often totally hidden from view. Shelter occupancy was, without exception, the behavioural response to light above the "boundary zones" of all the lakes studied.

0.5x mag.

Plate 8
Adult crayfish on a mud substrate ...
Between pp 56,57

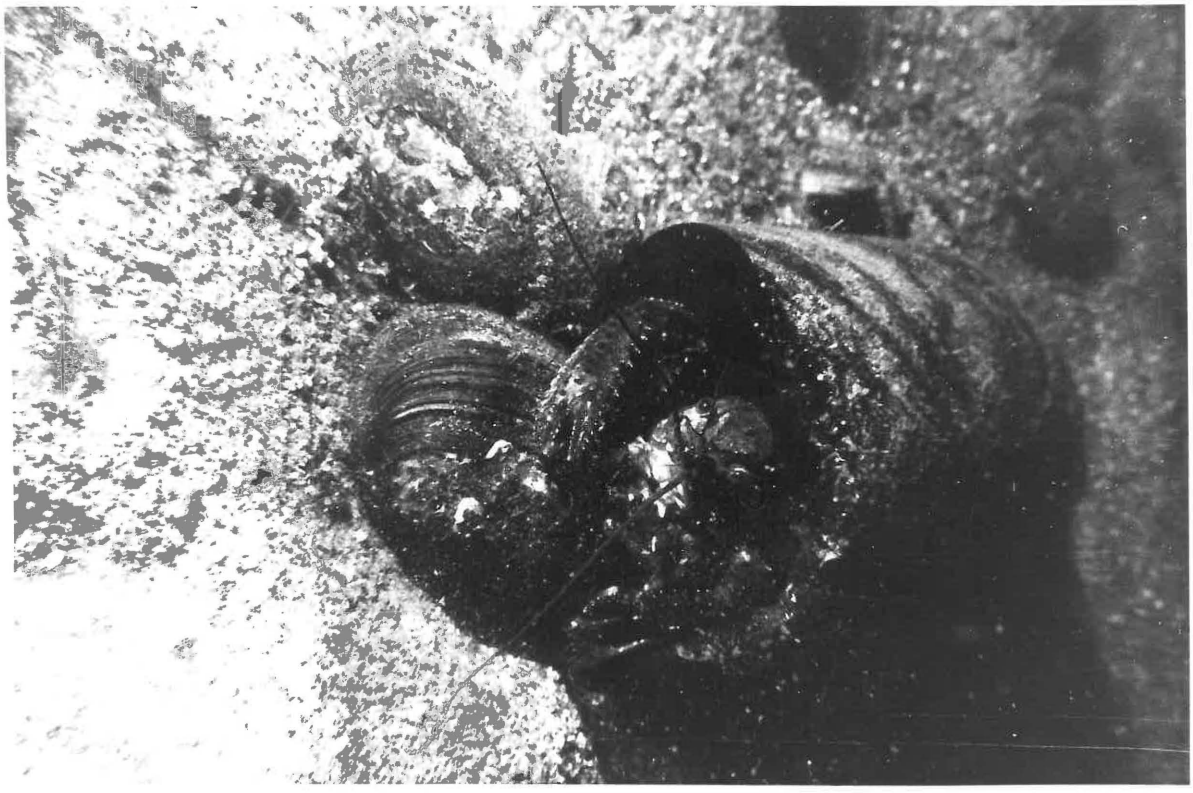


Plate 7
Adult crayfish within a shelter ...
Between pp 56,57

Table 13: Depths and associated light intensities where crayfish were first sighted in the open in 6 lakes.

Lake	Date	Depth (m)	Av. depth (m)	Light intensity (lux)	Mean light intensity (lux)	SD
Rotoiti	15 Jan '75	13.5		195		
"	16 Feb '75	12.8		190		
"	17 Apr '75	12.5		200		
"	16 Apr '77	10.7	14.3	205	182	21.8
"	15 July'76	16.5		155		
"	15 June'77	16.2		150		
"	9 Sept'77	17.7		180		
Okataina	11 Aug '73	16.5	15.9	350	555	290.0
"	20 Dec '73	15.2		760		
Rotoma	3 Apr '76	20.7	19.5	430	420	14.1
"	16 Apr '77	18.3		410		
Tarawera	17 Apr '77	12.2		860		
Taupo	4 Mar '78	24.4		800		
Tikitapu	24 Apr '77	13.8		210		

crayfish occur fully exposed, while above this depth, crayfish are always found under cover. This zone was termed the "boundary zone" and its position defined the upper limit if the high density band in L. Rotoiti.

Also shown in Table 13 are results from 5 other lakes. These lakes had smaller population densities than L. Rotoiti, so their boundary zones appeared less distinct and consequently, may account for the associated broader ranges in light values (e.g. L. Okataina). A significant feature was that the average depth of each boundary zone and the associated mean light intensity differed quite markedly between the 6 lakes.

All crayfish above the boundary zone in L. Rotoiti were concealed to varying extents. Crayfish in water shallower than about 5 m were always totally hidden from view, whereas those between this depth and the boundary zone were often visible within the entrances to shelters. The relationship between ambient light and crayfish location above the boundary zone was assessed by removing a crayfish from its shelter, then positioning a photocell as near as possible to the original site of the crayfish's eyes and recording the light intensity. Results are shown in Table 14 and indicate that crayfish tolerate light intensities up to 220 lux, which was similar to the levels of the boundary zone.

Overall, the results illustrated that during daytime, the crayfish population is confined to areas with light intensities below ca 200 lux.

Table 14: Light intensity at the location of crayfish eyes at depths above the boundary zone

Crayfish number	Shelter type	Depth (m)	Light intensity (lux)
1	bottle	8.1	15
2	bottle	8.0	20
3	rock	9.1	undetectable
4	rock	5.3	undetectable
5	can	3.2	100
6	rock	2.7	60
7	log	6.5	undetectable
8	rock	9.0	40
9	can	10.4	220
10	log	1.5	undetectable

Behaviour with respect to light depends on the relationship between the spectral sensitivity of crayfish and the spectral composition of water. Spectral sensitivity is determined by the absorption spectrum of the photosensitive pigment in the retina (Waterman 1961). Studies on northern hemisphere freshwater crayfish (table 15) have revealed that retinular cells possess two categories of receptor elements, one maximally sensitive to yellow-orange wavelengths, while the other shows peak sensitivity at wavelengths in the violet region of the spectrum. The absorption spectrum of *P. planifrons* has yet to be determined but from the evidence presented in Table 15, similar dual peaks in wavelength sensitivity are likely. A consequence of *P. planifrons* showing an increased responsiveness to certain wavelengths, would be that behavioural responses to light are influenced mainly by such wavelengths. The boundary zone depth is therefore most likely to be controlled by wavelengths in either the yellow-orange or violet regions of the spectrum.

The generalised spectral composition of lake waters is shown in Figure 12. However, this pattern is readily modified by gilvin content, even to the extent of being reversed in lakes that are deeply coloured (Hutchinson 1957). Therefore, the transmission of violet and yellow-orange light in the lakes may not accord with the pattern indicated in Figure 12.

Of the lakes listed in Table 16, L. Rotoiti has the lowest Secchi reading, which suggests that this lake has the highest gilvin and/or content of suspended material.

Figure 12. Attenuation of light of different wavelengths by lake waters. Upon entering a lake light is attenuated as a result of absorption. The water itself, colour or gilvin (the dissolved yellow substance in water) and suspensoids all contribute to the absorption process (James and Birge 1938, Kirk 1977). Each of these 3 groups has its own type of absorption curve. Water selectively absorbs wavelengths at the red end of the spectrum and its effect is generally constant for all lakes. Suspensoids show no selective effects, while gilvin strongly absorbs at the blue end of the spectrum. Thus lake gilvin content will modify the pattern shown in the figure, by controlling the depth of penetration of shorter wavelengths relative to longer wavelengths.

The depth scale represented in the figure is arbitrary. Actual values depend on both gilvin and suspensoid contents within the lake.

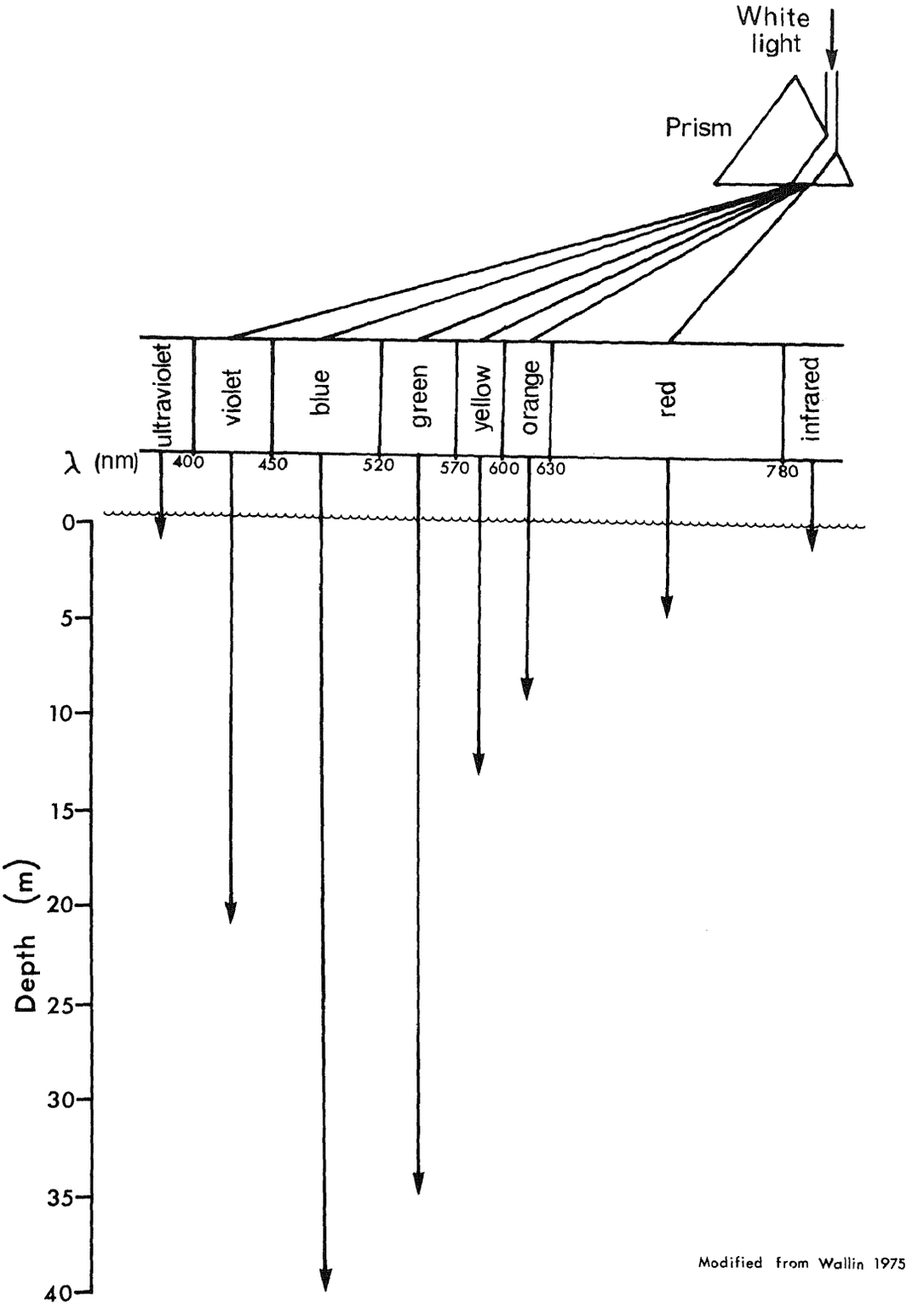


Figure 12
Attenuation of light ...
Between pp 60,61

Table 15: Peaks in spectral sensitivity of 3 freshwater crayfish species.

Species	Max. wavelength sensitivities (nm)	Source of reference
Procambarus clarkii	594 & 440	Waterman and Fernandez 1970
P. clarkii	>600 & 460 (summer) 560 & ? (winter)	Nosaki 1969
P. clarkii	575 & 450	Wald 1968
Orconectes virilis	565 & 435	"
O. virilis	565 & 425	Goldsmith and Fernandez 1968
O. immunis	565 & 425	"

Table 16: Secchi depths recorded from 6 lakes.

Lake	Secchi depth (m)	Reference	Date
Rotoiti	4.5	present study	26 March 1978
"	4.5-9.0	Jolly (1968)	1955-56
Okataina	13.0	present study	11 March 1978
"	6.0-14.2	Jolly (1968)	1955-56
Rotoma	12.0	present study	12 march 1978
	10.0-10.5	Jolly (1968)	1955-56
Tarawera	9.0	Green (1975)	10 Aug. 1972
	5.6-9.0	Jolly (1968)	1955-56
Tikitapu	5.0-10.0	"	"
Taupo	8.0-18.0	"	"

This means that light at its boundary zone would comprise less blue and green wavelengths (to which *P. planifrons* is probably relatively insensitive) than in the other, clearer lakes. Therefore, it follows that the differences in light intensity between each boundary zone (table 13) were probably due mainly to the amounts of blue and green light present at those depths. Boundary zone depths were generally deeper in the clearer lakes mainly because of greater attenuation of either violet or yellow-orange, or both wavelengths.

Clearly the spectral composition of L. Rotoiti and microspectrophotometry studies on the photocells of *P. planifrons* are necessary before a better understanding of the regulatory effect of light on crayfish distribution is possible.

b) Substrate

L. Rotoiti has an irregularly contoured floor. Most of the bottom at depths of over 20 m appears relatively barren and consists of a smooth, soft, pale coloured mud, dotted with occasional rock outcrops. Many of these are deeply dissected and protrude up to 15 m from the lake floor. The more exposed shallower areas have coarse-grained materials including sand, pumice, stones, gravels and rocks, in varying proportions, while protected bays are predominantly muddy. Weed bed sediments are mainly mud and sand.

The lake is used by many people for recreational purposes (McColl 1974), consequently its floor (especially above 20 m depth) is littered with debris such as cans,

bottles, bricks, tyres, iron sheets and sunken craft. These objects along with the accumulations of allochthonous debris (leaves, twigs and logs which often accumulate at the bottom of steep slopes), rock piles and crevices, include the main types of shelter utilised by crayfish. Also, empty *Hyridella menziesi* shells often serve as shelters for the larger juveniles and smaller adults especially. Svärdson (1972) comments that *Astacus astacus* prefers a firm bottom but *P. planifrons* was seen in large numbers on bottom substrates ranging from rock to quite soft mud. As in all the lakes studied, muds usually became softer with increasing depth. In localised areas at about 23 m depth, imprints made by crayfish were commonly seen (plate 9). Deeper down crayfish sometimes sank into the softer deposits and so produced networks of tracks as they moved across the lake floor (plate 10). Here crayfish numbers were always very low (<0.01 crayfish m^2). As these crayfish partially sank into the mud, greater oxygen demands would have been created in order to maintain activity. Also, since movements were always accompanied by a sediment cloud, the gill filaments might become partially clogged, which could restrict respiratory exchange. It is possible therefore, that the problems associated with living on soft mud bottoms are physiological as well as physical, which may account for the low densities observed on these bottoms.

The presence of walking tracks was accepted as an indicator of the softest mud bottom able to support

Plate 10. Tracks formed by crayfish walking across a very soft mud substrate at 33 m depth in L. Okataina. The area shown is ca 2.5 m^2.

Plate 9. Imprints formed by crayfish on a soft mud substrate at 24 m depth in L. Okataina. The area shown is 176 cm^2.

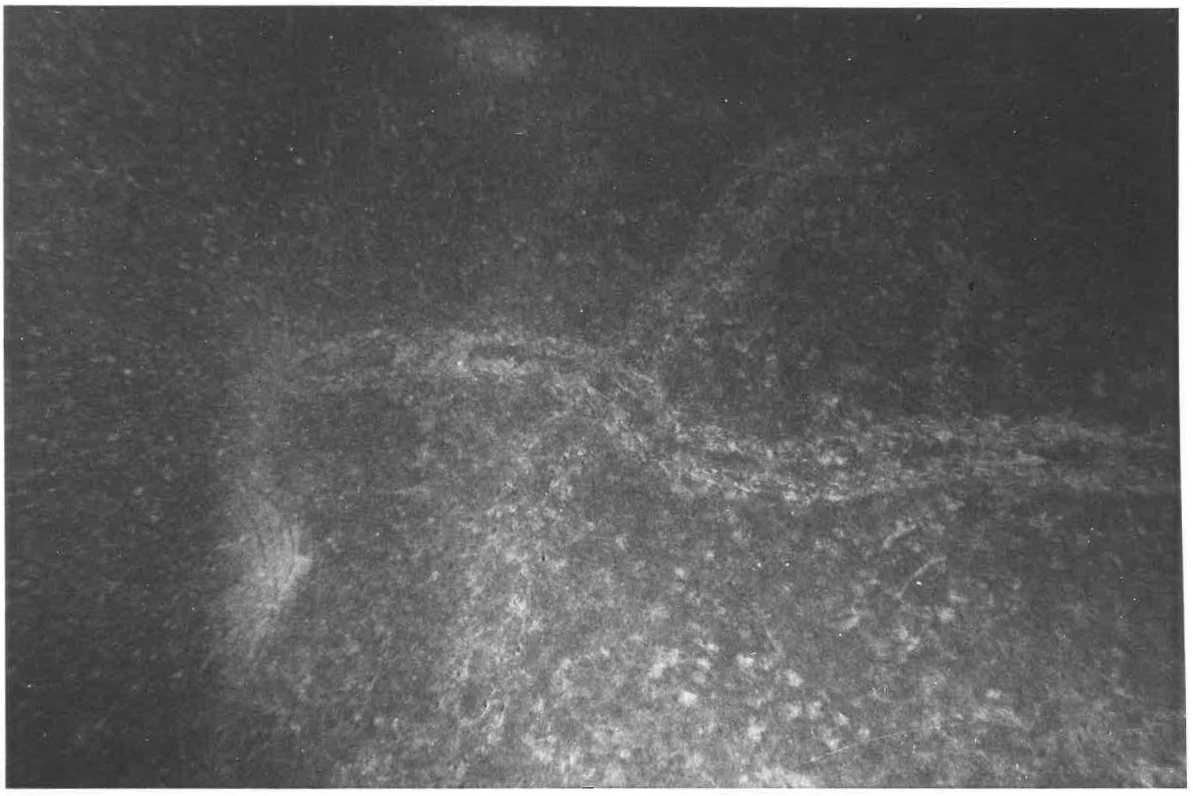


Plate 10
Tracks formed by crayfish ...
Between pp 63,64

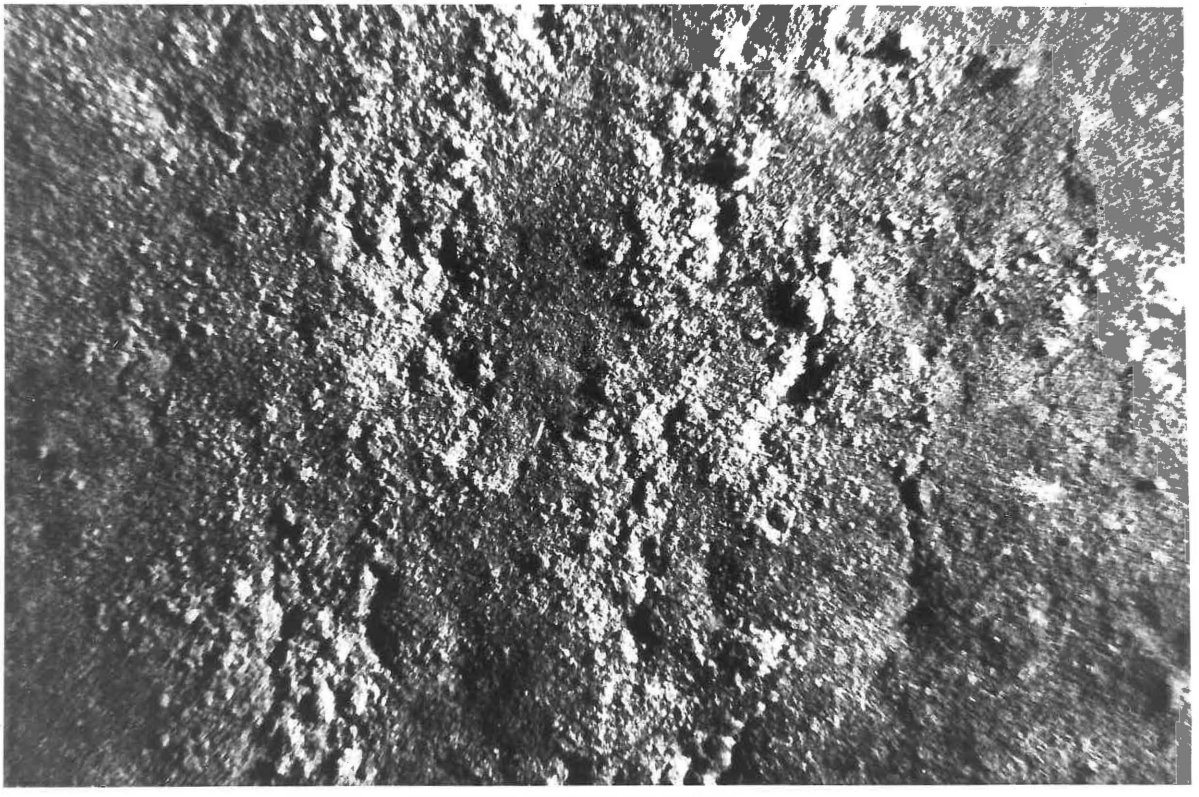


Plate 9
Imprints formed by crayfish ...
Between pp 63,64

P. planifrons. Where the muds became softer crafish may not survive. However, such areas appear to be localised and confined mainly to the deeper basins.

Substrate instability can also affect distribution by other means. Leigh (pers. comm.) observed areas within L. Waikareiti that were layered with a highly unstable, partially decomposed, detrital 'fluff', overlying a mud base and devoid of crayfish. It was likely that the grossly unstable nature of this material offered inadequate support for crayfish.

Abrahamsson and Goldman (1970) reported that storm-induced heavy wave action caused the dislodgement of rocks in the shallows of L. Tahoe, resulting in heavy crayfish mortalities. This was never apparent in L. Rotoiti but in lakes with a long fetch and thus greater wave-induced turbulence, e.g. L. Taupo, this form of substrate instability may occur. The shifting of shallow water sands in L. Rotoiti by storm wave action was thought to discourage crayfish moving into the shallows at night.

To summarise, substrate type has a marked influence on the patterns of spatial distribution of both adults and juveniles above the boundary zone in L. Rotoiti. Here, noninhibitory light occurs only where the substrate is irregular, therefore light and substrate function together as controllers of distribution. For this reason crayfish do not occur on the more open mud or sand bottoms but are restricted to areas with suitable shelters. Since these areas are randomly spread, densities above the boundary zone tend to vary greatly around the lake. Distribution

patterns below the boundary zone are probably controlled principally by substrate type, since light is no longer inhibitory. Here *P. planifrons* freely exist at similar densities on rock, sand and mud bottoms, indicating the wide adaptability of this species to various substrate types. Limits to its tolerance are probably reached on very soft muds.

Figure 13 summarises some of the ways by which the daytime spatial distribution pattern might be controlled by light and substrate. These two parameters would appear to be major controllers, as they can account for the actual daytime pattern established earlier.

A habit commonly seen below about 23 m was congregations of crayfish around or under objects lying on the bottom (plate 11). This behaviour may be a protective response to either light or predators.

2. The Night-time Pattern

Food

Food is a basic requirement for all animals, hence its location must influence consumer distribution, especially at times of feeding. *P. planifrons* feeds at night, therefore food would be most likely to exert an influence on distribution during these hours. Flint and Goldman (1975) found that *Pacifastacus leniusculus* had a regulatory effect on the productivity of periphyton and aquatic macrophytes within the littoral zone of L. Tahoe. Periphyton productivity was inhibited where crayfish biomasses exceeded 203 g m^{-2}, whereas a crayfish biomass

Figure 13. Typical section of L. Rotoiti to 30 m depth, illustrating the effects of light and substrate on adult spatial distribution. Crayfish above the "boundary zone" (area between broken lines) are present only where cover is available, while those deeper are mainly in the open and form the high density band. Here crayfish occur on all types of substrate, except the softest muds. The gradient of light intensity is shown by stippling.

Figure 13
Typical section of L.Rotoiti ...
Between pp 65,66

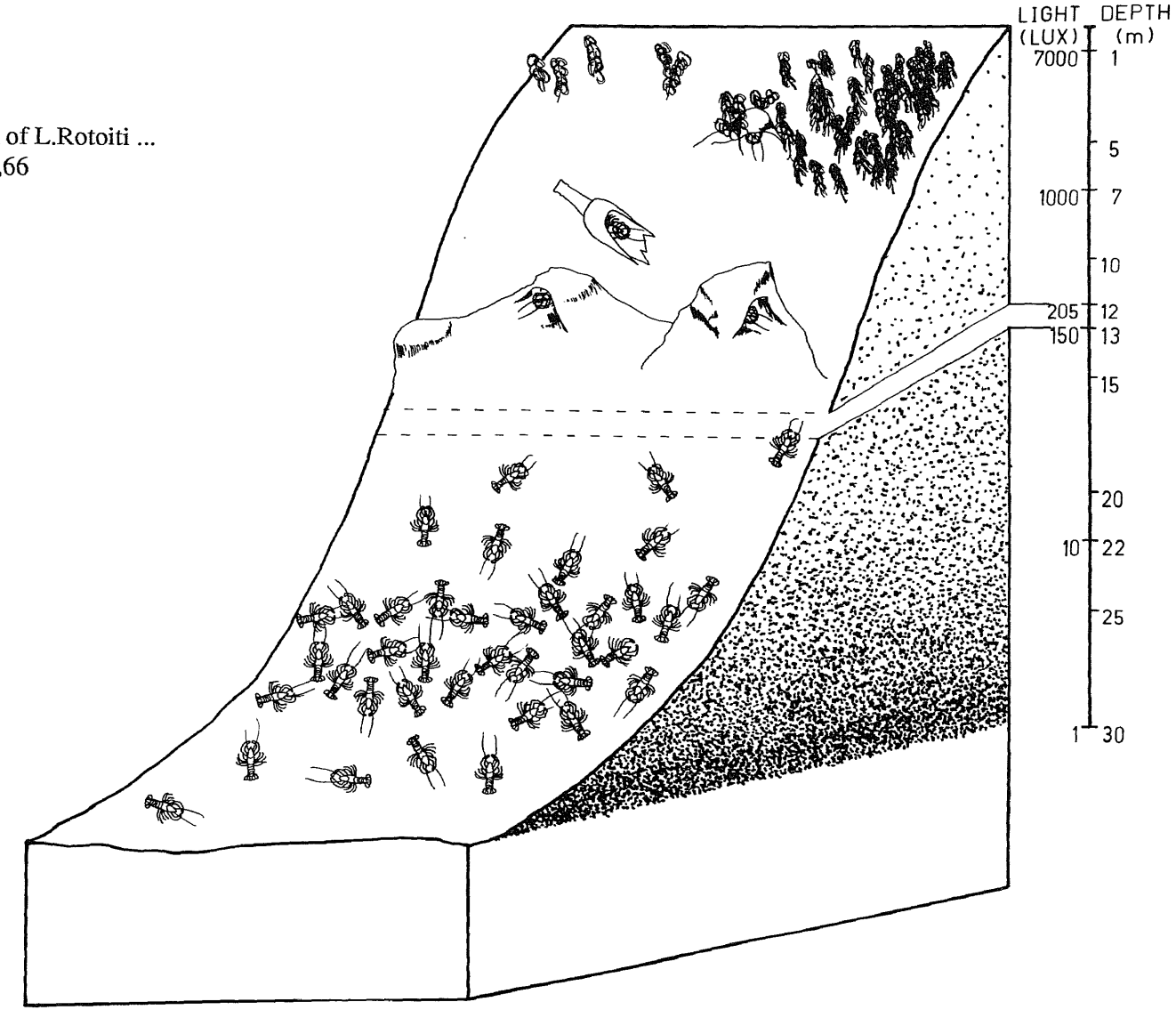


Plate 11. Crayfish under branches at 35 m depth in L. Taupo. Concentrations of crayfish around and under objects were a common behavioural feature below the "boundary zone" of Lakes Tarawera, Okataina, Rotoiti, Rotoma and Taupo.

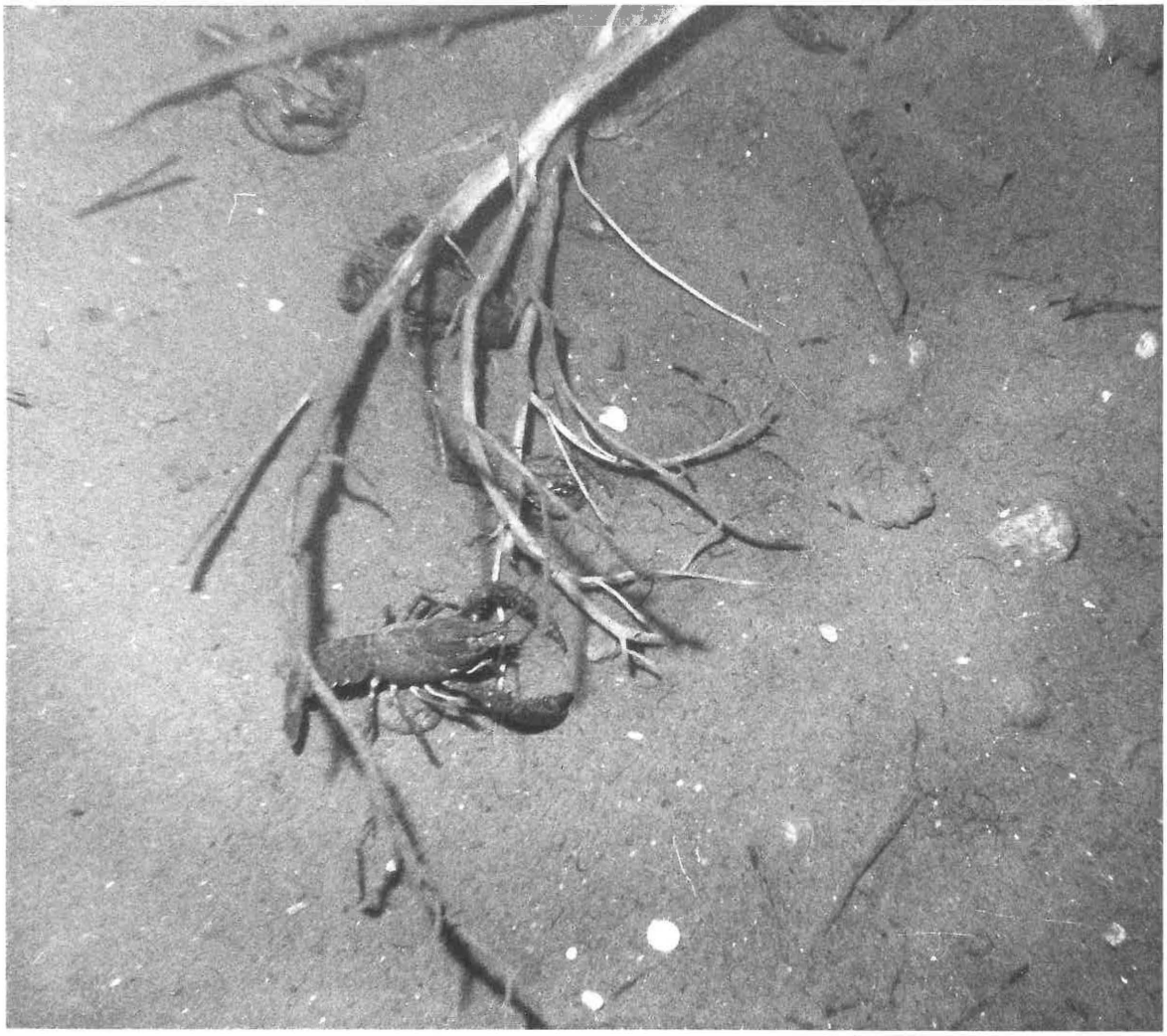


Plate 11
Crayfish under branches ...
Between pp 65,66

above about 69 g m^{-2} reduced the standing crop of *Myriophyllum* sp. In the earlier study (Devcich 1974), it was found that 80% of the diet of *Paranephrops planifrons* was detritus, while 10% was vascular plant material and the remaining 10% was animal parts, including crayfish carapace.

In this section the distribution and abundance of the food source of *P. planifrons* was established and then related to the population density. Also, it was determined whether food quality or food abundance was the factor most likely to have influenced the abundance of crayfish at night.

Crayfish are opportunistic omnivores playing a polytrophic role in aquatic ecosystems (Flint and Goldman loc. cit., Lorman and Magnuson 1978, Momot, Gowing and Jones 1978), thus it is difficult to accurately assess the abundance of their food. However, since crayfish are bottom feeders, the organic content of surface sediments can be used as a general indicator of food abundance.

Food distribution and relative abundance throughout L. Rotoiti was assessed as the amount of organic material per unit weight of surface sediment at 1, 10, 20, 30, and 50 m depths. Figure 14 clearly shows that sediment food value was greatest in the littoral zone, while food levels at greater depths were relatively constant but some 80% lower.

Crayfish distribution patterns could be affected by either food quality or food abundance. To assess whether crayfish were selective in their feeding habits and

Figure 14. The distribution and relative abundance of the food supply of *P. planifrons* in L. Rotoiti. Means were derived from 12 samples collected at the same site from January – December 1975.

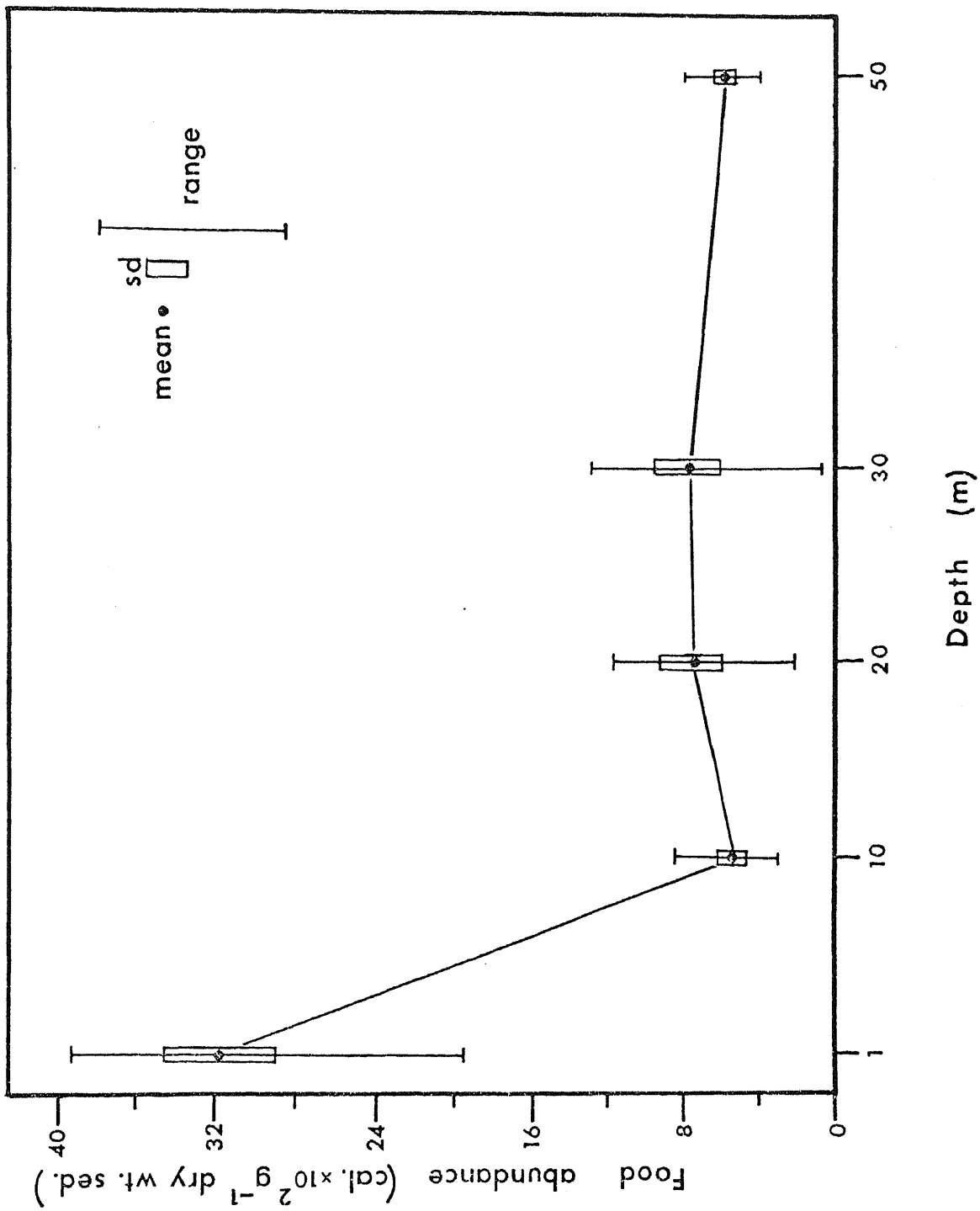


Figure 14
The distribution and relative
abundance ...
Between pp 66,67

whether their diet differed in quality throughout the lake, the mean energy content of stomach contents of crayfish captured from 1, 10, 20, 30 and 50 m depths was measured (table 17). Results suggested that crayfish are able to obtain food of a calorific value in excess of the general sediment values (cf. figure 14) regardless of depth, implying that high value food is available at all depths. Thus, distribution patterns are likely to be determined more by the abundance of food in the sediment, rather than by absolute food quality.

The relationship between crayfish density and food abundance was examined by comparing the monthly mean crayfish densities with the monthly mean sediment organic content. During 1975 crayfish were trapped and sediments sampled each month from 1, 10, 20, 30 and 50 m depths. At each depth both crayfish and sediments were sampled within the same area of L. Rotoiti and within the same 24 hour period. Values for March at 30 m depth and from January - May at 50 m depth were omitted because of the absence of crayfish at these depths during these months (see later). Results are given in Table 18 and show a strong positive correlation ($r = 0.96^{***}$, $n = 10$).

The vertical range of the rich littoral feeding ground was determined from the energy content of surface sediments taken at 1 m depth intervals between the 1 m and 8 m contours in Te Puhoe Bay. One sample was taken at each depth and the results are presented in Table 19. Values were consistently high down to 6 m depth but dropped markedly below this depth, which implied that the lower depth limit of the main feeding ground was around 6 m.

Table 17: Mean energy levels of stomach contents of crayfish from 5 depths in L. Rotoiti.

Date 1975	Energy of stomach contents (cals g^{-1} dry wt) 1 m	10 m	20 m	30 m	50 m
16 Jan.	5206	4690	4220	3874	-
17 Feb.	4414	4217	3702	3523	-
17 Mar.	4054	4058	4412	-	-
16 Apr.	5171	4521	4176	4235	-
12 May	4178	4567	4307	3753	-
15 Jun.	4892	4083	3463	3848	3979
14 Jul.	3920	3716	3343	3583	3375
15 Aug.	4484	4275	4421	4400	4230
15 Sep.	3825	4348	4769	3025	5009
15 Oct.	3884	5207	4736	3462	3067
13 Nov.	4408	4495	3540	3976	3817
15 Dec.	2991	3389	2914	3674	4586
No. stomachs examined	80	70	68	55	37
Duncan's New Multiple Range Test:					
Mean energy content (cals g^{-1} dry wt)	4286	4297	4005	3759	4009
Grouping: p = 0.05					

Table 18: Correlation between food abundance and numbers trapped at respective depths.

Depth	Food abundance (cals g^{-1} dry wt sed)	SD	N	SD
1	3183	563	136	28.7
10	539	162	47	15.1
20	739	345	42	13.9
30	763	338	21	11.3
50	574	128	26	6.5

Table 19: Energy content of surface sediments from 1-8 m depth in L. Rotoiti.

Depth of sample (m)	Surface sediment energy content (cals g^{-1} dry wt)
1	3278
2	3754
3	3600
4	3925
5	3457
6	3400
7	820
8	930

The depth range of these high values coincided exactly with that of aquatic macrophytes within this lake (Chapman et al 1971), so the weed bed zone may be regarded as the prime feeding ground of *P. planifrons*.

Overall, the results suggest that the distribution and relative abundance of food within L. Rotoiti strongly influences the crayfish distribution pattern at night. Food quality was found to be within the same range throughout the lake, while its abundance was greatest in the weed bed zone, that is, above the 6 m contour. That *P. planifrons* displays migratory behaviour after sunset, would appear to be of high adaptive significance, for it ensures that crayfish feed where conditions are optimal.

3. The Twilight Migration

a) Timing of locomotor activity

The twilight hours are transition periods in the behaviour of *P. planifrons*: from active to inactive at dawn and from inactive to active at dusk. In this study a difference in the timing of the initiation of activity with depth was observed.

Dusk observations showed that crayfish at 20 m depth became active 44 minutes before those at 1 m depth (table 20). It may be inferred from Table 12 (p. 53) that at dawn the timing of the beginning of inactivity also varied with depth but in the opposite manner; crayfish at 1 m becoming inactive about 90 minutes before crayfish at 15 m.

Closely related *P. zealandicus* is also nocturnally active and its locomotor activity is endogenously timed

Table 20: Timing of initial locomotor activity with depth during dusk.

Time of initial locomotor activity (00 hrs)	Depth (m)
1826	20
1830	15
1835	10
1840	5
1910	1

27 March 1978
Sunset at 1827 hrs.

(Quilter 1975). Quilter suggested a circadian clock may operate some time before dusk to induce the appropriate physiological conditions in order that locomotor activity coincides with the onset of darkness. Marler and Hamilton (1966) state that before the locomotor rhythm appears in animals, an external stimulus is often necessary. Light is generally regarded as the dominant Zeitgeber affecting circadian activity patterns (Brown 1972), so it may activate the clock mechanism proposed by Quilter. It seems feasible that the clock mechanism (if it exists at all) could be triggered when light attains a critical threshold intensity, perhaps perceived by the compound eye which discriminates intensity (Kennedy and Baylor 1961).

The feasibility of this hypothesis was assessed by relating light levels at dusk to crayfish locomotor activity. Light intensity was recorded at 1, 5, 10, 15 and 20 m depths every 10 minutes, from 1 hour before sunset, until zero intensity occurred at 1 m . During this period the depths of mobile crayfish were noted.

The general reduction in light intensity as dusk advances is shown in Table 21, which also shows the way in which light intensity is reduced to zero first at 20 m, and then at a depth of 1 m 30 minutes later. Crayfish activity with depth showed a similar trend (table 21 and cf. table 20). Thus, as dusk advances, the depth of the "threshold" light intensity would become progressively shallower. By this means light may induce the differences in timing of initial locomotor activity between crayfish at different depths.

Table 21: Decreasing light levels (as lux) associated with dusk and the timing of initial locomotor activity by crayfish.

Time (00 hrs)	Depth (m) 1		5		10		15		20	
	L	C	L	C	L	C	L	C	L	C
1630	1240	-	460	-	160	-	40	-	10	-
1640	1170	-	380	-	113	-	28	-	6	-
1650	780	-	280	-	74	-	17	-	4	-
1700	540	-	212	-	45	-	10	-	3	-
1710	380	-	145	-	28	-	6	-	<2	-
1720	240	-	90	-	15	-	4	-	<1	-
1730	130	-	40	-	5	-	2	+	0	+
1740	50	-	15	-	2	+	1	+	0	+
1750	15	-	4	+	<1	+	0	+	0	+
1800	0	+	0	+	0	+	0	+	0	+

- crayfish inactive.
+ crayfish active.

L = Light
C = Crayfish

6 February 1978
Sunset at 1730 hrs.

An experiment similar to the one performed at dusk was conducted at dawn (table 22). Results showed that as dawn advanced, bottom light intensities increased from the surface downwards. Accordingly, the timing of crayfish inactivity followed a similar path. Roberts (1944) found for *Cambarus virilis* that light caused the release of a chemical from the eyestalks which induced a decrease in locomotor activity. It may be that light affects quiescence similarly in *P. planifrons*. Crayfish in shallow water would be affected first and crayfish deeper down later, as dawn advanced.

As well as light, temperature also affects the timing of free-running rhythms (Brown 1972, Palmer 1976). The differences in timing of activity with depth around dusk (table 20) were recorded in autumn when the lake was thermally stratified, so temperature could have also been a contributing Zeitgeber. As a means of assessing whether temperature was important, the timing of initial activity between 1 and 25 m depths was determined in winter, when L. Rotoiti is homothermal. Results are presented in Table 23 and indicate a similar sequence of events to that recorded when the lake was stratified. Therefore, it would seem that temperature does not contribute to the differences in timing of activity with depth. In the opinion of Professor F.A. Brown Jr. (pers. comm.), differing light transitions, rather than any other Zeitgeber, are the most probable factor initiating activity in *P. planifrons*.

Blaxter (1975) states that the fact that vertical migratory behaviour tends to occur around dusk and

Table 22: Increased light levels (as lux) associated with dawn and the timing of locomotor inactivity by crayfish.

Time (00 hrs)	Depth (m) 1 L	1 C	5 L	5 C	10 L	10 C	15 L	15 C	20 L	20 C
0530	0	+	0	+	0	+	0	+	0	+
0540	1	-	0	+	0	+	0	+	0	+
0550	3	-	1	+	0	+	0	+	0	+
0600	10	-	5	+	1	+	0	+	0	+
0610	40	-	10	-	3	+	1	+	0	+
0620	188	-	62	-	10	+	3	+	0	+
0630	372	-	160	-	30	+	3	+	0	+
0640	775	-	295	-	45	+	5	+	0	+
0650	1185	-	345	-	88	-	10	+	0	+
0700	1600	-	450	-	120	-	15	-	1	-
0710	2260	-	566	-	160	-	28	-	10	-

\- crayfish inactive.
\+ crayfish active.

L = Light
C = Crayfish

26 March 1978
Sunrise at 0629 hrs.

Table 23: Timing of initial activity with depth at dusk and under homothermal conditions.

Time of initial activity (00 hrs)	Depth (m)
0521	25
0526	15
0530	9
0545	6
0610	1

14 July 1978
Sunset at 0522 hrs.
Water temp. 10±0.5°C.

dawn is good circumstantial evidence of the role of light. *P. planifrons* follows a receding light gradient at dusk, while at dawn the downward migration is accompanied by an intensifying light gradient. Viewed in this sense, light is the likely ultimate determinant of the time and rate of crayfish movements at dusk and dawn.

b) Migratory behaviour

i) Rhythmical activity

Activity rhythms in some crayfish species display bimodal peaks at dusk and dawn (Roberts 1944, Page and Larimer 1972, Quilter 1975). This almost certainly occurs in *P. planifrons* too, for Whittle (unpub. data) found a free-running bimodal increase in oxygen uptake during the hours of twilight for crayfish collected from L. Rotoiti. These increases in metabolic rate coincide well with periods of migratory activity. It may be that these endogenously induced bursts in metabolism are an adaptation helping to satisfy the increased energy requirements associated with migratory activity. This seems reasonable, for the twilight migrations are fairly rapid events dominated by locomotor activity (foraging activity was never apparent) and may include quite large distances (up to ca 500 metres).

ii) Evidence for a circadian rhythm

An experiment to verify the existence of a dual circadian migratory rhythm was conducted in a blacked

out aquarium, the bottom of which was tilted at 20° to the horizontal (plate 12). The open substrate of sand and small pebbles was divided into 5 unmarked sectors of equal area in the following depth ranges: <0.2 m, 0.2-0.4 m, 0.4-0.6 m, 0.6-0.8 m, >0.8 m. Crayfish were not fed throughout the experiment and a dim red light was used to observe them. [Crayfish are probably blind to wavelengths in the red end of the spectrum (Kennedy and Bruno 1957, Goldsmith and Fernandez 1968)]. To ensure against loss of overt behaviour, which, according to Bunning (1973), may result from adaptation to certain environmental conditions, the experiment was run 1 day after the crayfish were taken from L. Rotoiti. Indeed such a loss may occur in *P. planifrons*, for after about 10 days in the aquarium, their daytime distribution pattern changed from a concentration at the aquarium's deep end, to an even spread along the bottom. (As a precaution all subsequent experiments were run within 3 days of collecting crayfish from the lake.)

One half hour before natural sunset (1830 hrs, 28 March 1978), 30 adults (15 males and 15 females) were released into the deep end where they stayed relatively inactive. At 1 hour after sunset and at every subsequent half hour thereafter until midnight, the number within each depth range was noted. From these readings the overall night-time distribution pattern was assessed.

Half hourly readings were recommenced one half

Plate 12. Aquarium. Note crayfish at bottom of slope.

Plate 12
Aquarium
Between pp 77,78

hour before natural sunrise (0625 hrs) and continued for 2 hours, by which time all crayfish were quiescent. The final reading (0800 hrs) therefore indicated the general daytime pattern.

Statistical analyses of this experiment and of data in subsequent experiments were made using the Kolmorgorov-Smirnov and Chi-square goodness of fit tests. The Kolmorgorov-Smirnov test is more powerful than Chi-square when n is small (Zar 1974), so for $n > 50$ Chi-square was applied. Tests for significance were determined at the 5% level.

Results are shown in Figure 15. After dusk crayfish moved up the slope in a negative geotactic response and then back down again before dawn in a strongly positive geotaxis, which showed that migratory behaviour is under circadian control. This behaviour produced a highly significant difference between their overall night and daytime distribution patterns ($\chi^2 = 428$, $p << ***$, $n = 150$). The actual difference is best illustrated when the night and day patterns are compared at their respective theoretical peaks, that is, at 12 pm and 8 am ($D = 0.533$, $p <<< ***$, $n = 30$).

iii) Effect of size

The relationship between size and rate of movement was assessed in situ. 4 crayfish of varying size were placed on a slope with a constant gradient of 16° 41', in L. Rotoiti. The slope angle was

Figure 15. Distribution pattern of crayfish maintained in darkness in the aquarium with a sloping bottom (see plate 13) over a 24 hour period. The results demonstrate the existence of a dual circadian migratory rhythm. One migration occurs after dusk and the other before dawn.

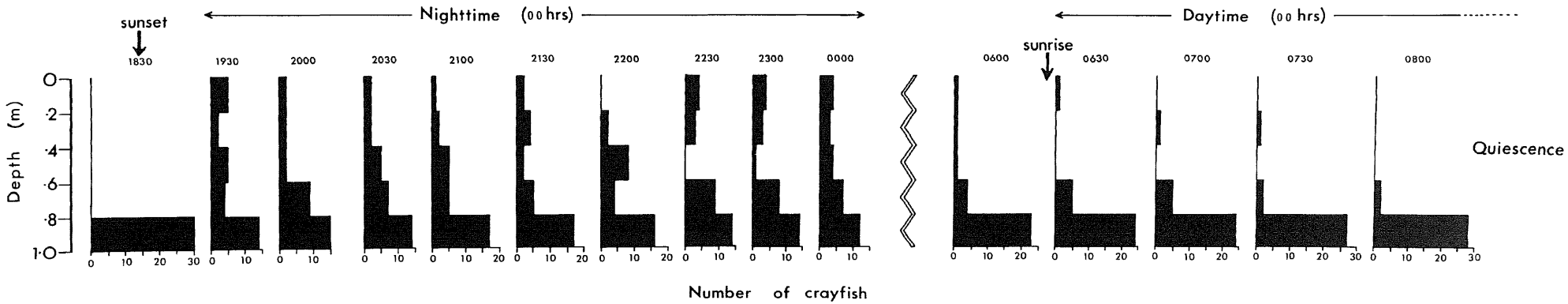


Figure 15
Distribution pattern of
crayfish ...
Between pp 78,79

calculated geometrically from the straight line distance along the bottom and the difference between two depths. (It was assumed that the effect of slope and changes in light intensity associated with increasing depth was similar for crayfish of different size.) Once normal locomotory behaviour had re-established (2-10 minutes), the time each crayfish took to move between two depths down the slope was noted. The distance travelled in a straight line was calculated and to this value a 13% correction was added, thus giving the actual distance travelled. (Crayfish deviate about 13% from a straight line when moving down a 16° 41' slope)(see later). From this, the locomotor rate was calculated (table 24).

There was a significant difference in locomotor rate between the juvenile and the adults ($t = 25.0$, $p = **$, $n = 4$), although the rate for adults did not vary with size. It may be expected that progressively smaller juveniles would display increasingly slower rates of movement. Locomotor rate of the adults was 1.1-1.8 times and 1.8-2.3 times faster than recorded for adults at dawn and dusk respectively (see later). Nevertheless, the results do indicate that *P. planifrons* is capable of traversing large distances in a relatively short time, which strengthens the impression that the migrations were rapid events, as mentioned earlier.

iv. Effect of slope in situ

The echsounding traces of the bottom of L. Rotoiti

Table 24: Effect of crayfish size on locomotor rate in situ.

Size (CL mm)	Initial (upper) & final (lower) depth (m)	Time (00 hrs)	Time of obs. (min)	Straight line distance (m)	Actual distance covered (m)	Locomotor rate (m min^{-1})
60.0	6.5 15.0	1310 1320	10	29.6	33.5	3.4
45.1	6.0 14.8	1332 1342	10	30.6	34.6	3.5
32.5	6.0 15.0	1350 1400	10	31.3	35.4	3.5
19.7 (juv.)	6.0 13.0	1414 1429	15	24.4	27.5	1.8

22 April 1978

(see figure 16) indicated that migrating crayfish probably traverse slopes of varying gradient and this was verified by dives made at twilight. To assess how gradient affects orientation behaviour in situ, adult crayfish of similar size were placed on 3 slopes with different gradients. The slopes were angled at 2°52', 8°31' and 16°41' to the horizontal and were relatively smooth so that orientation was not influenced by bottom irregularities. Slope angles were calculated geometrically as indicated previously. The starting location of each crayfish was marked with a stake and the depth noted. As each crayfish moved down the slope, it was followed and cord was let out to enable an accurate assessment of the actual distance covered. The number of times a crayfish stopped was recorded during the 11-20 minute experiments, after which the depth was noted and the straight line distance to the starting point measured. From the linear values, the extent crayfish deviated from the straight line distance was calculated and expressed as a percentage of that distance. Rates of movement were also calculated (table 25).

There was an inverse relationship between gradient and extent of random movement, orientation becoming progressively less directed as the gradient decreased (see figure 17). Casual observation at night verified that the relationship also held for crayfish migrating upward. Rates of movement showed a more or

Figure 16. Bottom topography from the shoreline to about the 30 m contour at 10 locations in L. Rotoiti. Locations and associated bottom traces are numbered similarly. Horizontal lines drawn through each trace depict 10 m depth intervals.

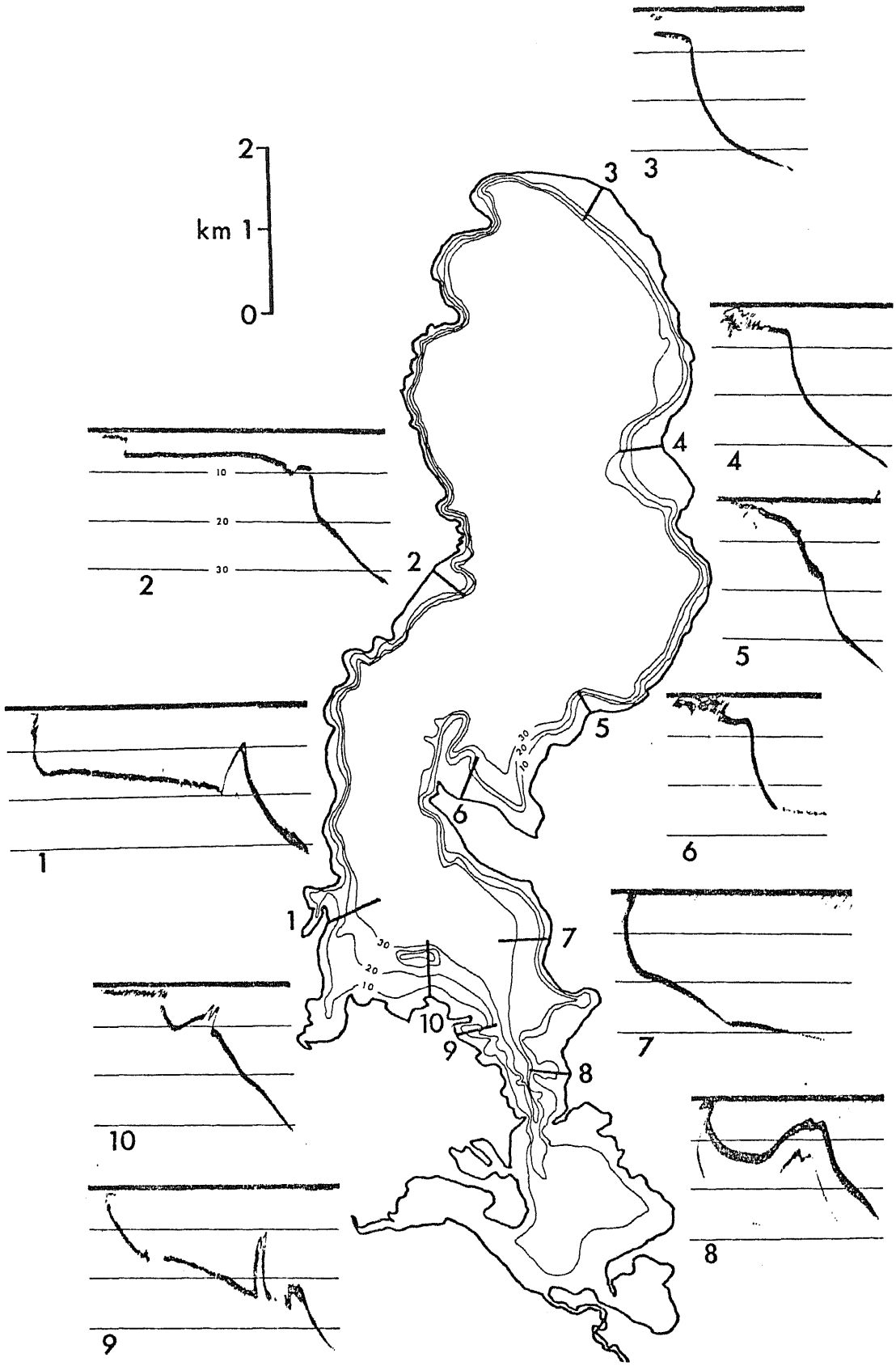


Figure 16
Bottom topography ...
Between pp 81,82

Table 25: Effect of slope on crayfish orienation and rate of movement in L. Rotoiti.

Sex	Angle of slope	Depth range (m)	Exptl. period (min)	No. stops	Direct line distance (m)	Deviation from direct line (%)	Actual distance covered (m)	Rate of movement ($m\ min^{-1}$)
F	16°41'	6.0-17.0	11	1	38.3	13.1	43.3	4.3
M	8°31'	9.0-13.5	20	11	30.4	117.1	66.0	3.3
M	2°52'	11.0-12.0	20	26	20.0	165.0	53.0	2.7

Figure 17. Effect of slope angle on orientation behaviour of *P.planifrons* in situ during daytime. Slope angles and straight line distances travelled are given and the arrow indicates the general direction of movement. The patterns displayed are near replicates of those made by the crayfish.

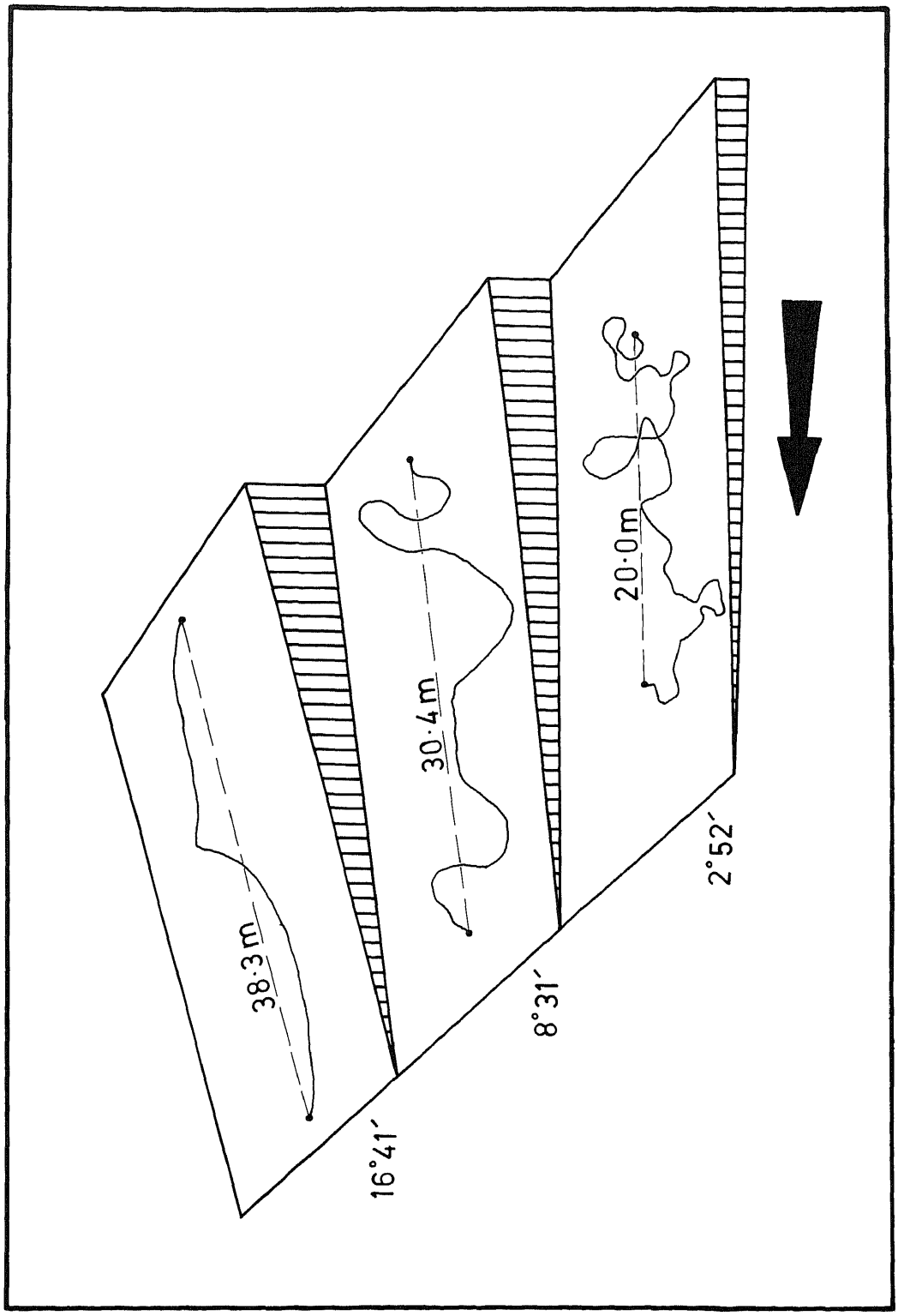


Figure 17
Effect of slope angle ...
Between pp 82,83

less direct relationship with gradient and appeared to be mainly a function of the number of stops taken. Each stop usually resulted in a change of course.

It is apparent from these results that slope angle directly affects rates of straight line movement, consequently migrations would take longer to complete wherever the littoral and high density zones are separated by low gradient slopes. Such differences in migration durations would be further accentuated by the fact that travel distance increases as gradient decreases.

The actual locomotor response associated with migratory behaviour is a taxis, as movement is from a source to a goal. Tactic responses are oriented reactions to external stimuli (Pardi and Papi 1961), which are perceived by receptor organs having certain thresholds of responsiveness specifying their sensitivity to varying intensities of stimulation (Marler and Hamilton 1966). It seems reasonable therefore, that the course taken by a migrating crayfish depends, at least in part, on the relationship between stimulus intensity and corresponding organ sensitivity. This relationship appears to be strongest on steeper gradients, as indicated by the strongly tactic response on the 16°41' slope. On lesser gradients, orientation behaviour changes to resemble a kinesis, which suggests that slope modifies the relationship, presumably by affecting receptor perceptivity.

v) Effect of slope in the absence of light

Experiments were conducted during daytime in a blacked out aquarium on bottom slopes of 0°, 10° and 20° respectively. The 0° and 10° slopes were established with a false bottom affixed to the aquarium by adjustable metal straps. Each slope was divided into 5 unmarked sectors of equal area (as noted earlier, p. 77) and numbered 1-5 in ascending order from the shallow end. There was a small variation in section areas between the 3 slopes.

30 adults (15 males and 15 females) were placed in the uppermost part of sector 1 of each bottom and retained by a metal plate until hyperactivity had ceased (about 2 minutes). The barrier was lifted and numbers within each sector were recorded every 2 minutes for a period of 10 minutes and subsequently at longer intervals until activity ceased.

The results are presented in Figure 18 and show that crayfish on slopes display a positively geotactic response. A comparison of each distribution after locomotor activity ceased, revealed highly significant pattern differences between crayfish on the flat (figure 18A) and sloping bottoms (figures 18B, 18C) (cf. 0° and 10° slope $D = 0.633$, $p << ***$, $n = 30$; 0° and 20° slope $D = 0.667$, $p << ***$, $n = 30$) but no difference between the two sloping bottoms ($D = 0.033$, $p >> 0.50$, $n = 30$). The response was similar on both slopes but numbers were consistently

Figure 18. Resultant distribution patterns of crayfish released on 3 different bottom gradients in the absence of light and during daytime.

A Flat bottom

B 10° slope

C 20° slope

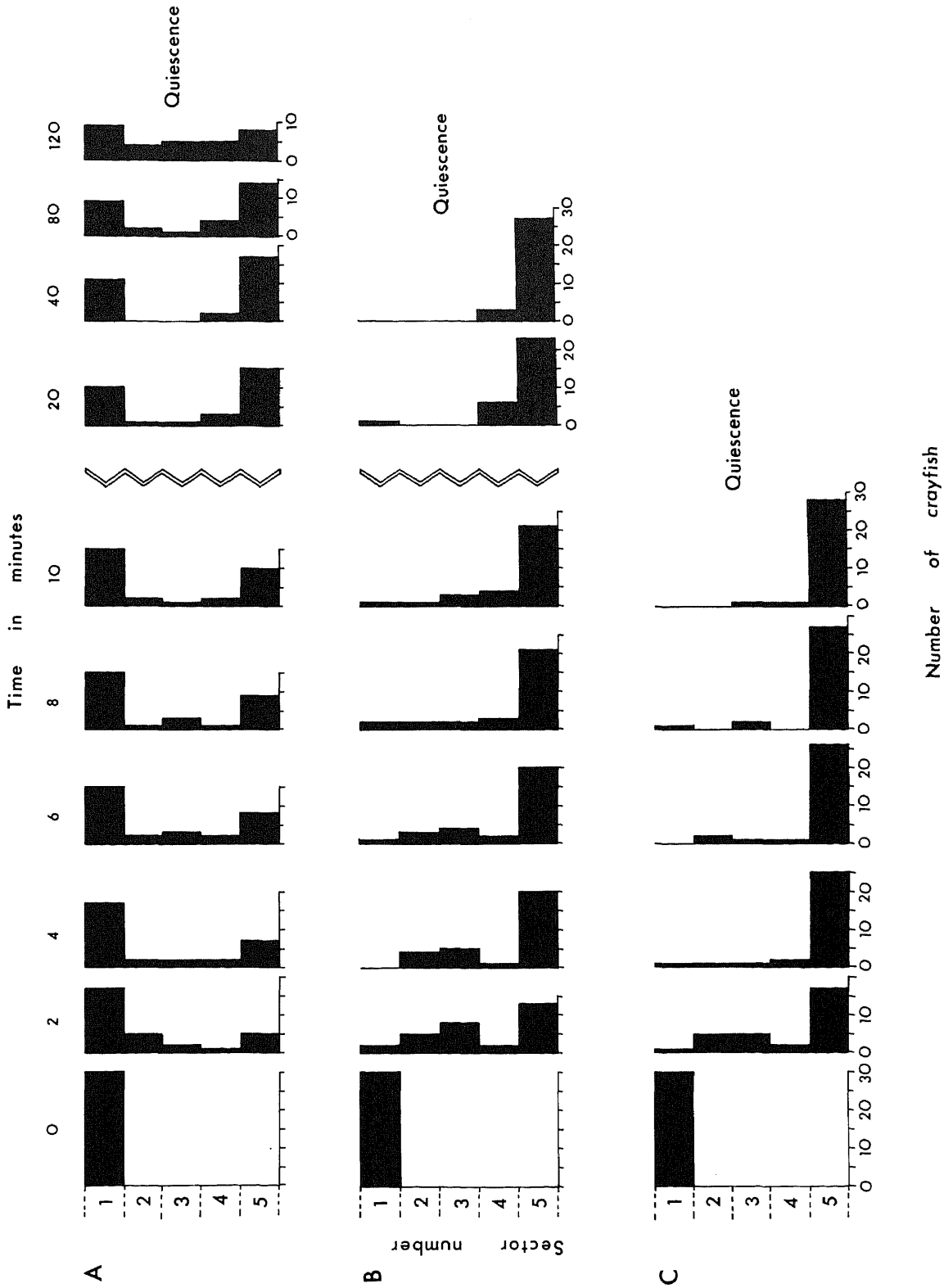


Figure 18
Resultant distribution
patterns ...
Between pp 84,85

higher in sector 5 of the 20° slope, which may indicate that the response to gravity was stronger on this slope. This seems reasonable since the increased angle of body tilt would tend to induce greater responsiveness to gravity by the mechanoreceptors.

Results also showed that slope affected the activity period in an inverse manner, such that crayfish on the flat bottom remained active 80 and 110 minutes longer than crayfish on the 10° and 20° slopes respectively.

vi) Effect of light in the absence of slope

The false bottom was affixed to the aquarium in a horizontal position. Light gradients of even (16±2 lux), weak (2-50 lux) and strong (8-2000 lux) intensity were established along the bottom on 3 separate occasions. Four 100-150 watt bulbs, placed strategically around the aquarium, produced the appropriate light gradients. For each run, 30 crayfish (15 males and 15 females) were introduced at the end with the lowest light intensity and retained by a metal plate for a few minutes, then admitted to the light gradient.

As before (p. 77) the bottom was divided into 5 equal sectors numbered from 1-5, and the number of crayfish within each sector was totalled every 2 minutes for the first 10 minutes and then less frequently until the crayfish became quiescent, which occurred within 2 hours.

Figure 19 shows the distribution pattern sequences as crayfish colonised each light gradient. Distributions within the even (figure 19A) and weak (figure 19B) light gradients did not differ significantly (see table 26). Under these light conditions a phototactic response was not expected, since intensities were below the critical 150-205 lux range already established for crayfish in L. Rotoiti. The behavioural pattern within the strong light gradient (figure 19C) was significantly different from that within the even and weak light gradients (see table 26). Nearly every crayfish in the strong light gradient displayed a strong negative response to light above the critical light range, by remaining in sectors 1-3 where the light intensity was least. Even so, a few individuals showed a positive phototaxis toward bright light (in sector 5) where they became quiescent against the aquarium walls.

It was interesting to note that many crayfish in the even and weak light gradients displayed thigmotaxis along the aquarium walls, which culminated in crayfish accumulating at the corners. This behaviour was not so apparent in the strong light gradient, which may imply that high light intensities suppress the thigmotactic response. However, only a few individuals entered the inhibitory light, so to hypothesise from their behaviour would be somewhat presumptuous.

Figure 19. Distribution patterns of crayfish subsequent to release within 3 different light gradients in the absence of slope. Distributions were assessed until crayfish became quiescent.

A Even light gradient of low intensity

B Weak light gradient

C Strong light gradient

Figure 19
Distributed patterns of
crayfish ...
Between pp 86,87

Table 26: Statistical analysis of data shown in Figure 19. p = ns when D<.242, p = * when .242>D<.290, p = ** when .290>D<.347, p = *** when D>.347 at n = 30.

Light gradient		Time (mins.) 2	4	6	8	10	20	40	80	120
even vs weak	D =	.067	.067	.133	.100	.167	.100	.167	.100	.133
	p =	ns	ns	ns	ns	ns	ns	ns	ns	ns
even vs strong	D =	.200	.300	.367	.400	.400	.433	.467	.433	.467
	p =	ns	**	***	***	***	***	***	***	***
weak vs strong	D =	.200	.267	.333	.400	.400	.333	.300	.367	.333
	p =	ns	*	**	***	***	**	**	***	**

Quiescence

vii) Effect of slope on the response to light

Behavioural responses of *P. planifrons* to a weak light gradient and then to a strong light gradient, while on 10° and 20° slopes, were examined as a means of gauging the relative strength of the positive geotactic response. Light gradients were greatest in intensity at the lower end of each slope, such that intensities decreased up the slope. During daytime, 30 crayfish (15 males and 15 females) were placed in the shallow end of the aquarium and the resultant distribution patterns were assessed as outlined previously.

Figure 20 shows that for each combination of slope and light gradient, crayfish readily moved in a positive geotaxis into the increasing light gradients. This behaviour was most pronounced within the weak light gradient (figures 20A and 20C), presumably because light levels never became inhibitory. However, there was a significant difference between the rates of movement down these two slopes (2 min. D = .267, 4 min. D = .400, 6 min. D = .367, 8 min. D = .333, 10 min. D = .300, 20 min. D = .400, 40 min. D = .433, 80 min. D = .400, p = * or less, n = 30 for each test). Movement was quickest on the 20° slope and this behaviour may be attributed to an increased responsiveness of mechanoreceptors to gravity, resulting from an increased angle of body tilt (mentioned earlier).

Crayfish in the strong light gradients readily

Figure 20. Distribution of crayfish on 10° and 20° slopes while in weak and strong light gradients.

A 10° slope, weak light gradient

B 10° slope, strong light gradient

C 20° slope, weak light gradient

D 20° slope, strong light gradient

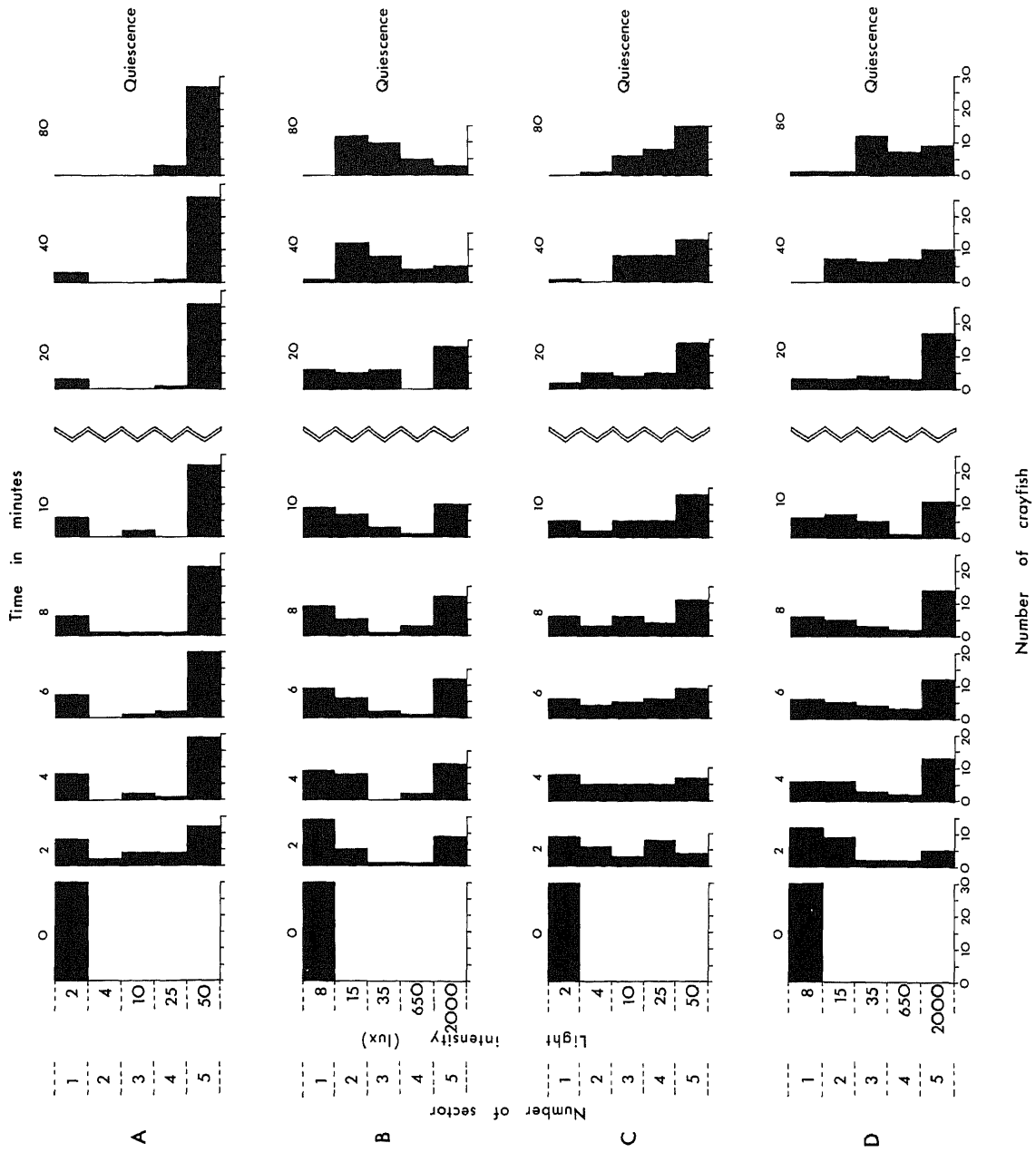


Figure 20
Distribution of crayfish ...
Between pp 88,89

entered the inhibitory light intensities in sectors 4 and 5, which suggested that the response to gravity was stronger than the response to inhibitory light. However, in some crayfish negative phototaxis became the dominant response after a variable latent period. This is best illustrated by those crayfish which moved back up the slope in Figure 20B. Of the 20 crayfish (figure 20D, 20 min sample) that entered sectors 4 and 5 on the 20° slope, 20% (4 crayfish) responded to light, whereas of the 15 like crayfish on the 10° slope (figure 20B, 8 min sample), 40% (7 crayfish) responded to light by walking back up the slope. This apparent difference in behaviour suggests that slope affects the response to light and probably in an inverse manner.

The findings above indicate that the positive geotactic response is very strong, for it even overrides the negative response to bright light. Geotaxis was strongest on the steeper slope.

2. The Sensory Mechanism

Of the environmental stimuli known to affect tactic response in decapods, light and gravity are the most likely to contribute migratory activity in *P. planifrons*. The major light receptor organ of crayfish is the eyes, while photosensitive cells also occur in the sixth abdominal ganglion (Prosser 1934, Welsh 1934, Hermann 1964, Page and Larimer 1972). Paired statocysts (Cohen and Dijkgraaf 1961, Horridge 1965, Marler and Hamilton 1966) and

proprioceptors (Cohen and Dijkgraaf 1961, Fraenkel and Gunn 1961, Horridge 1965, Marler and Hamilton 1966, Finlayson 1968, Mill 1976) function as gravity receptors. In the following experiments crayfish vision and statocyst functioning were supressed in order to elucidate the environmental stimuli and receptor organs involved in the twilight migrations.

i) The light sensors

Walking activity in crayfish results when the eyes (Schalleck 1942, Roberts 1944, Arechiga and Wiersma 1969, Hazlett 1971) and the sixth abdominal ganglion (Prosser 1934, Welsh 1934, Kennedy 1963) are stimulated with light. To establish whether retinal or extraretinal photoreception was more likely to contribute to migratory activity, the following experiment was conducted.

The eyes of 10 adult crayfish from L. Rotoiti were blinded with 3 applications of Miners nontoxic black nail varnish. (It was found that 3 layers of the varnish needed to be applied to a photocell positioned 25 cm from a 40 watt bulb before light became undetectable. Light intensity initially measured 1740 lux and was similar to the ambient light intensity of the lake at a depth of ca 3 m). Crayfish were placed in a tray (80 cm long x 30 cm wide x 10 cm deep) half filled with water. One half of the tray was dark and the other half was illuminated at 1500±50 lux. After 15 minutes the numbers in each half were noted. The distribution of 10 normal

crayfish was assessed similarly. Each experimental group was run 5 times and results were averaged.

The results are given in Table 27 and indicate that blinded crayfish were unable to differentiate between light and dark, which implies that the caudal photoreceptor is inactive below at least 1500 lux. As expected therefore, normal crayfish avoided the bright light, thus suggesting that the eyes are the dominant photosensors associated with locomotor activity.

Welsh (1934) suggested that a caudal photoreceptor may function to warn an animal of its exposure to light and hence susceptibility to attack. This specialisation is unlikely to be effective in adult *P. planifrons*, since all but a few adults reside below the depth of penetration of the very high light levels necessary to activate the response. Furthermore, the exoskeletons of adults in L. Rotoiti are generally very heavily pigmented, hence light would not readily penetrate to body tissues. However, juveniles in this lake, and stream dwelling crayfish would be more likely to utilise a caudal photoreceptor. Juveniles have lighter pigmented exoskeletons, while crayfish in the generally shallow lotic habitats are normally in close proximity to high ambient light levels.

ii) Field experiments

Experiments were conducted on the 16°41 slope off Whangamoa Point during the twilight migrations. Crayfish of both sexes in the 40-50 mm CL size

Table 27: Reactions of normal and blinded crayfish to a strongly inhibitory light intensity.

Experiment number	Number of crayfish: Blinded, Dark side	Blinded, Lit side (1500±50 lux)	Normal, Dark side	Normal, Lit side (1500±50 lux)
1	4	6	10	0
2	5	5	9	1
3	7	3	10	0
4	4	6	10	0
5	5	5	9	1
Total	25	25	48	2

D = 0.004, $p >> 0.50$, n = 25 D = 0.04, $p >> 0.50$, n = 50

range were tracked individually between the 6 m and 18 m contours. Each crayfish performed two runs, firstly as a control and then with either visual or gravistatocyst responses supressed. For this, a crayfish was removed from the lake and either blinded with black nail varnish as explained above, or its statocysts were extirpated. This small operation involved inserting a needle into the cuticular invagination of the basal segment of each antennule and macerating the tissue within. [In crayfish a statocyst lies in an invaginated cuticular vesicle of the basal segment of each antennule (Cohen 1955, Cohen and Dijkgraaf 1961, Horridge 1965, Laverack 1968, Sandeman 1976)]. The crayfish was returned near to the original position of its control run and its movements were tracked. Depths and time at the start and finish of each run were recorded to assess the direction and rate of movement.

To aid recognition of the experimental animals, a 1 cm diameter aluminium foil disc, painted luminescent green, was attached with fine wire onto the dorsal surface. By positioning an underwater torch such that only the luminescence was visible, it was possible to track the crayfish with relative ease and without disturbance to it. The torch light was screened with an orange-red filter to reduce illumination.

Crayfish were recaptured and appropriate receptor organs examined to verify their deactivation. The

blinded crayfish were found to be unresponsive to intermittent flashes of bright light (ca 2000 lux) and to hand movements directly above the eyes. (Normal crayfish generally raise chelae or show the tail reflex response to these treatments.) The basal regions of antennules of those crayfish with destroyed statocysts were scrutinised under a microscope. In both cases the statocysts were severely damaged and had separated from the statocyst nerve. It was concluded therefore, that photoreception and gravity perception via statocysts had been supressed.

Results of the field experiments are shown in Table 28. All crayfish displayed migratory activity. Those treated, readily migrated, which indicates that the migratory mechanism can still operate without the photoreceptors and gravistatocyst receptors. However, the slower rates of movement by treated crayfish (especially the blinded crayfish) at dawn suggested some involvement of these receptor organs.

All crayfish, except those treated at dusk, behaved in accordance with other migrating crayfish in the lake. These two crayfish may have moved downward in response to handling and post-operative stress, for when a torch light is directed at crayfish in situ at night, avoidance is always by a movement downwards. This suggests that when stressed, crayfish react in a positively geotactic manner.

Table 28: Orientation of 4 crayfish without vision or statocysts in L. Rotoiti during the twilight migrations.

	Sex	Experiment	Direction of movement	Duration of expt. (mins)	Depth range (m)	Rate of movement (m min^{-1})
BEFORE DAWN	M	control	↓	23	6.0-17.5	1.97
		no stato.	↓	22	7.0-14.5	1.34
	F	control	↓	11	6.0-17.0	3.12
		blind	↓	20	6.0-17.0	1.72
AFTER DUSK	M	control	↑	14	16.5-9.5	1.97
		no stato.	↓	10	13.0-17.5	1.77
	F	control	↑	23	15.0-6.0	1.53
		blind	↓	25	10.0-17.8	1.23

iii) Laboratory experiments

Experiments were conducted in the aquarium on the 20° bottom slope and in a low daytime illumination of 16±2 lux. Apart from the presence of light, the experimental protocol followed that of the circadian rhythm experiment (p.76-78).

Two groups of 30 crayfish each (15 males and 15 females) were treated similarly to the crayfish in the field experiments, that is, blinded and statocysts destroyed. A third group received both treatments (blinded with statocysts destroyed). Before experiments were run, the eyes and statocysts were verified as nonfunctional, as outlined above (p. 93). As in Figure 15, which also served as the experimental control for each group. distribution patterns were assessed from the start of activity from midnight and from 6 am until crayfish became quiescent. Night-time and daytime results are shown in Figures 21 and 22 respectively.

A comparison of the night-time patterns revealed no significant differences between the control group and each experimental group (see table 29). In the group with destroyed statocysts the levels of insignificance increased with time. This suggested a slight initial delay in the geotactic response. However, a similar trend was not apparent in crayfish both blinded and with statocysts destroyed, so it would seem that the statocysts are relatively unimportant mediators of the negative geotactic

Figure 21. Effects of suppressed photoreception and gravistatocyst reception on the negative geotactic response associated with migratory behaviour after dusk. Experiments began at sunset (1830 hrs) and the sequence of distribution patterns from the start of activity until midnight is shown. Night-time data comprising Figure 15 has been included as the control.

A Control

B Statocysts destroyed

C Blinded

D Blinded and statocysts destroyed

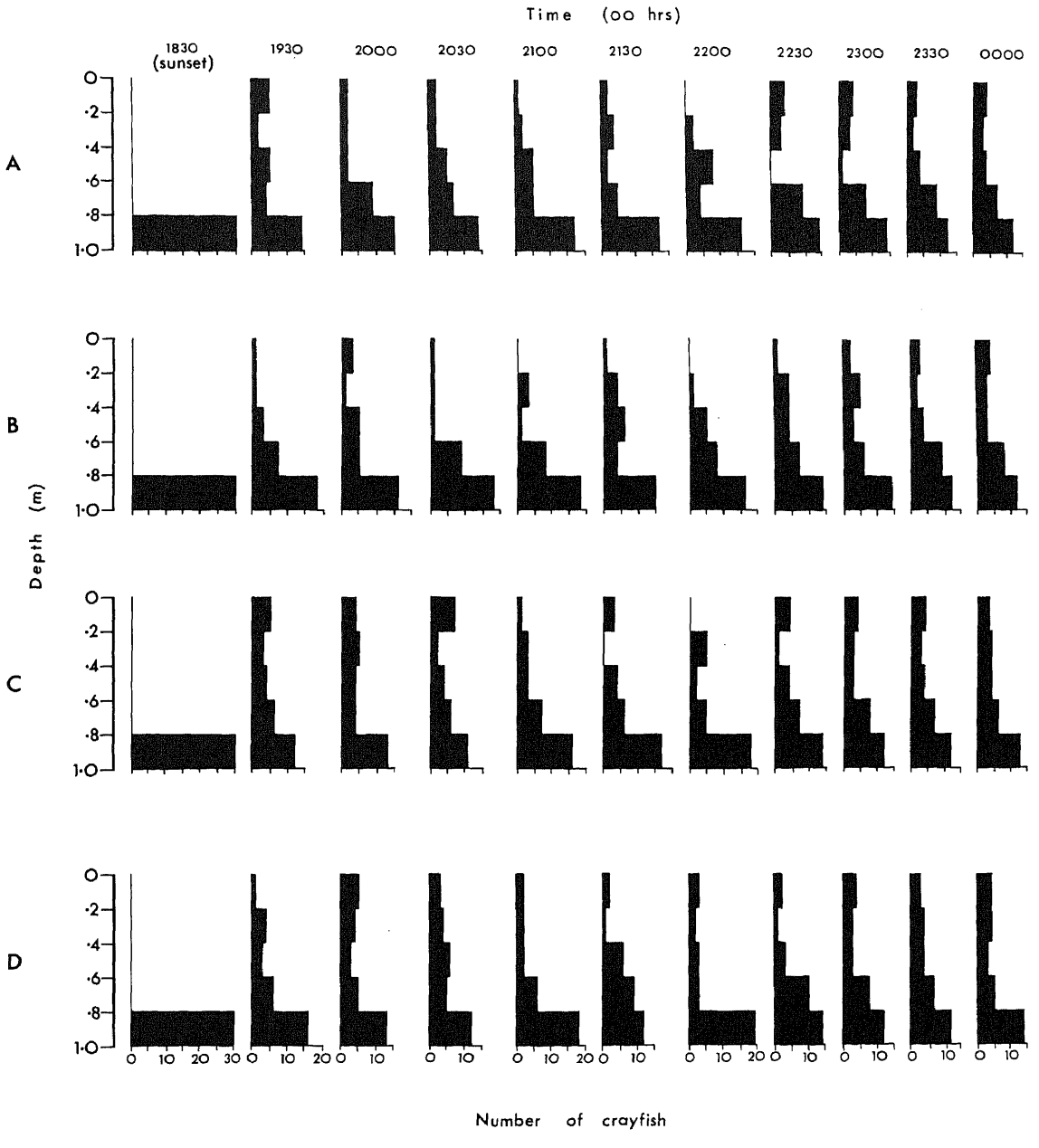


Figure 21
Effects of suppressed photoreception ...
Between pp 96,97

Figure 22. Effects of suppressed photoreception and gravistatocyst reception on the positive geotactic response associated with migratory behaviour at dawn. Distribution patterns from one half hour before natural sunrise until crayfish became quiescent are shown. Daytime data from Figure 15 has been included as the control.

A Control

B Statocysts destroyed

C Blinded

D Blinded and statocysts destroyed

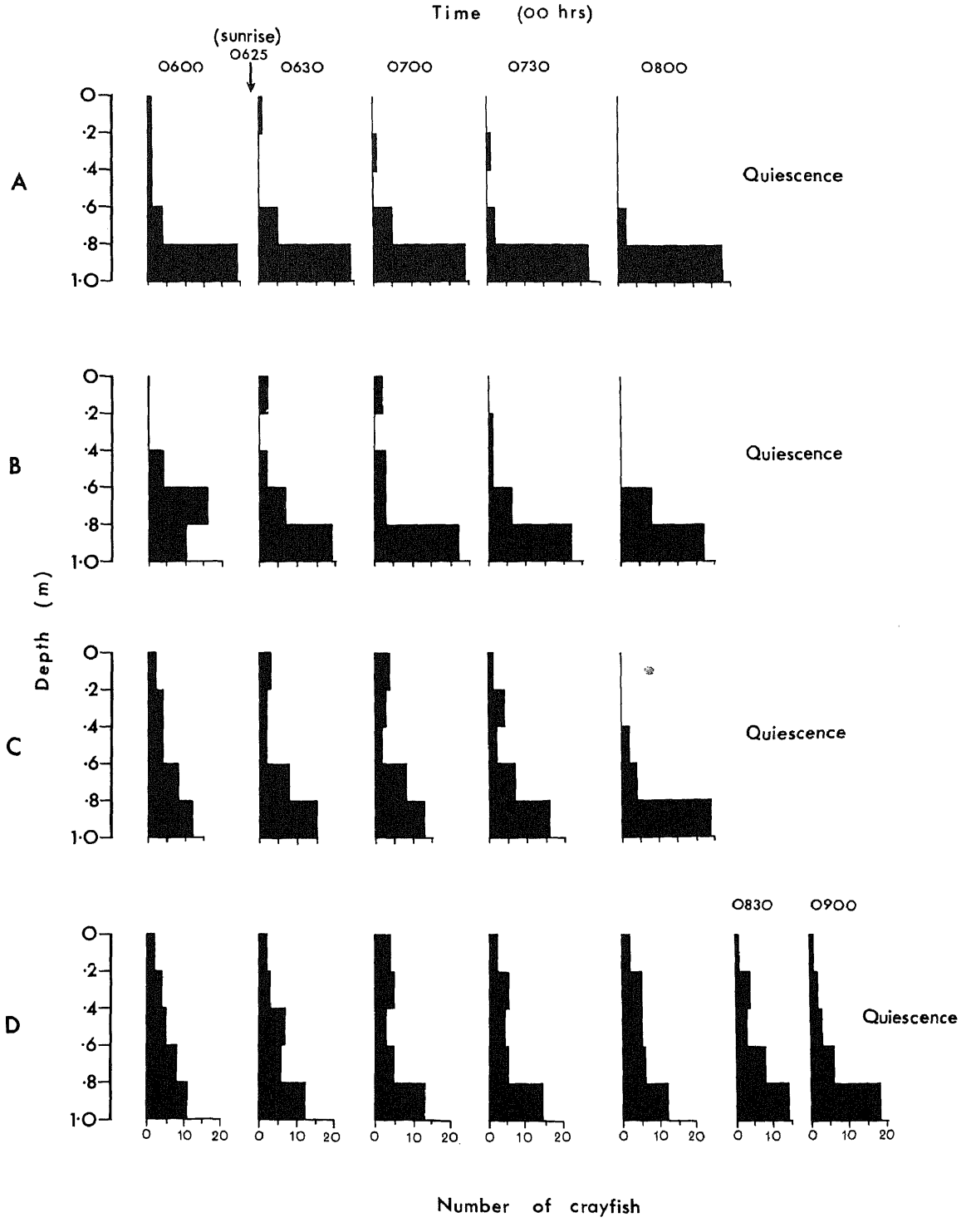


Figure 22
Effects of suppressed photoreception ...
Between 96,97

Table 29: Statistical analyses of data comprising Figure 21. p = ns when D<0.242 at n = 30.

		Time (00 hrs)									
		1930	2000	2030	2100	2130	2200	2230	2300	2330	0000
control vs statocysts destroyed	D =	.233	.167	.200	.133	.100	.133	.100	.067	.000	.033
		←increasing level of insignificance→									
	p =	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
control vs blind	D =	.067	.233	.167	.033	.100	.100	.067	.067	.067	.033
	p =	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
control vs blind with statocysts destroyed	D =	.133	.200	.133	.067	.133	.100	.133	.067	.067	.067
	p =	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

response. Overall, the results imply that upward movement after dusk is mediated via receptor elements other than the eyes and statocysts.

In contrast to night-time results, the daytime pattern of each group (figure 22) differed from the control group (see table 30). There was an apparent delay of about 30 minutes in the positive geotactic response by crayfish without statocysts. The delay was extended a further 90 minutes for blinded crayfish, while geotactic behaviour by crayfish with the combined treatments never attained a significant level. Delay times were assessed as the period until no significant difference between experimental and control distribution patterns occurred (see table 30). Another feature was that crayfish with the combined treatments remained active one hour longer than crayfish in the two other groups.

The inference, therefore, is that both vision and the statocysts are associated with the mechanism(s) regulating the positive geotactic response at dawn. Of these two receptors, photoreception appeared to have the greatest influence.

The positive geotactic response of treated crayfish was re-examined under more controlled conditions, in order to establish better the relative importance of statocysts and vision regarding migratory behaviour at dawn. Experiments were run on a 20° bottom slope of the aquarium during daytime and in a low light environment (16±2 lux). Three groups of 30 crayfish each (15 males and 15 females) were

Table 30: Statistical analyses of data comprising Figure 22. p = ns when D<.242, p = ** when .290>D<.347, p = *** when D>.347 at n = 30.

		Time (00 hrs)					
		0600	0630	0700	0730	0800	0900
control vs statocysts destroyed	D =	.433	.167	.133	.167	.167	
	p =	***	ns	ns	ns	ns	
control vs blind	D =	.367	.433	.367	.367	.133	
	p =	***	***	***	***	ns	
control vs blind with statocysts destroyed	D =	.400	.433	.367	.433	.533	.333
	p =	***	***	***	***	***	**

given identical treatments to those in the previous experiment. Crayfish were retained at the top end of the aquarium (sector 1) for a few minutes then allowed full access. Resultant distribution patterns were assessed every 2 minutes for the first 10 minutes, then less frequently until crayfish became quiescent. The distribution of a control group was assessed similarly. Results are illustrated in Figure 23 and statistical analyses are presented in Table 31.

The distribution patterns of each group followed a similar sequence to that of its comparable group in Figure 22, but some subtle differences did occur. Crayfish with destroyed statocysts did not show the same initial delay in the downward response as before, yet there was a slight delay after 4 minutes (see table 31). Findings, therefore, suggest some involvement of statocysts in the migratory mechanism, although its operation is not dependent on statocyst functioning. In contrast to the crayfish with only one type of sense organ destroyed, those with both vision and statocysts destroyed differed very significantly from the control group throughout the experiment (tables 30 and 31). This indicated that these two receptor types were part of the same mechanism controlling orientation. However, as in the earlier experiment, this group displayed a marked decrease in the level of significance at quiescence, which implies some downward movement had occurred. Therefore other receptors were also involved in postural control.

Figure 23. Effects of suppressed photoreception and gravistatocyst reception on the positive geotactic response during daytime. Distribution patterns of the variously treated groups were assessed until crayfish became quiescent.

A Control

B Statocysts destroyed

C Blinded

D Blinded and statocysts destroyed

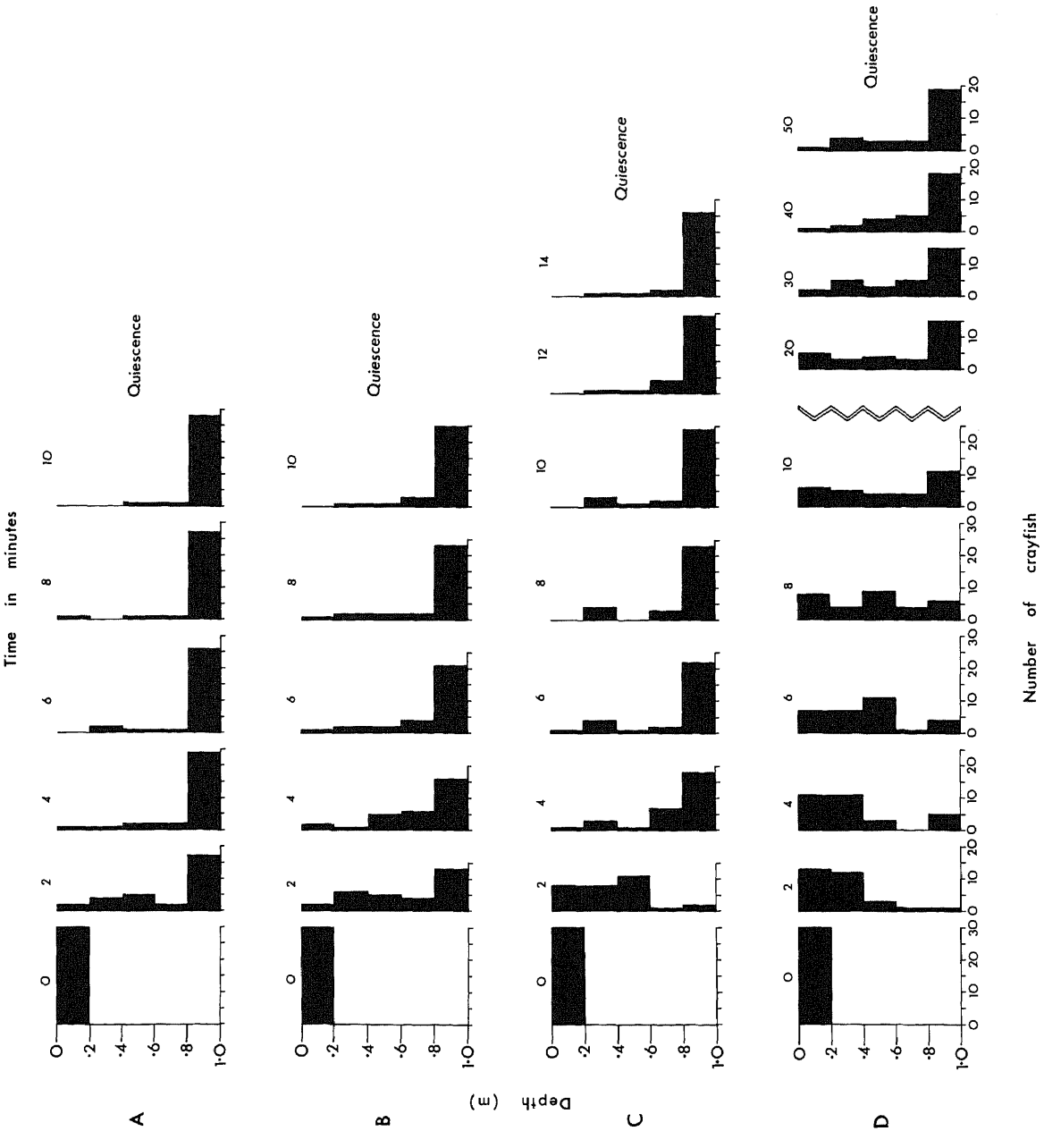


Figure 23
Effects of supressed photoreception ...
Between pp 100,101

Table 31: Statistical analyses of data comprising Figure 23. p = ns when D<.242, p = * when .242>D<.290, p = ** when .290>D<.347, p = *** when D>.347 at n = 30.

		Time (mins.)					
		2	4	6	8	10	Quiescence
control vs statocysts destroyed	D =	.133	.267	.167	.133	.100	.100
	p =	ns	*	ns	ns	ns	ns
control vs blind	D =	.533	.200	.133	.133	.133	.133
	p =	***	ns	ns	ns	ns	ns
control vs blind with statocysts destroyed	D =	.633	.700	.733	.700	.567	.300
	p =	***	***	***	***	***	**

Although the eyes and statocysts seem to be important components of the mechanism affecting the dawn migration, other receptor elements must also be involved. The night-time results indicate that the migration at dusk is influenced even more so by these unnamed receptors, since movement was significantly unaffected after gravistatocyst and visual responses had been suppressed.

Before a fuller interpretation of the above results can be made, it is necessary to consider the complex mechanisms associated with walking and the attainment and maintenance of posture. In decapod crustaceans, postural control operates continuously and is achieved through the sensory integration of photoreceptor (Hisada et al 1969, Hisada 1975), gravity receptor (Marler and Hamilton 1966, Schone 1971, Hisada 1975, Neil 1975a, Stein 1975) and proprioceptor (Clarac et al 1976, Sandeman 1976, Schone et al 1976) systems. Sandeman (1976) states that postural control is dependent on multiple cues rather than a single set of receptors. Less is known of the mechanism associated with walking in decapods. However, it has been established that certain leg proprioceptors are involved (Mill 1976) and the statocysts have also been implicated in limb movements (Schone 1961; 1971).

One aspect of the posture controlling mechanism manifests itself through the eyestalk compensation reaction, whereby displacement of the body about its axis is compensated by a change in eye position. In this way crayfish are able to perceive changes in body position relative to gravity. Eyestalk compensation is modulated by

two main sources of sensory information: the statocysts, functioning as gravity receptors and the eyes. Hisada (1975) found that the visual contribution involved detection of differences in illumination (the field effect) and the movement of objects within the visual field (the optokinetic effect), while stimulation of the statocysts' sensory hair cushion induced a complementary eyestalk compensatory response (Stein 1975). A lesser contribution to eyestalk movement involves leg proprioceptors (Horridge 1965).

Postural control also involves the cuticular stress detectors. These are proprioceptors located in the coxo-basipodite, mero-carpopodite and pro-dactylopodite joints and are thought to modulate the posture of the entire leg (Clarac 1976). Other leg proprioceptors thought to regulate posture and which are also implicated in locomotion, include the mero-carpopodite joint of each leg (Mill 1976) and the chordotonal organ of the thoracic-coxal joint (Bush 1976). These receptors and those associated with eyestalk compensation generally function together in order to achieve the correct posture, although inputs from some receptors may dominate (Sandeman 1976).

My results showed that the amount of geotactic behaviour differed between day and night following the suppression of visual and statocyst responses. At night the negative geotactic response remained significantly unaffected, whereas in the daytime, positive geotaxis was reduced. The reduction was most pronounced in crayfish with both receptor types inoperative. Such a difference in

behaviour indicated a diel change in emphasis of the receptor organs operating within the system of postural control.

Light, rather than gravity, which remains constant, was the environmental factor most likely to initiate such a change. The initial delay in locomotor activity of blinded *P. planifrons* during daylight indicated that light was a significant contributor to the eyestalk compensation reaction. Hence, light was likely to affect the integrity of the eyestalk response and consequently postural control. For this reason, eyestalk compensation was likely to operate best during the day, while at night it probably functioned with a reduced integrity. This implies a greater dependence on the gravity receptors for postural control. Since statocystectomised crayfish could still walk normally at night, it was probably the leg proprioceptors, rather than the statocysts, which functioned as the principal controllers of posture during the hours of darkness.

It was mentioned earlier that vision and statocysts function as integral components of the eyestalk compensation reaction. Therefore, during the day, crayfish with these receptor organs supressed, would have had difficulty in achieving adequate postural control to enable walking, even though their walk receptors were intact. However, because of the switch in emphasis to the leg receptors at night, these crayfish were easily able to achieve postural control and, as a result, walk activity was possible.

In applying these findings to *P. planifrons* in situ, it may be said that the mechanism controlling posture undergoes a reorganisation of its receptors every diel period. The presence or absence of light is postulated as the factor determining the course of this reorganisation. During the dawn migration and during daytime, the emphasis is on the receptors associated with the eyestalk compensation reaction, whereas at night and during the migration at dusk, the leg proprioceptors are emphasised.

With regard to the statocysts it seems that their status within the mechanism controlling posture is not particularly high. This finding was somewhat surprising, since statocysts are generally regarded as important contributors to the control of spatial orientation in decapods (Cohen and Dijkgraaf 1961, Horridge 1965, Neil 1975a; 1975b). In *P. planifrons* the statocysts displayed maximal involvement during the day, while at night their involvement was not detectable. Further work on these seemingly well developed organs is clearly necessary in order to understand better their relationship in the mechanism controlling body orientation. Perhaps their functioning as temperature receptors is important, for Horridge (1965) comments that the statocyst units of *Homarus americanus* have a $Q_{10}>5$, which suggests a heightened sensitivity to temperature change.

B. THE SEASONAL DISTRIBUTION PATTERN

1. Trapping Results

The seasonal distribution pattern at night-time of the adult population within L. Rotoiti was assessed throughout 1975 and 1976. Results are presented in Figure 24. The pattern recorded in 1975 recurred in 1976 which indicated that events are cyclical.

During winter and spring, crayfish were fairly evenly distributed throughout the lake. At the onset of summer, crayfish began to evacuate the deeper waters, as indicated by the lowered relative abundances at 50 m depth in January 1976 and in December of the same year. This mass migration continued until March of both years, when no crayfish below 30 m depth were trapped. This was not an artefact of the sampling method at this time of year, as checks with SCUBA verified the absence of crayfish below 28 m depth. During autumn the crayfish gradually redistributed downwards such that by June 1975 and by May 1976 the whole lake floor was again recolonised.

The patterns shown by adult males and females are separately shown in Figure 24 also. Although the overall trends were similar, some differences between the sexes were distinguishable. Firstly, movement of females from deeper waters began approximately one month earlier than that of males. This was evident from the December 50 m depth results for both years. Secondly, the lower depth limit of females during summer and autumn was slightly higher than for males. Thirdly, during summer and autumn

Figure 24. Seasonal trends in depth distribution of the adult population as a whole and of males and females separately in L. Rotoiti at night. Assessments were made by trapping at the 1, 10, 20, 30 and 50 m contours each month during 1975 and 1976. For each month the numbers caught at each depth interval were calculated as a percentage of the total captured. The 227% correction (p. 40) has been applied to 1 m numbers and is included in the calculation. The total monthly number trapped is given.

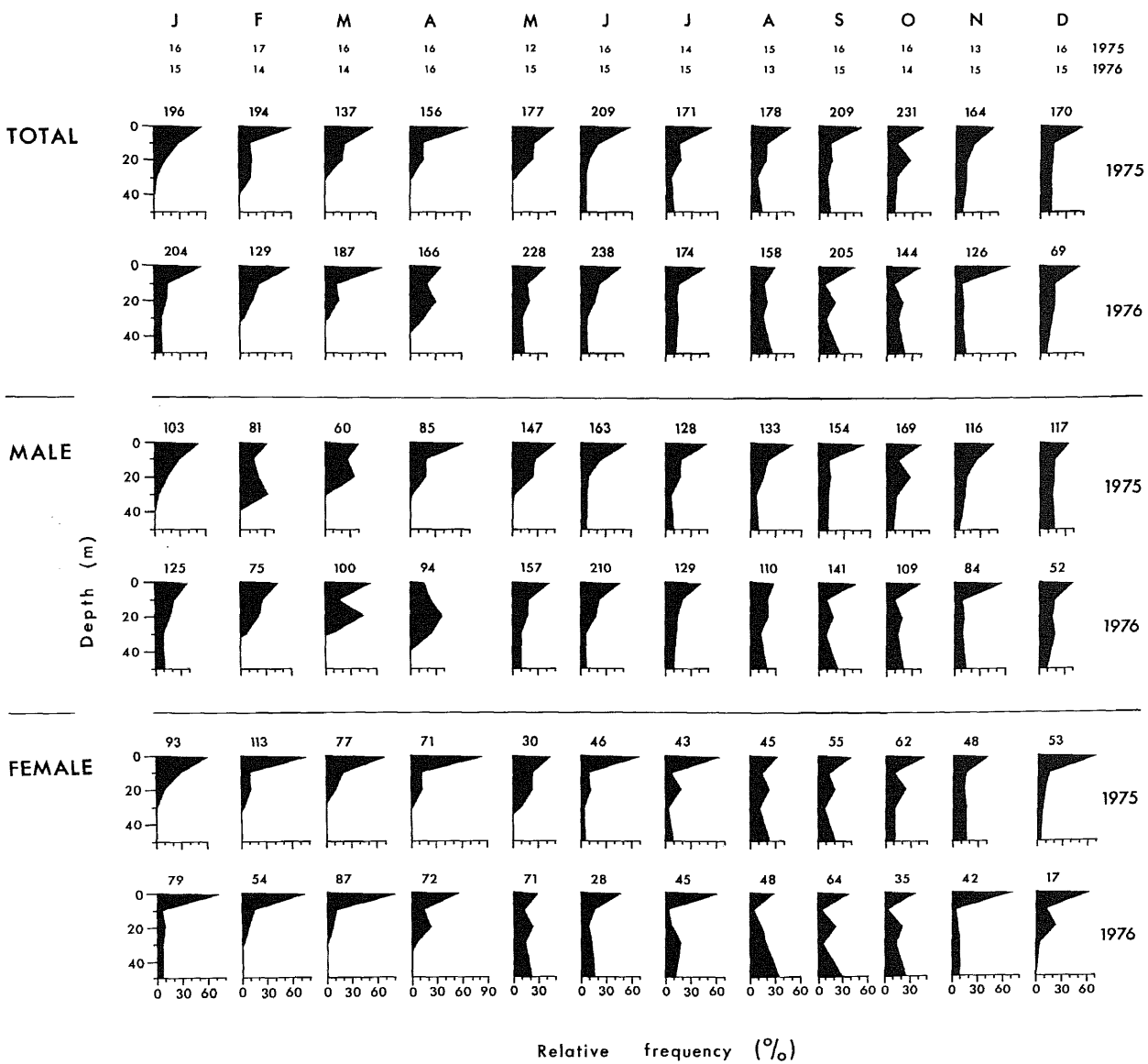


Figure 24
Seasonal trends ...
Between pp 106,107

(December - April) female numbers at 1 m depth ($\bar{N}$ = 91) were significantly greater than corresponding male numbers ($\bar{N}$ = 51) (t = 3.180, p = **, n = 18). The difference may be increased by a factor of 2.07, since trap catch ratio over the two year period favoured males by 2.77:1. Fourthly, during each summer/autumn period, females were preponderant at the 1 m depth, whereas males were more evenly distributed down to the 20 m contour.

2. SCUBA Results

Trapping revealed night-time patterns only, so SCUBA was used to determine seasonal trends during daytime. Dives were made in L. Rotoiti at infrequent intervals during which the mean depth of the boundary zone (upper limit of crayfish out in the open), the approximate mean depth of the high density band, its approximate vertical range and maximum density, were assessed. Results are presented in Table 32 and indicate that there was a seasonal shift in depth of the high density band. In the summer/autumn period the band was about 3.3 m shallower than in winter/early spring. Accordingly, the boundary zone had shifted down some 4.1 m in the colder months. The band was slightly broader throughout the summer and autumn and maximum densities were relatively lower during this period.

It was established earlier that densities were generally maximal around the band's midpoint. Here crayfish tended to concentrate in localised areas ranging in size from 1-10 m^2, rather than distributing uniformly

Table 32: Seasonal variations in characteristics of the high density band off Whangamoa Point, L. Rotoiti.

	Date	Boundary zone depth (m)	Approx. band mean depth (m)	Approx. vertical range (m)	Max. density seen (crayfish m^{-2})
SUMMER/ AUTUMN	15 Jan.1975	13.5	18.2	11.5	25
	16 Feb.1975	12.8	18.9	12.2	20
	27 Mar.1978	14.5	19.2	9.5	22
	17 Apr.1975	12.5	18.7	12.5	28
	16 Apr.1977	10.7	16.3	11.3	28
Mean		12.8	18.3	11.4	24.6
WINTER/ EARLY SPRING	15 Jun.1977	16.2	21.1	9.8	34
	14 Jul.1978	16.8	22.0	10.2	38
	9 Sep.1977	17.7	21.8	8.3	50
Mean		16.9	21.6	9.4	40.7

across the apparently uniform bottom, as might have been expected. This feature appeared most pronounced during the colder months, which may explain the greater maximum densities encountered over that period. There were no obvious seasonal differences in the overall band density, although total numbers were greater in summer, since the band's area had increased some 17.5%.

In winter inadequate light restricted diving to 30 m depth. However, as the density here was far lower (ca 0.2 crayfish m^{-2}) from that a few metres shallower (ie. in the lower quartile of the high density band), it was assumed densities below the band remained fairly low.

Observed maximum densities within the high density band of each lake varied widely and are given as follows: Rotoiti (50 crayfish m^{-2}), Taupo (21 crayfish m^{-2}), Tarawera (19 crayfish m^{-2}), Okataina (18 crayfish m^{-2}), Rotoma (5 crayfish m^{-2}) and Tikitapu (3 crayfish m^{-2}). These figures also give a broad indication of the differences between these lakes.

From casual observation in L. Rotoiti, it appeared that more adults occurred above the boundary zone in summer than in winter. This was verified quantitatively by counting the number of adults within specific permanent shelters in Te Puhoe Bay during February and July 1977. The results are given in Table 33 and indicate 4.25 times more crayfish above 13 m depth in February than in July. A similar trend was found in the previous study (Devcich 1974), whereby of 200 beer cans distributed evenly between the 1 and 15 m contours, the number of

Table 33: Number of adults occupying the same shelter areas from 1-13 m depths in summer and winter.

Location	Depth (m)	Number observed Summer 14 Feb. 1977	Winter 16 July 1977
iron sheet	9.0	3	1
tyre	4.4	1	0
log	7.5	4	1
wood debris	12.0	6	4
rock pile	1.0	6	2
rock pile	3.2	6	0
70 beer cans	5.0-13.0	42	8
	Total	68	16

cans occupied by crayfish increased from 2 in July 1973 to 75 in January 1974.

The daytime distribution patterns for summer and winter are summarised in Figure 25. The main features include a difference in abundance above the boundary zone, a difference in the vertical displacement of the high density band and the presence of crayfish below 30 m depth in winter but not in summer.

The ratio of adult males:females collected by hand in L. Rotoiti was 1.34:1. This ratio was determined from a total of 2671 adults taken at random on 19 occasions above 30 m depth throughout the study. On 2 February 1979, 100 adults were collected at random from above 6 m depth and produced a ratio of 3:1 in favour of males. This tentatively indicated that relatively more males occupied shallow depths by day during the warmer months at least. By contrast, females were in greatest abundance within these depths at night, which suggested that mainly females migrated between the littoral and high density zones during the warmer months, whereas males comprising the high density band showed less tendency to migrate.

In 1975 the number of females trapped at 1 m depth was 69.6% higher from January - April ($\bar{N}$ = 45) than from July - October ($\bar{N}$ = 14) ($t = 4.288$, $p = **$, $n = 8$). Similarly, an increase of 70.8% was recorded in 1976 (January - April, $\bar{N}$ = 39; July - October, $\bar{N}$ = 11) ($t = 3.756$, $p = **$, $n = 8$). However, for males this tendency was reversed, with a 44.6% increase in the numbers trapped during July - October ($\bar{N}$ = 42) over the January -

Figure 25. A stylised depth distribution of the adult population in daytime during summer and winter in L. Rotoiti, based on observations while diving and the results in Tables 32 and 33.

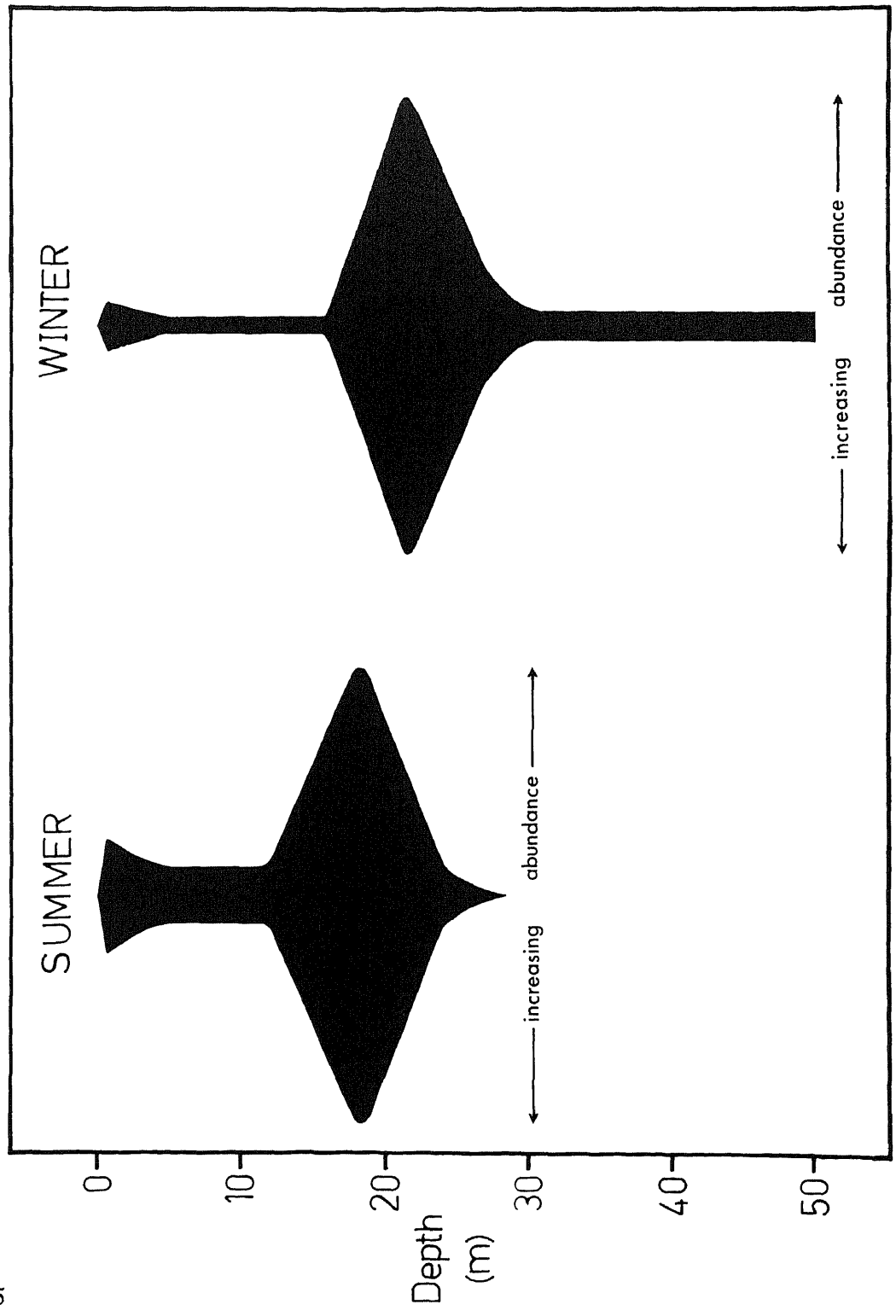


Figure 25
A stylised depth distribution ...
Between pp 111,112

April ($\bar{N}$ = 15) period in 1975 (t = 2.793, p = *, n = 8) and with a 20.4% increase in 1976 (July - October, $\bar{N}$ = 27; January - April, $\bar{N}$ = 22) (t = 0.777, p = ns, n = 8). The above findings suggested that from around midsummer - midautumn, predominantly females migrated in accordance with the model of diel spatial distribution (figure 11, following p. 54), whereas from around midwinter - midspring mainly males fitted the model (as determined from trapping results).

Dives made during all seasons revealed that the juvenile population remained in the littoral zone throughout the year and did not undergo the seasonal movements displayed by mature crayfish.

FACTORS AFFECTING THE SEASONAL PATTERN

1. Oxygen

Oxygen profiles of L. Rotoiti were recorded at monthly intervals throughout 1975 and 1976 and are shown in Figure 26. Surface waters stayed more or less fully saturated, whereas waters below about 20 m depth underwent marked seasonal fluctuations in oxygen concentration. Throughout the warmer months the pattern of oxygen distribution was clinograde. Oxygen concentrations were uniformly high throughout the lake during winter and early spring. Bottom waters began to deoxygenate at 50 m depth around October and by February/March of 1975 and March of 1976 only 0.5 g m^{-3} O_2 was recorded below about 30 m depth. In March of 1976 a strong oxycline had established and lay near the 20 m contour. As autumn progressed the oxycline slowly sank and was followed by reoxygenated waters as it sank. Between May and June the oxycline had totally dispersed, after which winter conditions prevailed.

Table 34 indicates weak relationships existed between ambient oxygen and crayfish abundance down to 20 m depth, suggesting that oxygen was never a limiting factor above this depth. This was substantiated by direct observation which verified the all year presence of crayfish at these depths. At both 30 and 50 m depths strong correlations occurred, so oxygen levels could have affected seasonal abundances within the deeper regions of L. Rotoiti.

Details of the relationship between crayfish numbers

Figure 26. Oxygen profiles from L. Rotoiti, recorded at monthly intervals from January 1975 to January 1977. Readings were taken at 1 m depth intervals and within the main area of research. Surface and 50 m depth values are shown for each date.

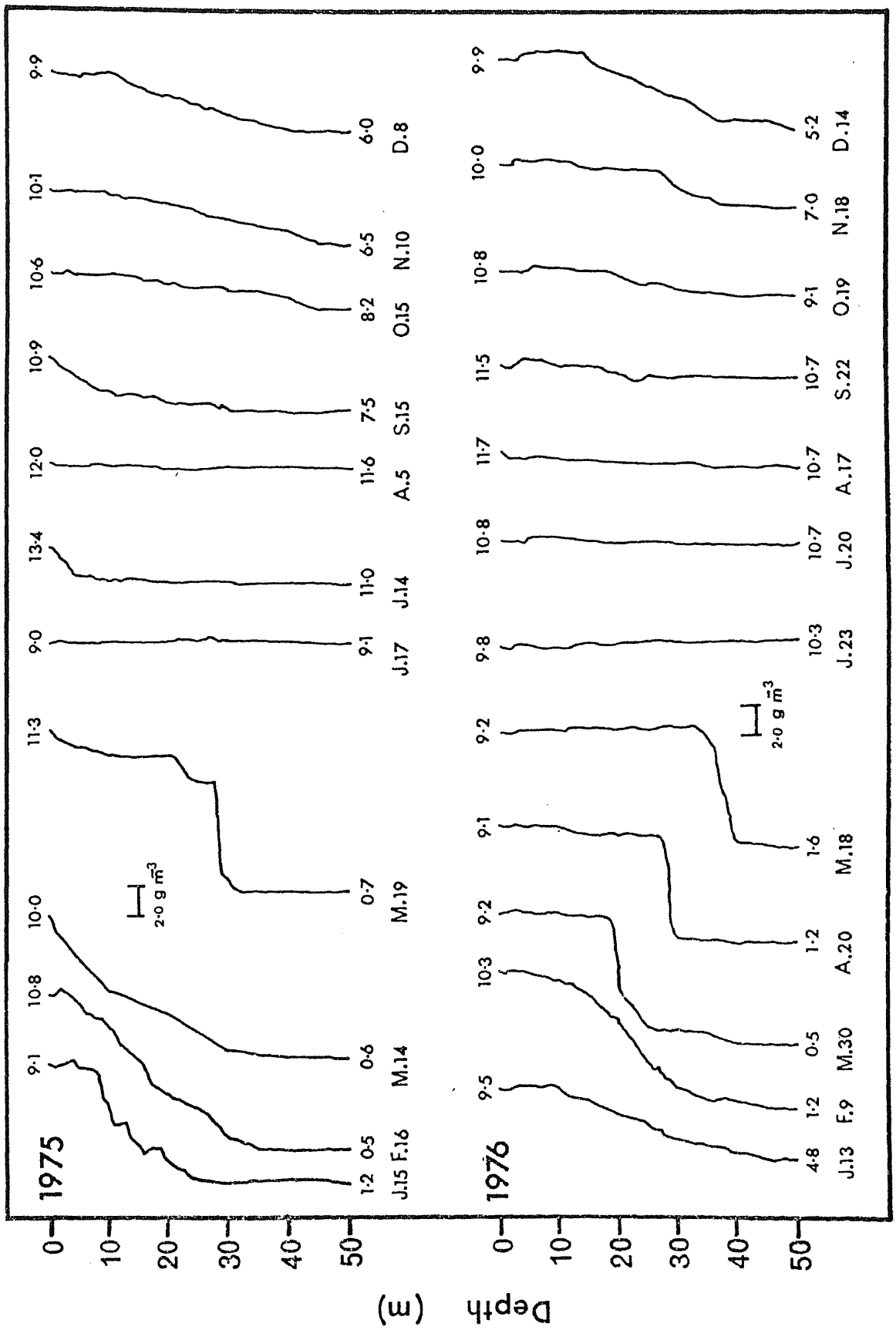


Figure 26
Oxygen profiles from
L.Rotoiti ...
Between pp 113,114

Table 34: The correlation coefficients of the relationship between the number of crayfish trapped each month at specific depths and corresponding ambient oxygen concentrations from January 1975 to December 1976.

Depth (m)	r
1	-0.44
10	-0.51
20	0.08
30	0.81
50	0.84

and ambient oxygen concentrations at 50 m depth are presented in Figure 27. The results show that crayfish were present when oxygen concentrations were above 1.6 g m^{-3} but there was an appreciable decline in crayfish numbers when oxygen fell below about 5.0 g m^{-3}. Crayfish were absent below 1.2 g m^{-3} O_2 but reappeared in late autumn once oxygen levels exceeded this amount.

Table 35 gives the maximum depths attained by males and females and their corresponding ambient oxygen tensions for 8 months in 1975 and 1976. In each instance female lower depth limits were not as deep as those of males and accordingly, the corresponding oxygen tensions for females were slightly above those for males. The mean depth limit for males was found to be 3.3 m deeper than the females' one, and corresponded to a 0.2 g m^{-3} O_2 difference. These results suggested that 1.1 g m^{-3} O_2 for males and 1.3 g m^{-3} O_2 for females were the respective critical values of tolerance. Below these levels feeding probably became suppressed and or survival was jeopardised.

Whittle (1973) found that adult *P. planifrons* could survive ambient oxygen levels down to 1.0 g m^{-3} and when subjected to decreasing oxygen tensions from 9.0-1.0 g m^{-3}, crayfish display increased oxygen consumption and activity within the 6.0-4.5 g m^{-3} O_2 range. These values were calculated from curves established at 10°C and 15°C, and refer to 12°C, which was the mean temperature at 50 m depth in L. Rotoiti in early summer. He suggested that the increase in activity may be associated with migratory

Figure 27. The relationship between ambient oxygen (line) and crayfish abundance (histograms) at 50 m depth during 1975 and 1976.

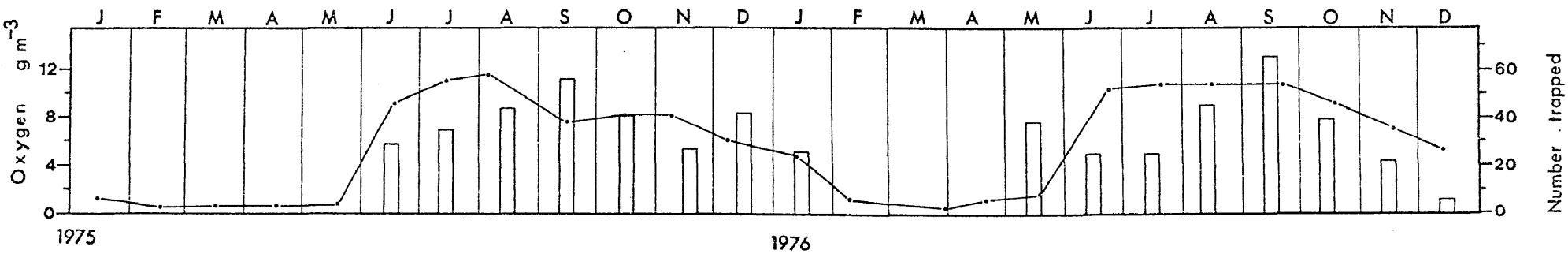


Figure 27
The relationship between
ambient oxygen ...
Between pp 115,116

Table 35: Projected lower depth limits of adults and associated oxygen concentrations (Data from figure 24)

Date	Lower depth limit of distribution (m) Male	Female	Associated ambient oxygen conc. ($g\ m^{-3}$) Male	Female
16 Jan. '75	41	38	1.5	1.5
17 Feb. '75	40	33	0.5	0.9
16 Mar. '75	31	28	1.1	1.6
16 Apr. '75	34	31	0.6	0.8
12 May '75	36	34	0.7	0.8
14 Feb. '76	35	33	1.8	2.1
14 Mar. '76	34	31	1.2	1.4
16 Apr. '76	39	36	1.2	1.4
Mean			1.1	1.3

$t = 1.047$, p = ns, $n = 16$

behaviour. This seems reasonable since the continuous reduction in crayfish numbers at 50 m depth from early to midsummer coincides well with the 6.0-4.5 g m^{-3} O_2 range. Unfortunately, Whittle did not distinguish between males and females in his experiments, however, since upward movement by females began earlier than it did for males, the migratory cue for females would appear to lie nearer 6.0 g m^{-3} O_2, whereas for males it may be nearer 4.5 g m^{-3} O_2.

Interestingly, crayfish apparently entered more oxygen depleted waters when foraging at night, for at the peak of the 1975 summer, baited traps at 30 m depth captured a few crayfish, while daytime diving indicated a maximum depth distribution to only 28 m depth. Also, in March 1978, no crayfish were observed below 25 m depth, yet crayfish imprints on the mud bottom extended to 27 m depth.

Seasonal fluctuations in lake oxygen content are considered to have influenced crayfish distribution patterns throughout the lake generally. In winter crayfish were distributed throughout the entire lake but in summer and autumn 62% of its bottom became unavailable due to deoxygenation. Consequently, most of the deep water crayfish probably entered the high density band, which may explain the increase in band breadth, while the remainder were accommodated in shelters above the boundary zone. The crayfish population in L. Rotoiti is large [Devcich (1974) calculated a conservative estimate for the adult population of approximately 1 million], so the

4.25 fold summertime increase in numbers above the boundary zone, indicated in Table 33 (p.110) would seem a fair approximation. The winter reduction in numbers above the boundary zone and the reduction in size of the high density band, were possibly the result of a 'dilution effect' due to crayfish recolonising the deeper waters which reoxygenate in late autumn. Factors other than oxygen could also have contributed to these trends in distribution and are considered later.

Oxygen may have also controlled the position of the high density band in midsummer to some extent. On 30 March 1976, lake deoxygenation was maximal and the migratory cue (4.5-6.0 g m^{-3} O_2 range) proposed above had ascended to 20 m depth. Consequently, the lower depth limit of the high density band would have been forced up to the 20 m contour and as a result, the whole band would have become displaced shorewards.

In contrast to L. Rotoiti, the summer hypolimnetic waters of the oligotrophic Lakes Okataina, Rotoma, Tarawera, Taupo and Tikitapu were all inhabited by crayfish. Fish (1969) reported mean minimum oxygen concentrations of 6.9 g m^{-3} in April 1966 for L. Okataina and 5.5 g m^{-3} in April for L. Tarawera, which are values well within the levels of tolerance for *P. planifrons*. Presumably intolerable oxygen tensions are also never attained in the hypolimnia of the other lakes, although McColl (1972) reported a brief period of total deoxygenation in the 2 m thin hypolimnion left in L. Tikitapu, just prior to the overturn.

The distribution pattern of crayfish in the crater arm (Awaatua Basin) of mesotrophic L. Rerewhakaaitu was unique in that no high density band existed and all crayfish occupied shelters in shallow water. The Awaatua Basin has a very low population density (<0.001 adults m^{-2}) compared to the other lakes [eg. L. Okataina 0.014 adults m^{-2} and L. Rotoiti 0.049 adults m^{-2} (Devcich 1974)], and it would appear that there are sufficient littoral zone shelters to fully accomodate the crayfish population. Thus, there is no high density band formation. An alternative, although less likely explanation, is that the deoxygenated zone may spread above the depth where light is no longer inhibitory to *P. planifrons*. Jolly et al (in prep.) found that although the water column becomes hypothermal in winter, the hypolimnetic zone does not become fully re-saturated with oxygen, probably due to the surrounding steep sided cliffs obstructing wind action.

2. Light

From photometer readings the vertical extinction coefficient (n") (Hutchinson 1957) in L. Rotoiti was calculated monthly, from January 1975 to January 1977 by the formula:

$$n'' = \frac{In.Ia - In.Ib}{z_b - z_a}$$

where Ia and Ib were light intensities at depths z_a and z_b respectively. Using n", the percentile transmission of light per metre was calculated as:

$$Pt/m = 100e^{-n''}$$

thus giving a record of seasonal trends in light penetration, as shown in Figure 28. Results indicated that the transmission of light was greatest during summer and least in winter.

It was established earlier that the boundary zone depth and its associated high density band are controlled by light intensity, therefore band vertical displacement could be expected to fluctuate more or less in accordance with the pattern indicated in Figure 28. However, this did not occur and in fact almost the reverse situation existed, whereby the band lay deepest when light penetration was least.

An explanation of this apparent anomaly may involve a seasonal shift in spectral sensitivity towards longer wavelengths in spring or early summer. Nosaki (1969) recorded a shift in wavelength maximum sensitivity of the predominant retinular cell type in *Procambarus clarkii*, from 560 nm in winter to >600 nm in summer, this being a total shift of 40-60 nm. This was thought to be caused by a seasonal change in the filtering action of screening pigment on incidental light. Whether a seasonal shift in wavelength sensitivity occurs in *Paranephrops planifrons* is unknown, but it could explain, at least partly, why boundary zone light intensities were higher in summer and autumn than in winter and early spring ($t = 4.142$, $p = **$, $n = 7$). Deoxygenation of the hypolimnion may also be a contributing factor and has already been considered on page 118.

Figure 28. Seasonal trends in percentile transmission (Pt/m) of light in L. Rotoiti. January – April 1975 readings appear excessively high because the photocell used was sensitive to a broader spectral range than the one used later. (See figure 4 for spectral response curves for the two meters.)

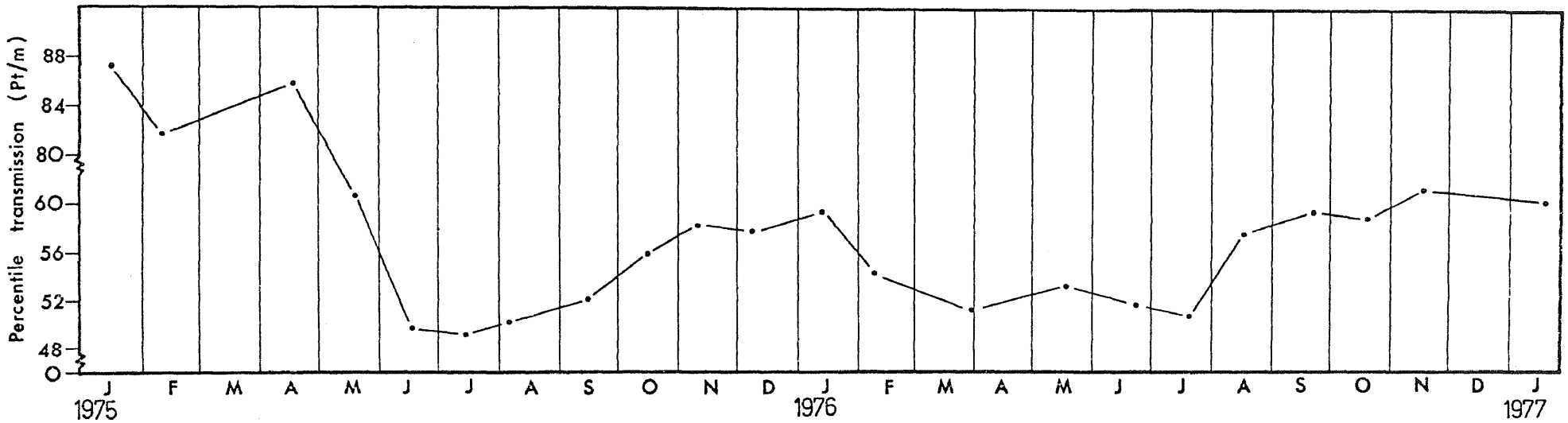


Figure 28
Seasonal trends ...
Between pp 120,121

3. Food

Trends in food abundance at 1, 10, 20, 30 and 50 m depths, and for the lake as a whole, throughout 1975 are shown in Figure 29. The general pattern was determined by averaging the summed calorific values of surface sediment from the 5 specified depths each month. This indicated that food levels in L. Rotoiti remained fairly consistent throughout the year but were somewhat higher in autumn and spring. These peaks coincided with periods of increased primary productivity generally (Burnet and Wallace 1973).

Food levels at 1 m depth remained consistently high throughout the year and as this depth formed part of the main feeding ground of *P. planifrons* (established earlier), it would appear that food never becomes a limiting factor to the population as a whole. However, in isolated deeper regions, food may have occasionally become limiting, as quite low levels were sometimes recorded (eg. at 30 m depth in February). To test the likelihood of food acting as a limiting factor, the relationship between number of crayfish trapped and food abundance at each of the 5 depths in 1975, was calculated (table 36). Very low insignificant values of r were recorded for 1, 20, 30 and 50 m, which suggested that the food supply at these depths probably exceeded the demand. A moderate correlation coefficient ($r = 0.58$) was recorded for 10 m, so food reserves here could have occasionally limited the number of crayfish present.

Although seasonal fluctuations in food abundance

Figure 29. Food abundance at various depths in L. Rotoiti during 1975. A mean value is also shown.

Figure 29
Food abundance ...
Between pp 121,122

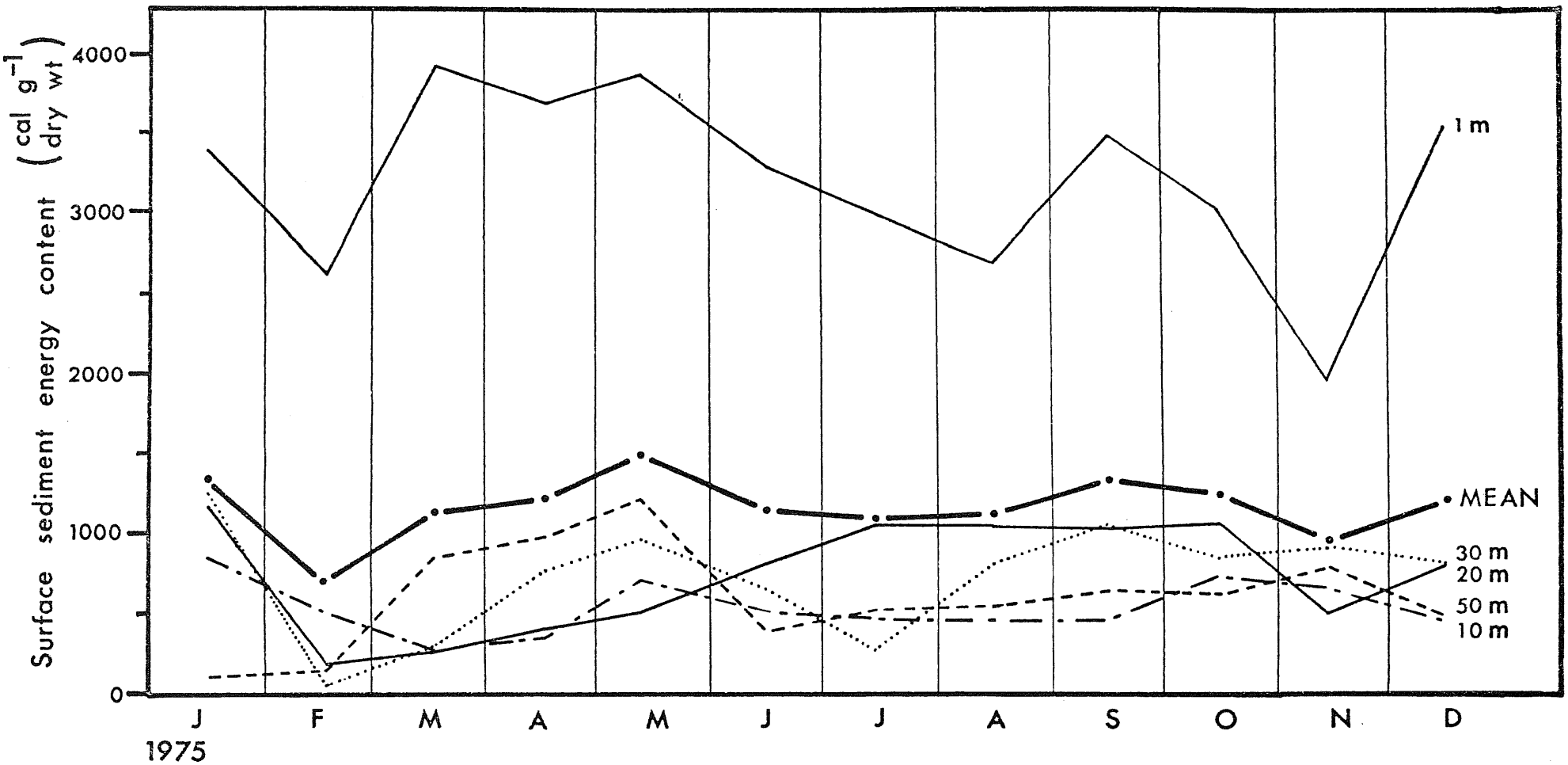


Table 36: Relationship between food abundance (as cals g^{-1} dry wt sed) and crayfish numbers at specific depths in L. Rotoiti during 1975.

Date 1975	Depth (m) 1 F	1 C	10 F	10 C	20 F	20 C	30 F	30 C	50 F	50 C
16 Jan.	3394	155	842	82	1161	36	1273	9	103 †	0
17 Feb.	2625	178	519	35	198	42	58	38	165 †	0
17 Mar.	3926	115	286	45	275	40	295 †	1	822 †	0
16 Apr.	3629	169	349	38	407	39	752 †	4	970 †	0
12 May	3871	119	692	62	511	55	945 †	7	1221 †	0
15 June	3328	176	523	64	815	29	656	19	387	19
14 July	3131	126	474	35	1057	42	288	15	532	23
15 Aug.	2712	110	469	43	1046	40	816	17	562	29
15 Sept.	3506	142	462	36	1032	44	1057	29	648	37
15 Oct.	3036	124	722	36	1076	80	828	33	624	27
13 Nov.	1948	95	672	47	495	28	908	29	784	18
15 Dec.	3572	108	453	35	794	33	812	26	480	28
r =	0.24		0.58		0.23		-0.37		0.13	
p =	ns		*		ns		ns		ns	

F = Food

C = Crayfish

† = Not included in calculation due to deoxygenation affecting catch rates.

below the littoral zone probably had little influence on the crayfish population overall, the fluctuations nevertheless illustrated something of the effects of crayfish grazing areas comparatively low in food content. For instance, anoxic conditions at 50 m depth from January - May meant that food levels could rise almost totally unchecked (as indicated in figure 31) but after reoxygenation in late May, subsequent grazing by recolonising crayfish may have been a major cause for the marked decrease in food reserves recorded in June.

Similarly, the increase in crayfish numbers within the high density band over summer and autumn may have kept food at 20 m depth to low levels.

4. Temperature

According to Barber (1961), crayfish are generally insensitive to small changes in temperature and therefore like many invertebrates (Fraenkel and Gunn 1961), they tend not to select a particular temperature but rather to avoid temperature extremes.

Temperature profiles of L. Rotoiti to 50 m depth were recorded at monthly intervals throughout 1975 and 1976 and are shown in Figure 30. The overall temperature range was 9.9-24.0°C. Surface waters varied between 10.3°C and 24.0°C, while at 50 m depth the range was 9.9-13.5°C. From June - September the lake was homothermal with temperatures reaching their lowest values in August (9.9°C on 5 August 1975). Surface water temperatures rose from October to January/February

Figure 30. Distribution of temperature with depth in L. Rotoiti, recorded at monthly intervals from January 1975 to December 1976. Values are in °C and readings were taken at 1 m depth intervals. Surface and 50 m depth temperatures are given.

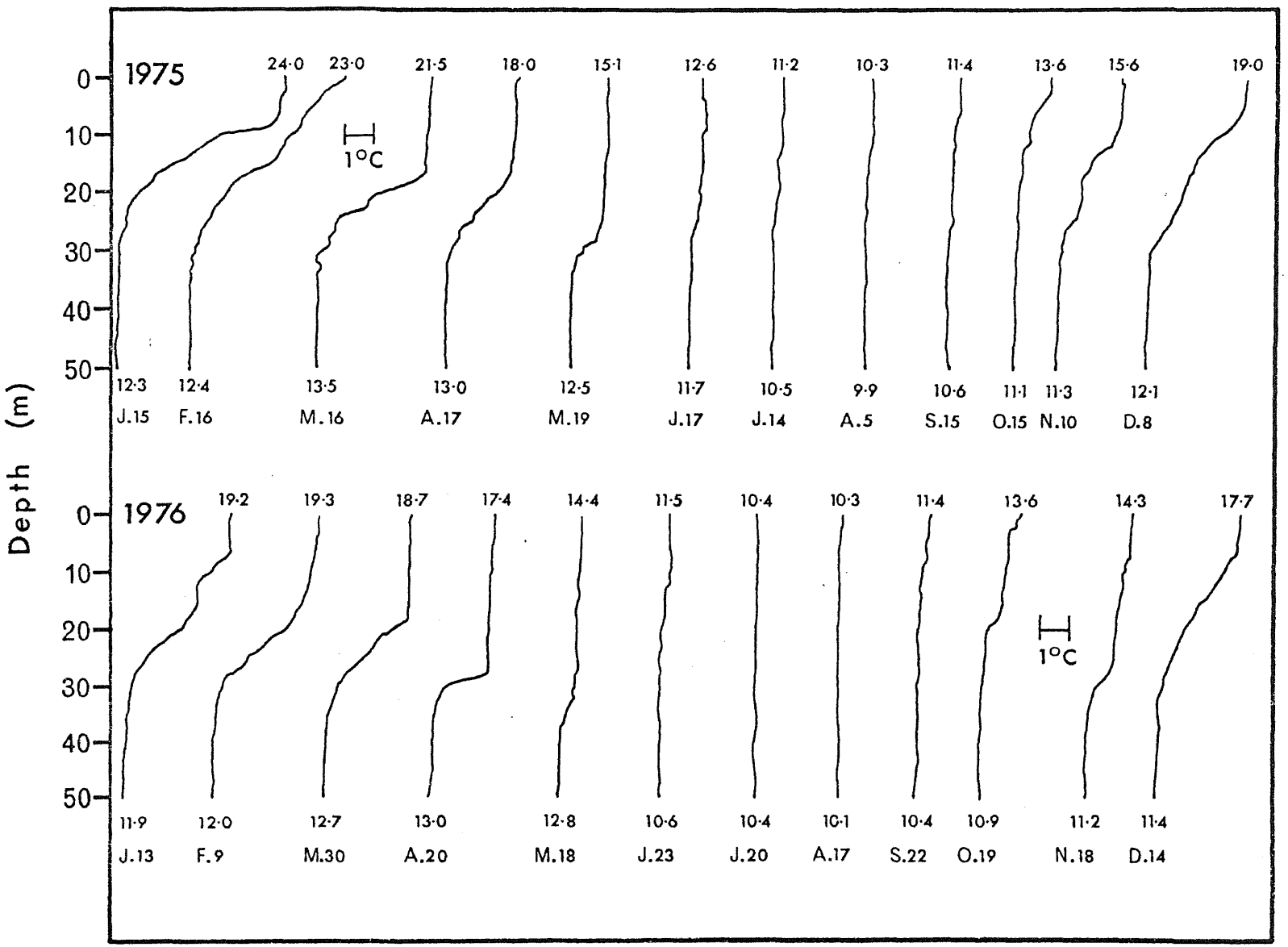


Figure 30
Distribution of temperature ...
Between pp 123,124

during which time the lake stratified. A moderately developed thermocline occurred between the 8 m and 20 m contours in midsummer and increased in depth as the epilimnion cooled. The thermocline lay near the 30 m contour by May, shortly after which the lake became homothermal.

The temperature range within which *P. planifrons* survives, was determined. 20 adult crayfish were acclimatised to 15°C for 3 weeks, then the water temperature was gradually lowered over a 7 day period to 5°C. All 20 crayfish survived. After 1 week at 25°C , these crayfish were subjected to increasing temperatures with a daily increment rate of ca 1.0°C, until death resulted. The results are shown in Figure 31 and indicate that the thermal death point was ca 35°C.

Thus *P. planifrons* can survive temperatures from 5-ca 34°C, which is similar to the 1-35°C survival range reported by Frost (1975) for *Cherax destructor*. Whittle (1973) found that maximal Q_{10} values occurred for *P. planifrons* from 10-21°C and declined markedly outside this range. This latter temperature range was similar to the thermal regimes of the lakes in this study (table 37), which indicated that crayfish were well adapted to the full range of temperatures encountered. Furthermore, as lake temperatures were well within this species limits of tolerance, temperature was unlikely to have ever markedly limited its depth distribution.

Apart from the apparent involvement of light and oxygen as determinants of the position of the high density

Figure 31. Determination of the thermal death point of *P. planifrons*. For details see text page 124.

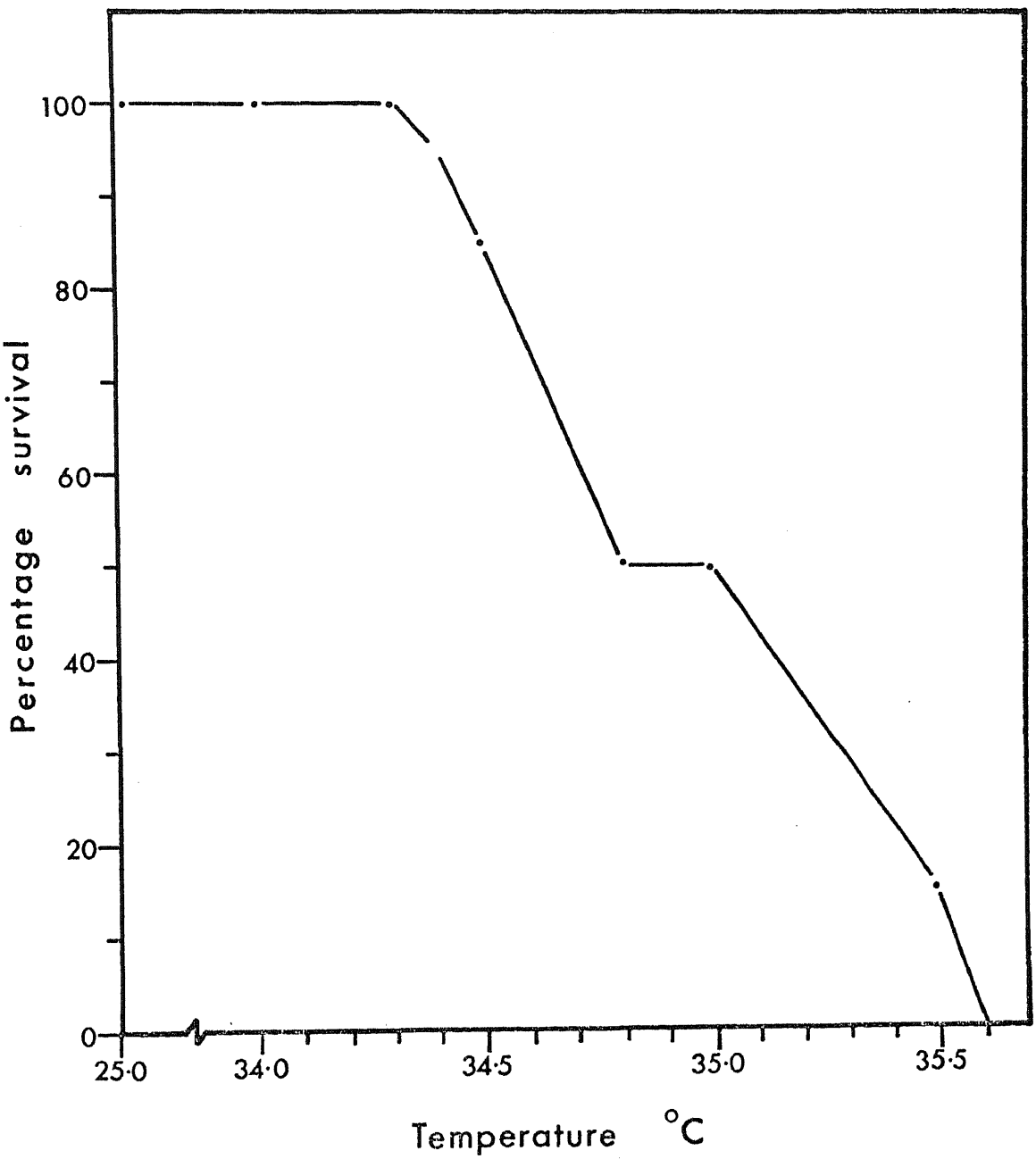


Figure 31
Determination of the thermal death point ...
Between pp 124,125

Table 37: Maximum and minimum temperatures recorded for the 7 lakes studied.

Lake	Maximum temp. (C)	Minimum temp. (C)	Year	Reference
Rotoiti	24.0	9.9	1975-76	present study
Okataina	20.6	11.0	1955	Jolly 1968
"	22.0	10.6	1970-71	McColl 1972
Rotoma	21.5	10.5	1955-56	Jolly 1968
"	24.0	10.4	1970-71	McColl 1972
Tarawera	22.8	10.6	1955, 1957	Jolly 1968
Tikitapu	20.5	9.5	1955-56	"
"	22.1	9.6	1971-72	McColl 1972
Taupo	19.1	10.6	1955-56	Jolly 1968
Rerewhakaaitu	18.2	8.5	1955-56	"

band, temperature could have conceivably contributed to its seasonal changes in depth. To check this, temperatures at 18.3 m depth and at 21.6 m depth (mean depths of the high density band in summer and winter respectively) were compared for the 5 warmest months in 1975 and 1976 (table 38). No significant difference was found, which suggests that temperature is unlikely to influence high density band position.

Crawshaw (1974) found that *Orconectes immunis* occurred within a wide range of temperatures over a diel period but selected significantly cooler water for its daytime inactivity period. A similar situation may exist for *P. planifrons* throughout summer and autumn because temperatures at the high density band were found to be significantly cooler than at the weed bed night-time feeding ground (table 39). It therefore seems possible that temperature could influence the diel distribution pattern throughout the warmer months. However, temperature would have no effect on the diel pattern during winter and early spring when homothermal conditions prevail.

Momot (1967a) and Fast and Momot (1973) found that adult *Orconectes virilis* moved into shallow water in early summer and suggested that this was in response to a preference for warmer water. In this study the number of *P. planifrons* females trapped within the littoral zone was low in winter and spring but increased markedly in early summer and remained high until midautumn. By contrast, there was no corresponding increase in the number of males trapped at the littoral zone during the warmer months.

Table 38: Comparison of temperatures at 18.3 m depth and 21.6 m depth during the 5 warmest months of 1975 and 1976. The depths correspond to mean depths of the high density band in summer and winter, respectively.

Date	Temperature (°C) at 18.3 m depth	at 21.6 m depth
15 Jan. '75	14.6	13.4
16 Feb. '75	15.3	14.8
16 Mar. '75	19.9	17.2
17 Apr. '75	17.0	15.9
8 Dec. '76	14.7	14.4
13 Jan. '76	16.2	14.8
9 Feb. '76	17.4	16.0
30 Mar. '76	18.3	16.6
20 Apr. '76	17.1	17.0
14 Dec. '76	14.4	13.6
Mean	16.5	15.4
SD	1.8	1.4
	t = 1.570, p = ns, n = 20	

Table 39: Temperatures at the high density band and weed bed feeding ground during summer and autumn.

Date	Temperature (°C) High density band. (mean depth 18.3m)	Littoral feeding zone. (mean depth 3m)
15 Jan. '75	14.6	23.8
16 Feb. '75	15.3	21.5
16 Mar. '75	19.9	21.4
17 Apr. '75	17.0	17.7
8 Dec. '75	14.7	18.9
13 Jan. '76	16.2	19.2
9 Feb. '76	17.4	19.3
30 Mar. '76	18.3	18.6
20 Apr. '76	17.1	17.3
14 Dec. '76	14.4	17.7
Mean temp.	16.5	19.5
SD	1.8	2.1
	$t = 3.516$, $p = **$, $n = 20$	

These findings may suggest that females have a greater preference for warmer waters than males.

Night-time temperature preferences were assessed in an aquarium with a sloping bottom (plate 12, following p. 77) and with a vertical temperature gradient. A refrigeration unit positioned at the deep end produced a temperature gradient along the bottom of 10-20°C, such that there were 5 groups comprising temperature ranges of 2°C each and covering approximately equal areas.

Group:	1	2	3	4	5
Temp range (°C)	10-11.9	12-13.9	14-15.9	16-17.9	18-20
Corresponding depth range (m)	1.0-0.8	0.8-0.6	0.6-0.4	0.4-0.2	0.2-0.

A bare substrate of sand and small pebbles was provided but no food or cover. A dim red light was used to observe the crayfish.

25 adult males were placed in the aquarium after dusk and the number within each temperature range was recorded 1 hour later and subsequently every half hour thereafter for a total of 10 trials. 25 adult females were treated similarly. Controls were obtained by repeating these experiments at night in homothermal conditions at 18°C. Results are shown in Figure 32. The Kolmogorov-Smirnov goodness of fit test was applied to each experimental run and its corresponding control run.

On every occasion there was a significant difference between the distribution of females comprising the

Figure 32. Temperature selectivity by adult *P. planifrons* within a 10-20°C thermal gradient, at night.

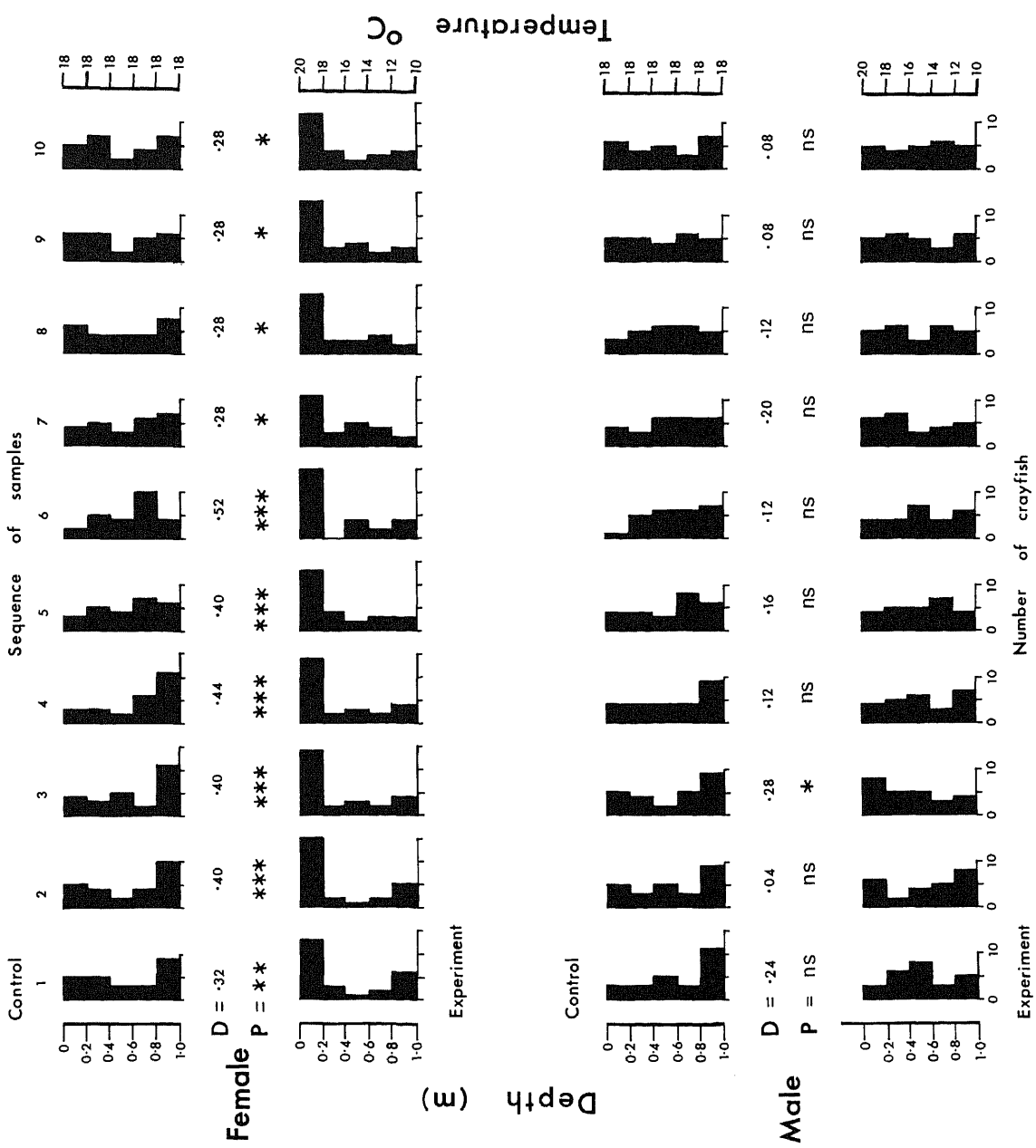


Figure 32
Temperature selectivity ...
Between pp 129,130

experimental group and control group (figure 32, upper). This was caused by a tendency to select the 18-20°C temperature range. There was no significant difference overall between the distribution of males within the temperature gradient and that of the control group (figure 32, lower). This indicated that males did not select a particular temperature but rather tended to be distributed fairly evenly throughout the 10-20°C temperature range.

Such an apparent difference in temperature selectivity between the sexes could, in part, explain why females occurred predominantly in the shallow water during the warmest months, at least during night-time, while males tended to be more or less evenly distributed down to 30 m depth. The reasons for such a temperature selectivity mechanism in females but not in males may involve differences in energy requirements associated with the reproductive cycle and possibly the moulting cycle. These aspects are considered further in the remaining part of the study, which concentrates mainly on the biological cycles of adult *P. planifrons* and their effects on distributional behaviour.

PART II SEASONAL BIOLOGICAL CYCLES

A PATTERNS OF BREEDING AND MOULTING ACTIVITY

1. Introduction

Seasonal migratory behaviour in some species of crayfish has been related to sexual cycles and to moulting. Henry (1951) believed that the downstream migration of *Astacus klamathensis* in spring was in response to the rearing of young and to moulting. Aiken (1969a) found that ovarian maturation in *Orconectes virilis* required 4-5 months of continuous darkness and low temperatures. These conditions prevail in deep water in winter and were thought to explain the downward movement of females in streams (Aiken 1968) and lakes (Momot 1967a, Momot and Gowing 1972) in late autumn.

Females of some species may sometimes necessarily shift into shallower, warmer waters for egg laying and egg hatching. Thus, Aiken (1969a) found that egg laying activity in *O. virilis* never occurred at temperatures less than 10-11°C. Eggs of *Pacifastacus leniusculus* did not hatch below 8.6°C in L. Tahoe (Abrahamsson and Goldman 1970) and consequently egg hatching was restricted to above 60 m depth in this lake. Low temperatures can also inhibit moulting in decapod crustacea (Van Deventer 1937, Hess 1941, Kyer 1942, Travis 1954, Passano 1960a; b, Mobberly 1963, Prins 1968, Aiken 1969b), so crayfish may sometimes migrate into warmer waters to moult.

In this section the breeding and moulting cycles of *Paranephrops planifrons* are outlined and their effects on

the spatial distribution patterns of males and females are considered in some detail. Behavioural adaptations associated with these cycles are presented and discussed in terms of certain environmental factors including temperature, depth and shelter distribution. Details on the breeding population are also given.

2. The Breeding Cycle

Breeding periods were defined as those times when females carried eggs on their pleopods, and when males were considered capable of producing spermatophores. Details of the breeding cycles of both sexes were obtained in 1975 and 1976 and are presented in Figure 33 and its overlay.

a) Females

Females with eggs were found throughout the year (figure 33A) indicating that breeding was continuous. However, breeding females were most common from May - July, when 40-50% of the population carried eggs. Another, slightly smaller rise in the breeding percentage occurred in November.

Periodicity of egg laying was determined from the percentage of females with newly laid eggs, that is, eggs in the EI = 1 stage of development (figure 33B). Egg laying was nearly continuous throughout both years, with peaks in late autumn and early spring. The largest of these began in April and ended in July (the late autumn lay), while the other extended from October to January of the following year (the early summer lay). The early

Figure 33. Annual breeding activity pattern of *P. planifrons* in L. Rotoiti and the activity cycles of associated events. Data was collected monthly from trapped crayfish during 1975 and 1976. Results are expressed as a percentage of the number trapped.

A Females with eggs

B Egg laying (EI = 1)

C Young release from parent (EI = 5)

Each arrow links the beginning and end of a single breeding period.

D Males with ripe testes, presented as the broken line on the 0-100% scale.

OVERLAY Adults with implanted spermatophores

Figure 33
Annual Breeding Activity ...
Between pp 132, 133

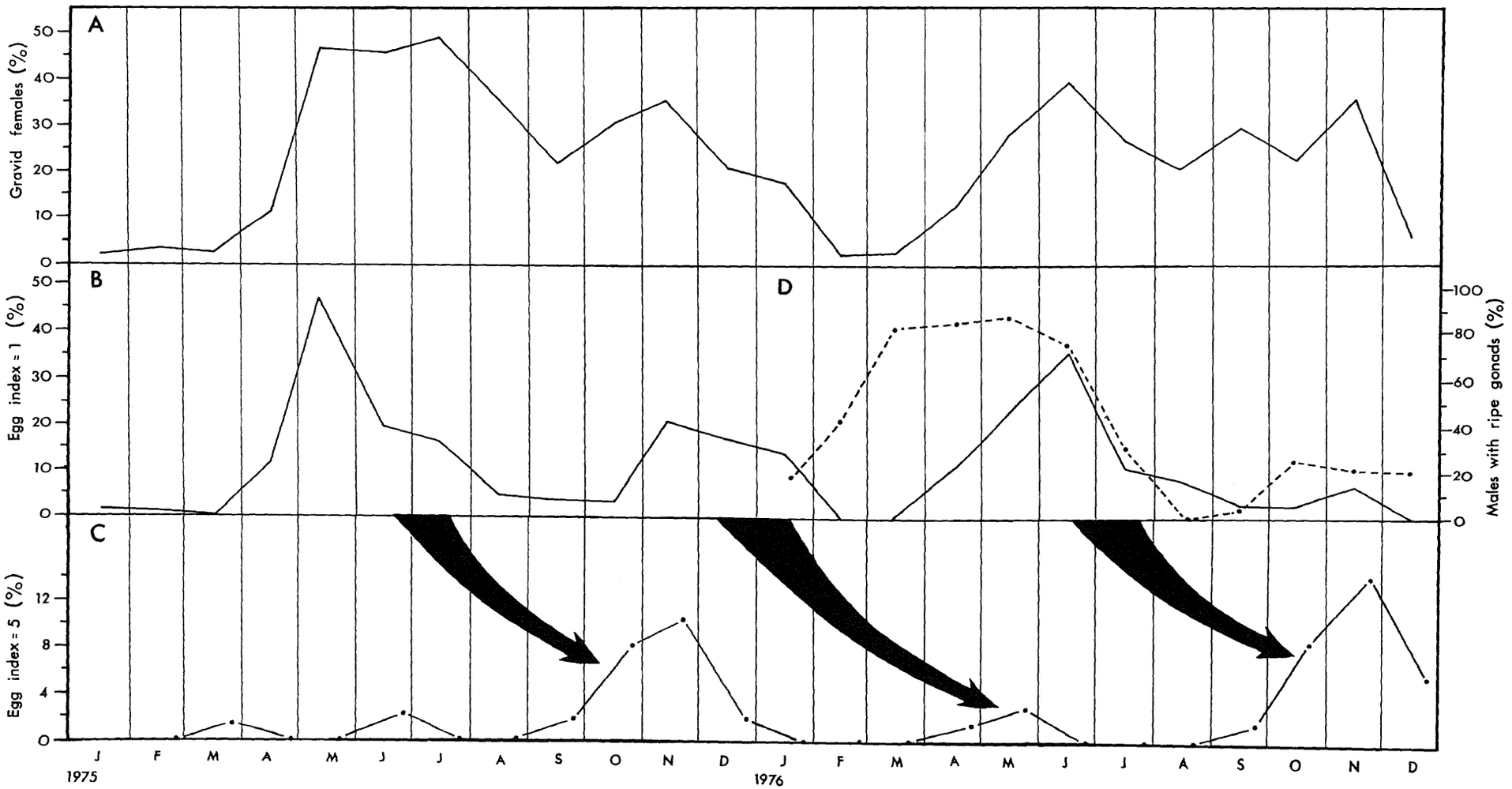
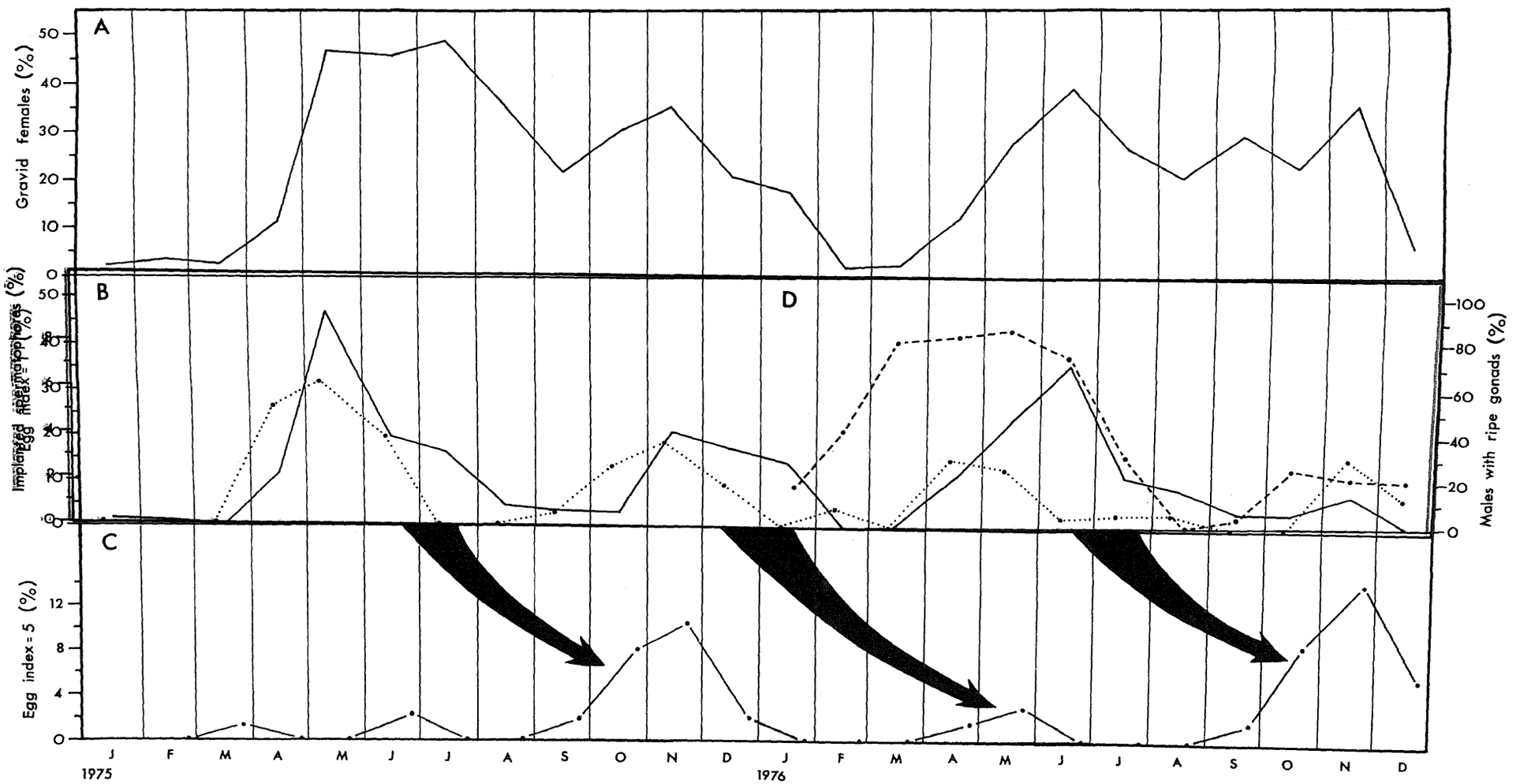


Figure 33
Annual Breeding Activity ...
Between pp 132, 133

Figure 33
Annual Breeding Activity ...
Between pp 132, 133



summer lay was not as apparent in the 1976 - 1977 season, possibly because too few females were captured from deep water in December (see later). Little or no egg laying activity occurred in late summer and early autumn.

The late autumn lay appeared the most important, as it included a greater percentage of the female population and was generally more consistent from year to year, than the early summer lay (table 40). Hopkins (1967a) found that the main laying period for a population of *P. planifrons* inhabiting the Mangatarere Stream system near Carterton, was also in late autumn. He made no mention of breeding activity at other times of the year but did observe a female with eggs in February, which implies that some egg laying may also occur around early summer

Females with offspring in the EI = 5 stage of development were used to determine the end of the two annual breeding seasons, which was defined as the period hatchlings left the parent. The EI = 5 stage lasts approximately 3 weeks, so young would have remained attached to the parent for a further 1-21 days after females were collected. To compensate for this the average, 10 days, was added to the results (figure 33C).

Results show that these young associated with the late autumn lay left their parents between late September and late December, while those associated with the early summer lay departed between the end of March and the latter half of June. By calculating the period between peaks in egg laying and peak times when young left the parent for each breeding season, the winter breeding season was

Table 40: Percentage of females laying eggs at peak times in late autumn and early summer in L. Rotoiti.

Late autumn Date	lay	Early summer Date	lay	Reference
29 Apr.1973	40.0	Nov. 1973	ca 10.0	Devcich 1974
12 May 1975	46.7	13 Nov.1975	20.8	present study
15 Jun.1976	35.7	15 Nov.1976	7.1	present study
Mean	40.8		12.6	
SD	5.5		7.2	

t = 5.360, p = *, n = 6

assessed at about 28 weeks, while the summer breeding season averaged 19-20 weeks. The 8-9 week longer incubation time for late autumn laid eggs was due to the lower temperatures associated with winter, since the rate of crayfish embryonic development is related to temperature (Andrews 1904, Lowe 1961, Frost 1975). Hopkins (1967a) calculated that the winter breeding season of *P. planifrons* lasted for 25-26 weeks.

b) Males

The presence of spermatophores on the exoskeleton of adults was the only external means of assessing breeding activity of male *P. planifrons*. Up to 13.3% of the female population (recorded on 12 May 1975) and, somewhat surprisingly, up to 4.8% of the male population (same date), carried spermatophores. From laboratory observations of males kept separately, it seemed that many of the spermatophores on males in situ were probably self-inflicted. Males may have also received spermatophores from other males. Mason (1970b) observed a pair of male *Pacifastacus trowbridgii* copulating, although he considered such behaviour to be rare.

The total number of spermatophores on crayfish (some individuals carried more than one spermatophore) captured each month from January 1975 - December 1976 was calculated as a percentage of the total number of crayfish caught each month. Results are presented in the Figure 33 overlay and indicate that spermatophore deposition occurred at discrete periods throughout both years and generally coincided with the late autumn and early summer laying periods. Little or no mating occurred at other

times of the year.

The periods at which males were considered capable of producing spermatophores were also assessed. These were determined by examining the testes of 637 adult males collected throughout 1976. Only males with testes that were robust, relatively large and filled with a thick, white seminal fluid were obviously mature, and hence probably capable of spermatophore production. The results are presented on Figure 33D and indicate that the male population is capable of almost continuous breeding activity. Their main breeding period extended from February to July and thus encompassed the late autumn egg laying period. A smaller peak in sperm production occurred in October and so preceeded the early summer lay by about one month. From November - January sperm production was generally lower (15-21% of the population) and it virtually ceased in August and September.

c) Size and age at maturity

The size of females at maturity was taken to be 31.0 mm CL, which was the length of the smallest female found to be bearing eggs. The smallest gravid female recorded by Hopkins (1966; 1967a; b) measured 25.0 mm CL (rostrum length included). He found that females matured in their second or third year, so on the basis of size, L. Rotoiti females probably matured in their third year.

Formalin injected into the thoracic cavity of males usually induced muscular contractions which emptied the testes of their contents, thus providing a simple, rapid method for distinguishing potent males. 20 males from

24.0-32.0 mm CL were taken from L. Rotoiti during the peak mating period of May 1976 and injected with 0.5 ml 10% formalin. The smallest male to extrude sperm from its gonopores measured 27.0 mm CL, indicating that males mature around this size. This was smaller than for females, so males may mature in their second, rather than third year. Woodland (1967) states that male crayfish tend to spawn at a slightly smaller size than females and suggested that this may be because less energy is devoted to the production of spermatozoa than to oocytes.

d) Size range of the breeding population

The largest crayfish caught in L. Rotoiti was a gravid female measuring 70.9 mm CL. A 63.2 mm male was injected with formalin and released sperm from its gonopods, indicating that this animal was sexually active. These findings suggested that the largest size classes contributed to the breeding population.

The size distribution of females forming the breeding population was assessed from the number of females with eggs in the EI = 1 stage of development expressed as a percentage of the total number trapped throughout the 1975 breeding period (ie April 1975 - January 1976). Females were grouped according to sizes which corresponded to single year classes (see later). The results are given in Table 41 and indicate that the breeding population includes mature females of almost every size, though mainly within the 37.5-53.4 mm CL range.

Table 41: The range in size of females forming the breeding population in L. Rotoiti for 1975 and the contribution of each size class towards recruitment.

Size class (mm CL)	Corresp. age (years)	No. with eggs in EI=1 stage	Total number trapped	Size of breeding population (relative %)
31.0 - 34.2	3	4	33	12.1
34.3 - 37.4	4	1	60	1.7
37.5 - 40.6	5	15	79	19.0
40.7 - 43.8	6	18	115	15.6
43.9 - 47.0	7	16	102	15.7
47.1 - 50.2	8	14	67	20.9
50.3 - 53.4	9	6	45	13.3
53.5 - 56.6	10	1	10	10.0
56.7 - 64.4	11-16	0	6	0.0

3. Mating

a) Stage of moult cycle

During the trapping series in L. Rotoiti from January 1975 to December 1976, 9 females were caught carrying a spermatophore each, though not eggs. All had soft exoskeletons which implied that mating occurred very shortly after females moulted (the prebreeding moult, see later). Meanwhile, the exoskeletons of males were in a more advanced state of hardness at mating time, for males had moulted up to 2 months earlier than females (see later). This pattern resembled that of *Homarus americanus*, for Templeman (1934; 1936) found that hard shelled males mated no later than 12 days and normally within a few hours or days of females moulting.

Crayfish are agressive but at moulting this aggressiveness has been found by Bovbjerg (1953) to be reduced and they cease to maintain their social hierarchy. Bovbjerg (1956) also describes mating as basically a tension contact, so it would appear advantageous that mating occurs when females are more passive than usual and when males are in a normal state of aggression. Therefore, the difference in timing of prebreeding moult activity between male and female *Paranephrops planifrons* may be an adaptation to ensure that copulation is successful.

b) Sexual dimorphism in chelae

The relationship between body length and length of the longest chelae for male and female *P. planifrons* was determined (figure 34). The results show that chelae

Figure 34. Relationship between body length and length of the longest chela for males and females from L. Rotoiti.

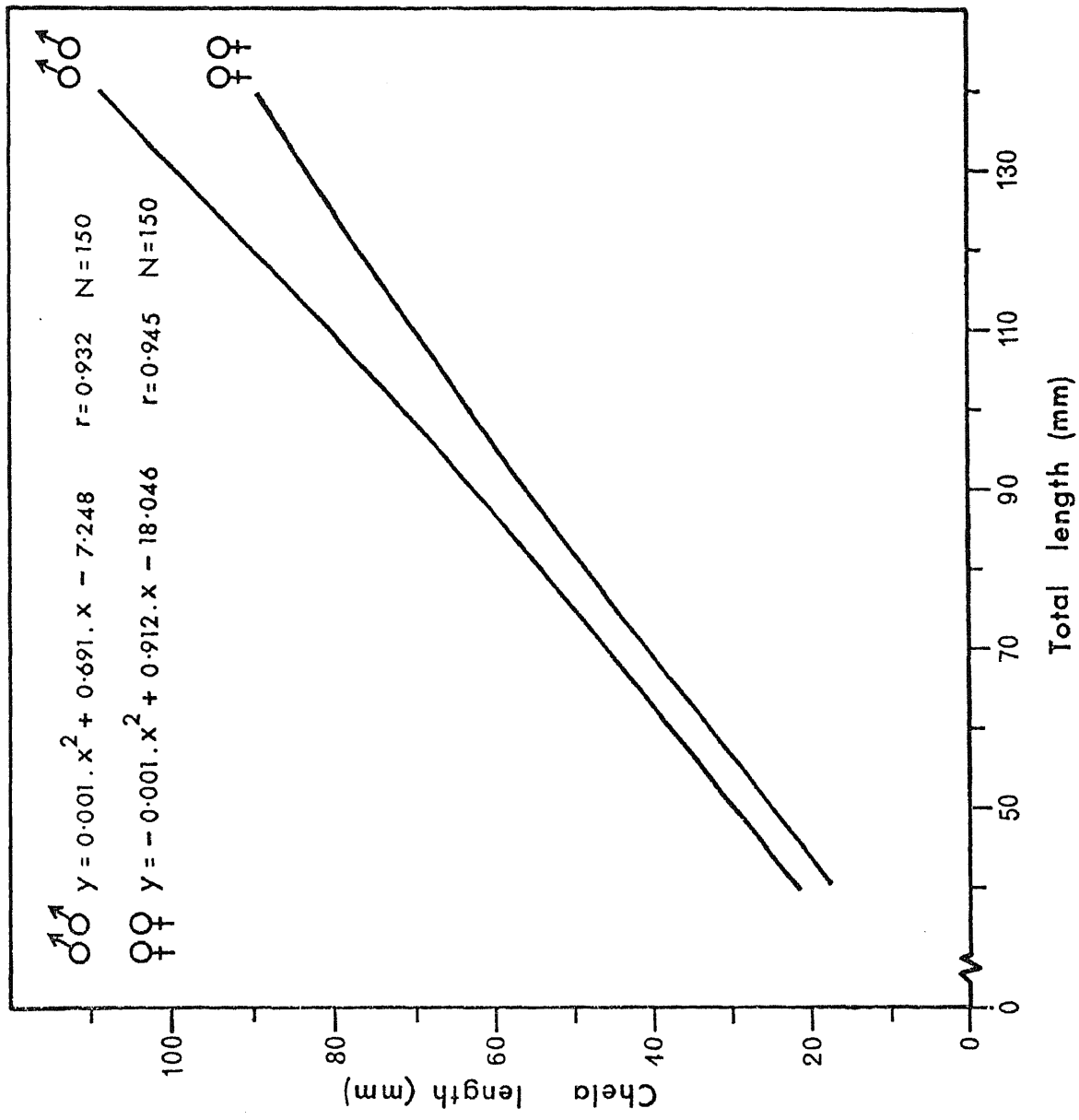


Figure 34
Relationship between body
length ...
Between pp 139,140

were sexually dimorphic and that their growth was allometric, especially in males.

Similar relationships occur in other species, including *Astacus astacus* (Abrahamsson 1966), *A. leptodactylus* (Kossakowski 1967), *Orconectes virilis* (Weagle and Ozburn 1970) and *O. kentuckiensis* (Boyd and Page 1978). Stein (1976) found that male *O. propinquus* with larger chelae were the most successful in copulating with females, tended to dominate male-male interactions and generally outcompeted males possessing smaller chelae, for females. Boyd and Page (1978) suggested that the greater increase in length of male chelae may be an adaptation to aid in the mating process, for the larger and more powerful chelae would give males greater control in manoeuvering and maintaining females in a copulatory position. This may apply to *P. planifrons* too. Therefore, it is possible there are at least two complementary mechanisms operating to ensure copulatory success: moult timing and chela size.

c) Spermatophore

At implantation the spermatophore of *P. planifrons* is soft, semi-transparent and usually about 1.2 cm x 0.8 cm x 0.7 cm in size. It firms within 48 hours, having acquired a slightly off white colouration during that period. 5 μ sections stained with methylene blue, revealed that spermatophores consist of a matrix pervaded with convoluted tubules containing great numbers of maturing spermatozoa. The spermatozoa are spherical non-flagellate bodies, each about 5 mμ in diameter (Devcich 1974) and appear typical of decapod spermatozoa

generally (Moses 1961).

d) Precopulatory behaviour in situ

Crayfish in copula were never seen either in situ or in the laboratory but some precopulatory behaviour was observed in Lakes Rotoiti, Okataina and Tarawera during the autumn mating periods in 1977 and 1978. A male would closely pursue a female, which usually walked at a faster than normal pace (ca 10 m min^{-1}, cf. 3.5 m min^{-1}; in table 23, p. 75) and would attempt to clamber onto her dorsal side from behind. All observed attempts to immobilise females failed and usually ended with the male toppling from the female as she continued walking. Unless females escaped, such attempts would continue for at least 30 minutes. On 1 occasion, 10 attempted mountings by a male were observed during a 30 minute period.

A more successful approach featured frontal contacts involving the chelae, in which a male would grasp both chelae of a female and hold them outstretched for varying lengths of time, up to and beyond 30 minutes. This behaviour was accompanied by a high frequency of pushing and shoving by both individuals. However, during periods of lesser activity males extended the first and second pair of walking legs toward the female's anterior end in an exploratory manner. Similar behaviour was described by Pippitt (1977) for male *Orconectes nais*. Andrews (1910), Mason (1970b), Ingle and Thomas (1974) and Pippitt (1977), all report that grasping of chelae preceeds the turning over of the female by the male and subsequent copulation.

The duration of the mating process was not determined

for *P. planifrons* but may be similar to the 8-20 minutes recorded by Mason (1970b) for *Pacifastacus trowbridgii* (family Astacidae, subfamily Astacinae), rather than the 2-10 hours for *Cambarus affinis* (family Astacidae, subfamily Cambarinae) (Andrews 1910). This difference may be due to the time spent in copula. The Cambarinae possess a complex reproductive anatomy, whereby the spermatophore is directed by the male into a specialised receptacle (annulus ventralis) on the female, to form a plug (Andrews 1904). In contrast, Astacinae (and Parastacidae) females have no annulus and, as in *Paranephrops planifrons*, the spermatophore is simply attached to the sternal plates of the recipient female (Payne 1978). Occasionally when handled, a male *P. planifrons* would spontaneously eject a sperm-filled spermatophore. This suggests that the copulatory position need be maintained for only a short time.

Tack (1941) described *Cambarus immunis* as promiscuous, since males and females mated more than once with the same or other individuals. Andrews (1904) reported similar behaviour in *C. affinis*, as did Mason (1970b) for *Pacifastacus trowbridgii*. Ingle and Thomas (1974) observed 1 female *Austropotamobius pallipes* mating with 5 males and larger males mated on at least 6 occasions. *Paranephrops planifrons* was no exception, for some females carried 2 spermatophores and 1 female in L. Rotoiti was found with 5 spermatophores. Since males had a long main breeding season (eg. March - June, in figure 33D, after p. 132) they were probably able to mate and produce spermatophores

continually over that period.

Successful copulation resulted in a spermatophore normally being deposited onto the sternal plates of a female at the bases of its last 2-3 pair of walking legs. However, quite often both females and males were found with spermatophores implanted indiscriminantly on the exoskeleton. This feature, and the fact that males actually chased females (see above), illustrated the strong mating instinct of males. Schone (1961) states that male crustaceans are usually the more active sexual partner.

v) Temperature, depth and time

The number of spermatophores deposited by males collected at peak breeding periods (eg. May 1975) was found to vary with temperature (see below), which suggested that male mating behaviour was affected by temperature. Adult males were collected from L. Rotoiti in May 1975 and May 1976 and separated into 8 groups of 30 crayfish each. These with spermatophores already implanted were excluded. Each group was placed in a tray (0.5 m^2) with a continuous water supply maintained at a set temperature between 10°C and 19°C. After 4 days the number of spermatophores produced by each group was recorded. Results are given in Figure 35 and show that most spermatophores were deposited between 14.5°C and 17.5°C, with maximum numbers at 15.8°C.

Since spermatophore deposition occurred predominantly within the 14.5 - 17.5°C temperature range, mating would have been largely confined to depths corresponding to this range. For the late autumn breeding period of 1975, this

Figure 35. The relationship between the total number of spermatophores produced by groups of 30 crayfish each maintained at a given temperature.

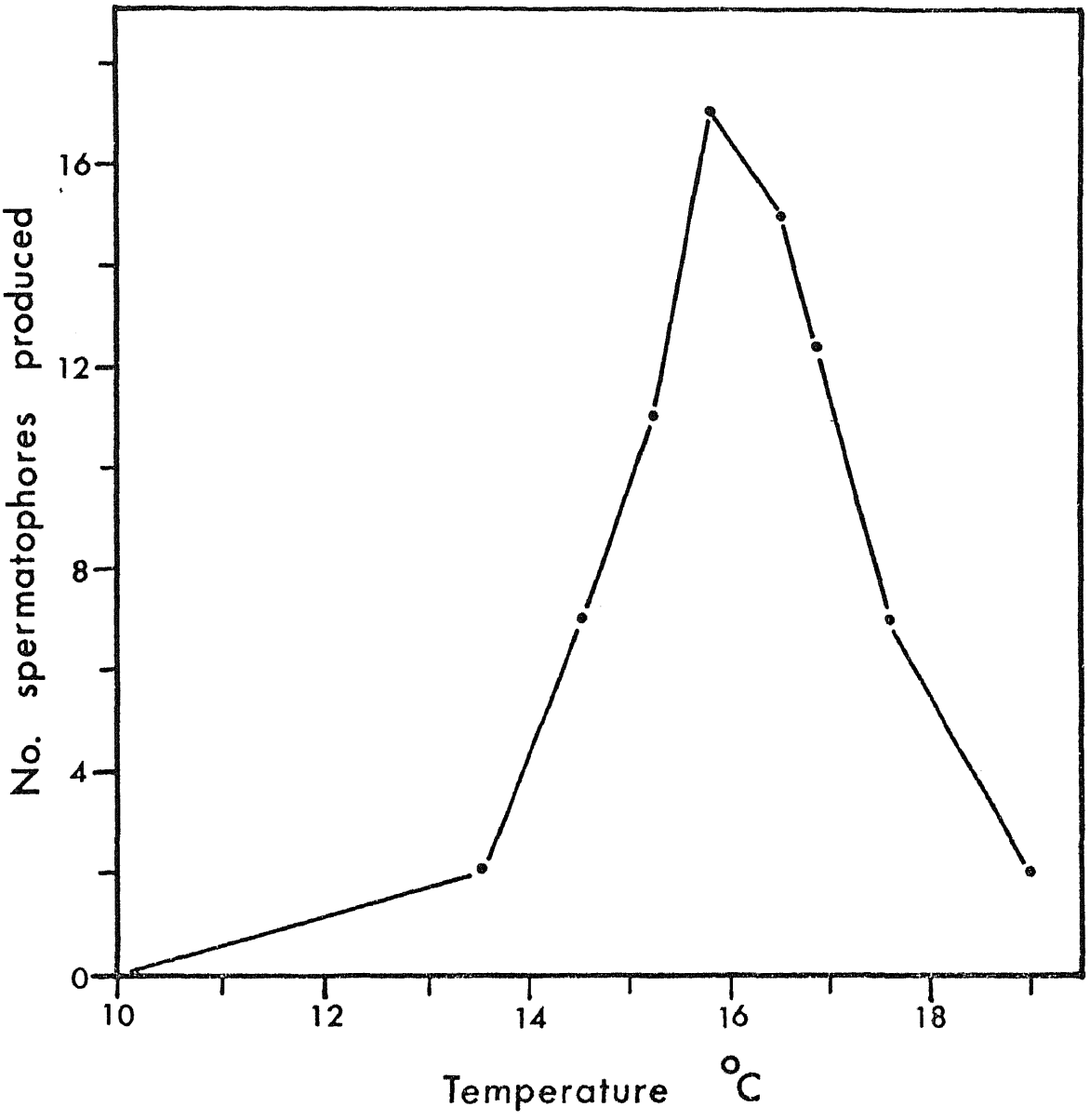


Figure 35
The relationship between the
total ...
Between pp 143,144

critical temperature range occurred between the 15 and 25 m contours on April 17 and above 26 m on May 19, while for the early summer breeding period it lay above 12 m depth on November 11.

Laboratory males deposited spermatophores almost exclusively at night, so mating in situ was probably a night-time event. This seems reasonable, for individuals would be most likely to encounter each other at night, rather than during the day when they are less active. However, some mating activity (described above) did occur in the daytime but was restricted to depths corresponding largely to the upper quartile of the high density band. Daytime precopulatory behaviour was observed in Lakes Rotoiti, Okataina and Tarawera in April and May of 1977 and 1978.

Pheremones have often been implicated in the mating of crayfish [reviewed by Dunham (1978)] as a means of sexual recognition by breeding males. Mason (1970b) found that although the frequency of male-male contacts was high, males bearing spermatophores were rare. This led him to suggest that there may be chemosensory information conveyed to females during the seizure-mount sequence. There is evidence that the active substance is released from the antennal gland and detected by antennular receptors (Barber 1961, Ameyaw-Akumfi and Hazlett 1975). In the above experiment (figure 35), *P. planifrons* males readily produced spermatophores without the presence of females, which suggested that pheremones were not essential for mating to occur. Sexual recognition may not

be particularly important in this species for successful copulation is almost certainly assured due to the moult-induced, highly passive nature of females throughout the mating season.

4. Egg Laying

a) Relationship to time of mating

Evidence presented previously (cf. the overlay in figure 33 and figure 33B, following p. 132) indicated that egg laying first occurred at about the time spermatophore implantation began, which implied that egg laying took place soon after mating. Since fertilisation most probably occurred at egg laying, from sperm released from the spermatophore (see later), the maximum time lag between mating and egg laying could be determined from the length of time spermatophores remained on females.

This period was found to be related to temperature. 15 females with newly implanted spermatophores were divided into 3 groups of 5 females each and maintained at different temperatures until their spermatophores had totally dissolved. The results are presented in Table 42 and suggest that the rate of reduction in spermatophore size was temperature dependent, occurring much more quickly at 20°C than at 10°C.

The mean temperatures of L. Rotoiti down to 30 m depth over the April-May and November-December mating periods of both 1975 and 1976, ranged from 14.6 - 15.6°C. Therefore, egg laying had to occur within 4 weeks of mating if the eggs were to be fertilised. It was likely

Table 42: Duration of spermatophores on females maintained at 10°C, 15°C and 20°C.

Crayfish No.	1	2	3	4	5	Average (weeks)
	Days for spermatophore to dissolve					
10°C	65	49	57	50	60	7.9
15°C	28	32	27	38	34	4.5
20°C	21	30	24	19	26	3.4

that the maximum quantities of sperm were released from the spermatophore between a few days and 2 weeks after implantation, by which time the spermatophore was considerably reduced in size. Females probably laid their eggs mainly within this period, as a means of maximising the chances of the whole egg clutch being fertilised.

b) Fertilisation and site

Since there is normally no physical connection between the implanted spermatophore and the oviduct openings, located on the basal joint of the third pair of walking legs, fertilisation appears to be external. Fertilisation most probably occurs at egg laying, when the extruded eggs pass over the dissolving spermatophore and gather within the 'chamber' formed by the abdomen and telson reflexed against the ventral cephalothorax. The dissolution of the spermatophore is thought to be due to chemical weathering by the water and, as a result, a steady stream of mature spermatozoa is released. Under tranquil conditions a sperm cloud forms in the vicinity of the eggs, which are consequently fertilised.

Female crayfish become secretive at the time of egg laying and seek the privacy of burrows and other refuges to lay their eggs (Mason 1970c, Riek pers. comm.). Such behaviour is undoubtedly in response to an increased vulnerability to predators, including other crayfish, while the females are laying and caring for the eggs. However, refuge seeking may also play a vital role in achieving fertilisation, as immobility would help ensure that spermatozoa are not swept away from the vicinity of the eggs.

P. planifrons females do not appear to be as secretive at egg laying as those of some other species, for on 30 April 1978, 3 females were found on an open mud bottom at 26 m depth in L. Rotoiti. Their eggs were still bathed in glair (mucous secretion) within the 'chamber' and were not yet attached to the pleopods, indicating that laying had just occurred. By contrast, Mason (1970c) reported that mated *Pacifastacus trowbridgii* females form burrows under large boulders in streams and apparently occupy them during spawning. He also found that females about to spawn became highly aggressive and did not tolerate other crayfish closer than about 0.7 m. Similar aggressive behaviour is perhaps not shown by *Paranephrops planifrons*, since the 3 females mentioned above were collected from an area where densities ranged up to 50 crayfish m^{-2}.

Shallow excavations within predominantly muddy and sandy substrates (see later, plates 14 and 15) were rathe common. These excavations were formed by both males and females and may have been utilised by females at egg laying, although apparently not extensively, since this was never observed during the numerous dives made throughout the egg laying periods. It was not determined whether females preferred any particular site for laying eggs but it would seem that this activity occurs within shelters, as well as on open bottom areas.

c) Temperature and depth

Aiken (1969a) showed that egg laying in *Orconectes virilis* was related to temperature and not to photoperiod,

as earlier suggested by Stephens (1952). Aiken found that a temperature threshold of about 10-11°C was required and that egg laying readily occurred at both 12°C and 20°C.

Since egg laying by *P. planifrons* did not appear to be confined to any single type of substrate, a knowledge of the temperature and temperature range over which eggs were laid could indicate the depth distribution of egg laying activity in L. Rotoiti. Unfortunately, these criteria could not be determined from experimental data, as the results obtained were inconclusive. Groups of 10 females bearing spermatophores were maintained at 10.0, 12.0, 15.0, 17.5 and 20.0°C. However, only 3 females (2 at 20.0°C, and 1 at 15.0°C) laid eggs and altogether 30 females (60%) died, whilst 17 (34%) did not lay eggs during the 4 week experimental period. However, egg laying did occur at 11°C in L. Rotoiti. This was about 1°C above the lake's minimum recorded temperature in 1975-76, therefore it seemed unlikely that temperature ever restricted the depth of egg laying activity.

In April 1978 the 3 females mentioned on page 148 were found laying eggs within the high density band, situated between the 11 m and 28 m contours. A large percentage (ca 70-80%) of the adult population occupied this depth range during the day, so much of the egg laying activity may have occurred there (see later). Observations with SCUBA revealed that during the warmer months, including the late autumn mating and egg laying period, crayfish within the band's upper quartile were

generally more active than crayfish at greater depths. It was therefore hypothesised that females about to lay sought the deeper regions of the high density band as a safeguard against interference by other crayfish during egg laying.

To check this, the high density band was sampled during a period of breeding activity (30 April 1978) and a period of nonbreeding activity (17 January 1979). The latter served as a control. Crayfish occupying the upper quartile (at 12-15 m depths on 30 April 1978 and 12-15.5 m depths on 17 January 1979) and lower quartile (at 22-26 m depths on 30 April 1978 and 23-27 m depths on 17 January 1979) were collected using the device in Plate 13. A series of 5 and 4 sample runs were conducted within each quartile on 30 April 1978 and 17 January 1979 respectively. Between 52 and 234 adult crayfish were captured per run. Male and female numbers per sample were totalled and female numbers within the upper and lower quartile expressed as a percentage, and compared. The number and distribution of females with newly laid eggs (EI = 1) on 30 April 1978 was noted also.

The results are presented in Table 43 and indicate an even distribution of females within the high density band during the nonbreeding period, whereas in the breeding period female numbers within the lower quartile were significantly higher. Also, 81% of the females with newly laid eggs occupied the lower quartile at this time. These findings, strongly suggest that egg laying activity occurred mainly within the lower region of the high density

Plate 13. Crayfish collecting device. The apparatus essentially comprises a collapsable entrance and collecting bag. The entrance consists of an aluminium frame, centrally hinged at each side and held open by a split pin, and the collecting bag is of wire mesh. In operation, 1 or 2 divers grasp the handles and swim at a moderate pace over the bottom so that crayfish are scooped into the bag. Up to 240 crayfish can be taken in a single run using this method

Plate 13
Crayfish collecting device
Between pp 150,151

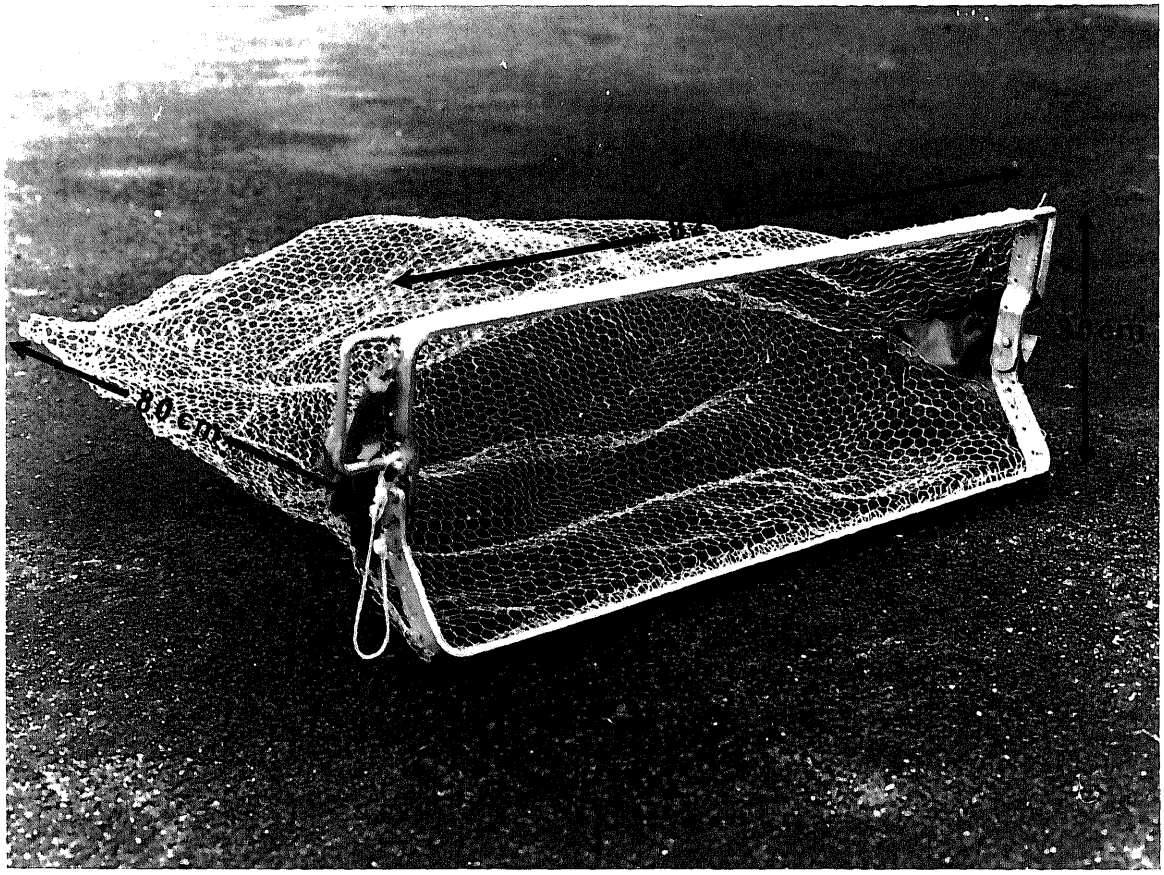


Plate 13
Crayfish collecting device
Between pp 150,151

Table 43: Distribution of females and males within the high density band of L. Rotoiti during a period of breeding and non breeding activity.

Breeding period - 30 April 1978

	Sample No.	Total no. taken	No. males	No. females	% females	SD	No. females EI = 1
Upper quartile	1	106	71	35	33.0	10.2	8
	2	62	52	10	16.1		5
	3	84	75	9	10.7		2
	4	57	50	7	12.3		2
	5	93	66	27	29.0		6
Lower quartile	1	234	119	115	49.1	8.1	26
	2	131	69	62	47.3		19
	3	70	43	27	38.6		10
	4	158	61	97	61.4		23
	5	120	59	61	50.8		20

% females: t = 5.019, p = **, n = 10

Nonbreeding period - 17 January 1979

Upper quartile	1	64	34	30	46.9	9.2
	2	76	44	32	42.1	
	3	116	67	49	42.2	
	4	52	20	32	61.5	
Lower quartile	1	68	32	36	52.9	2.3
	2	77	39	38	49.4	
	3	101	50	51	50.5	
	4	80	47	38	47.5	

% females: t = 0.403, p = ns, n = 8

band.

The shallow end of the high density band lay in the epilimnion (around 17°C at 12-15 m depth) in April 1978, while the deeper end lay at the bottom of the thermocline (around 13°C at 22-26 m depth). Therefore the decreased activity levels below the upper quartile of the band were conceivably due to the lower temperatures. (In winter L. Rotoiti is homothermal at around 10°C and throughout the band crayfish are inactive). The colder temperatures not only lowered activity levels generally, which was probably conducive to successful egg laying but would have increased the viscosity of water as well (Liley pers. comm.). Therefore, it is possible that such conditions may have enhanced the chances of fertilisation, as sperm would have tended to remain in the vicinity of eggs longer than if water temperatures were higher.

d) Depth distribution of egg bearing females

The depth distribution of females with eggs in the 5 stages of development (EI = 1, 2, 3, 4 and 5) and with egg shells attached was determined from crayfish trapped at 1, 10, 20 and 50 m depths, throughout 1975 and 1976 (table 44). The table shows a general movement by females from deeper waters into the shallows as eggs matured.

Figure 36 shows the night-time depth distribution of females with newly-laid eggs (EI = 1 stage) during the main egg laying periods. The most significant feature was that the late autumn breeders occurred almost exclusively above the 20 m depth, while early summer breeders remained

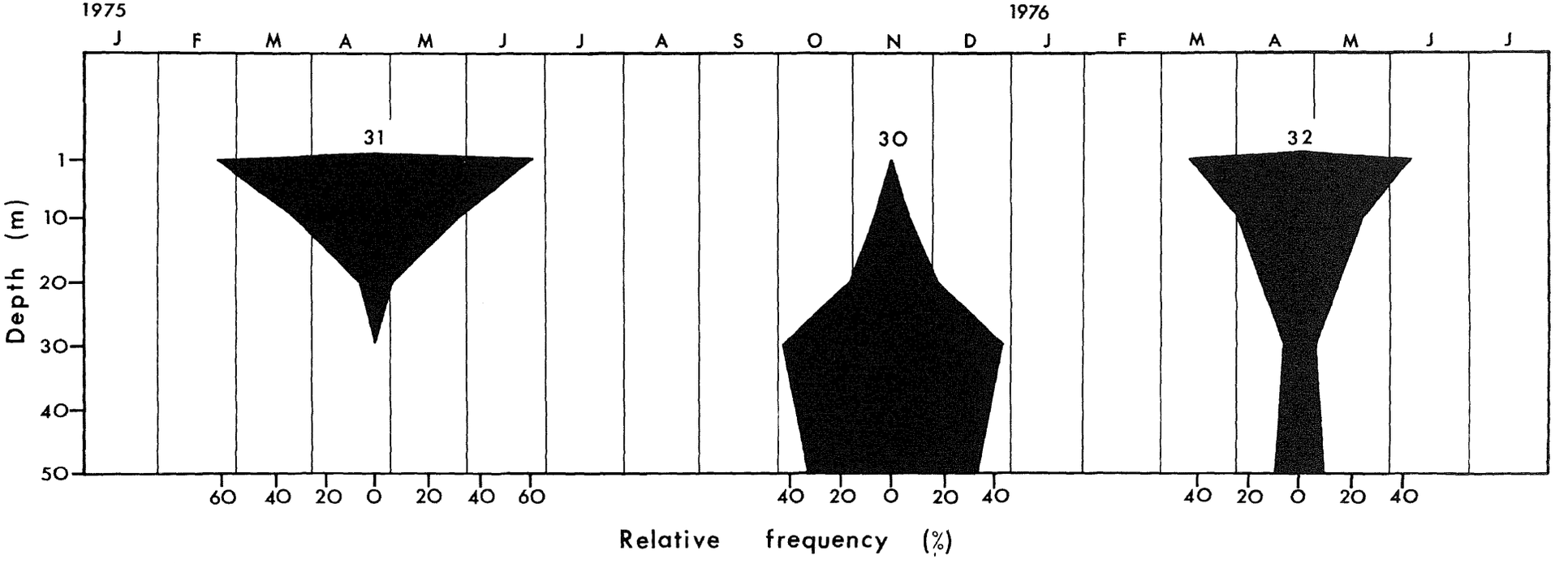
Table 44: Night-time depth distribution of females with eggs in the 5 developmental stages and also subsequent to release of the young. The results were derived from L. Rotoiti females trapped each month in 1975 and 1976.

Depth (m)	Depth distribution of breeding females. (%) EI = 1	EI = 2	EI = 3	EI = 4	EI = 5	†ES
1	32.8	43.4	32.5	50.0	67.8	20.0
10	19.2	13.2	18.9	19.2	14.3	6.3
20	16.8	20.8	32.4	19.2	14.3	31.6
30	16.0	11.3	10.8	7.7	0.0	23.2
50	15.2	11.3	5.4	3.9	3.6	18.9
N =	125	53	37	26	28	90

† Egg shell remnants on pleopods, denoting post-gravid females.

Figure 36. Night-time depth distribution of females with newly laid eggs (EI = 1), during during the late autumn egg laying periods of 1975 and 1976 and the early summer egg laying period of 1975, in L. Rotoiti. The number of females is given.

Figure 36
Night-time depth
distribution ...
Between pp 153,154



below this depth. Figure 36 is based on trapping results and therefore actually represents feeding activity of these females. It could be inferred that late autumn breeders had greater energy requirements because of their tendency to migrate into the rich littoral zone to feed, whereas early summer breeders remained at greater depths in L. Rotoiti, where food abundance was low. This aspect is further considered later.

5. Egg Hatching

Egg hatching (denoted by EI = 5 stage) (table 44) occurred almost exclusively above 10 m depth, which suggested that young became separated from the parent within this zone (shown in figure 6, following p. 48). Following the release of young, females dispersed to greater depths, as indicated by the distribution of females with egg shells attached to pleopods.

It seems unlikely that females undergo diel vertical migrations during the period when their young are leaving but rather that they remain in the shallows. Such behaviour would safeguard against the release of young in areas less favourable for growth (see later discussion). At 20°C in the laboratory there was a 5-10 day lag between the first and last young leaving their mother, so a female may stay in the shallows and at a reduced level of activity for a similar duration during this time.

6. Seasonal Adult Moult Activity

Periods of moulting activity of adult crayfish were determined throughout 1975 and 1976 (figure 37). Results showed that moulting activity was continuous in the male population and near continuous in the female population. The main peak for males was in March or early April and a smaller peak occurred from September to November. Male moulting frequency was low between June and early August and in December of both years. The female pattern was broadly similar to that of males, except that peak moulting periods were generally timed 1-2 months later. Virtually no females moulted in August and September and moulting activity was generally low between late December and early March.

a) Annual moult frequency

The annual moulting frequency of adults could not be determined precisely because of the presence of a second, temporally separate breeding period within the population, and so was derived indirectly. Generally, female crayfish moult either once [eg. *Cambarus propinquus* (Van Deventer 1937), *C. immunis* (Tack 1941), *C. clarkii* (Penn 1943), *Astacus astacus* (Svärdson 1949), *C. longulus longulus* (Smart 1962), *Orconectes virilis* (Momot 1967a), *O. rusticus rusticus* and *C. tenebrosus* (Prins 1968), *O. causeyi* (Dean 1969), *Procambarus hayi* (Payne 1972), *Parastacoides tasmanicus* (Lake and Newcombe 1975), *Pacifastacus leniusculus trowbridgii* (Mason 1975), *O. kentuckiensis* (Boyd and Page 1978)], or twice [eg. *O. clypeatus* (Smith 1953), *Cambarellus shufeldtii*

Figure 37. (upper) Seasonal moult activity patterns of adult males and females from January 1975 – December 1976 in L. Rotoiti. The number of crayfish trapped each month is given.

Figure 38. (lower) Frequency of females with empty egg shells attached to the pleopods in trap samples during 1975 and 1976.

Figure 37
Seasonal moult activity
patterns ...
Between pp 155,156

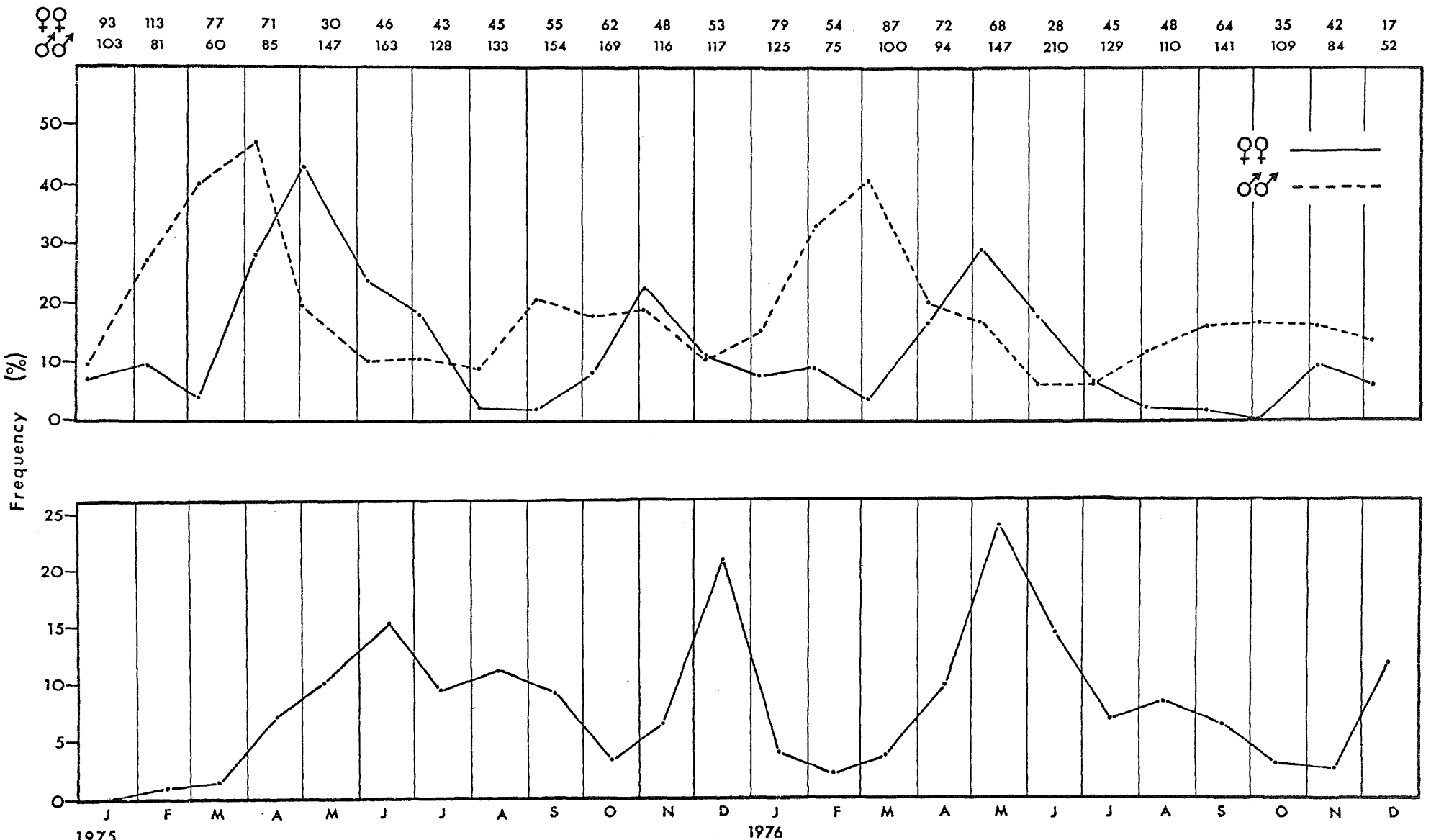


Figure 38
Frequency of females ...
Between pp 155,156

(Lowe 1961), *O. pellucidus inermis* (Jegla 1966)] every reproductive cycle. For those moulting twice, one moult closely preceeds egg laying (the prebreeding moult) and the other usually occurs shortly after have left the parent (the postbreeding moult). Females that moult only once do so in the interval between the young leaving and the following egg lay. This is usually defined as the annual moult. During the interim period between young leaving and the following (postbreeding moult), females retain empty egg shells on their pleopods, so the frequency of females in this state can be used to assess periods of postbreeding moult activity.

Figure 38 shows the numbers of females with attached egg shells, expressed as a percentage of the total number of females trapped each month in 1975 and 1976. The decreasing frequencies indicate periods of postbreeding moult activity, hence many of the 1975 late autumn breeding females moulted in December 1975 and January 1976, but some did not moult until February. In contrast, the postbreeding moult of the early summer breeding females was spread over a greater time span (from June-October in 1975 and from May-November in 1976). This was probably due to colder temperatures which are known to extend the duration of the moult cycle, as well as slowing moult initiation (Passano 1960a). Therefore, it seems that most females moulted within two months of their young leaving but some delayed moulting for considerably longer periods. A similar pattern was found in 10 females maintained at 20°C in the laboratory. One female moulted 16 days after

young had left and a further 5 within 2 months, yet 2 females had still not moulted after 23 and 29 weeks respectively.

There was a clear disparity between the periods of postbreeding moult activity shown in Figure 38 and the peaks in moulting activity of the female population overall (figure 37), which indicated the existence of another period of moulting. A moult always immediately preceeded egg laying (see later), so the peaks in Figure 37 were probably due mainly to females undergoing their prebreeding moult. Therefore, females appeared to moult twice during each annual reproductive cycle. However, there may have been exceptions.

Hopkins (1967a) showed that the pleopods of breeding *P. planifrons* females possess long nonpinnate or filose setae which form a cord attaching each egg to the parent, while the pleopod setae of nonbreeding females are fewer in number and of pinnate or plumose structure. In this study it was found that transition from one form to the other occurred at moulting. Therefore, filose setae occurred after the prebreeding moult, whilst plumose setae resulted from the postbreeding moult. On one occasion a female captured with empty egg shells attached, moulted and produced filose setae instead of the expected plumose setae, and laid eggs shortly after. This female was an early summer breeder and moulted about 6 months after young had left, therefore would have moulted only once in the preceeding 11 months.

It seems feasible that females with extended delays in their postbreeding moult may bypass this moult and have a prebreeding moult instead, in preparation for subsequent egg laying. Such females would therefore moult only once annually. However, Figure 38 shows that at certain times of the year very few females with empty egg shells occurred in the population, which implied that relatively few breeding females moulted once annually.

Figure 37 indicates an overall greater moulting activity by males compared to females, suggesting that males moulted at least as often as females. In conclusion therefore, adult females probably moulted twice annually and occasionally once, whereas adult males probably moulted at least twice each year.

The moulting frequency of crayfish decreases with age [eg. *Homarus americanus* (Templeman 1940), *Jasus lalandii* (Bradstock 1950), *Panulirus argus* (Travis 1954), *Paranephrops planifrons* (Hopkins 1967b) and *Pacifastacus leniusculus* (Flint 1975)], so very large *Paranephrops planifrons*, for example, over 55.0 mm CL, may have moulted only once annually. Hopkins (1967b) found that *P. planifrons* greater than 33.3 mm CL (max. size 43.8 mm CL) moulted once annually, while *Pacifastacus leniusculus* greater than approximately 33.0 mm CL (max. size 57.0 mm CL) had only a single annual moult (Flint 1975).

Hopkins (1967b) determined the moulting frequency of *Paranephrops planifrons* in streams to be 9 moults in the first year, 3 in the second year, 2 in the third year and once annually for the following 2 years. He found that

males and juveniles moulted at no specific time of the year and females moulted in summer after the young had left.

b) Effect of depth

Capelli and Magnuson (1975) reported that male *Orconectes propinquus* inhabiting deep water in Trout Lake, Wisconsin, moulted 8-10 days after males in shallower water, and considered the delay was at least partly due to the colder temperatures. To gauge whether the timing of moult activity in *P. planifrons* also differed with depth, the percentage of trapped crayfish with soft exoskeletons in deep (30-50 m depths) and shallow (1-10 m depths) water was determined each month during 1975 and 1976. From January to May in 1975 and from February to April in 1976, the hypolimnion was deoxygenated, so deep water numbers were supplemented by crayfish trapped at 20 m depth.

The results are given in Figure 39 and indicate that the 1975 late summer - early autumn moulting period for males peaked about one month earlier above 10 m depth than below 20 m depth. From January - April 1975 (and probably in late 1974 also) mean temperatures between 1-10 m depths and 20-30 m depths differed significantly from each other (table 45), so temperature probably influenced the difference in timing of peak moulting activity to some extent. A similar difference in timing was not evident for the equivalent moult in 1976. However, the difference between December 1975 - March 1976 mean temperatures at 1-10 m depths and 20-30 m depths was

Figure 39. A comparison of the timing of moult activity in males and females trapped each month between 1-10 m depths and 30-50 m depths from January 1975 – December 1976, in L. Rotoiti.

Figure 39
A comparison of the timing ...
Between pp 159,160

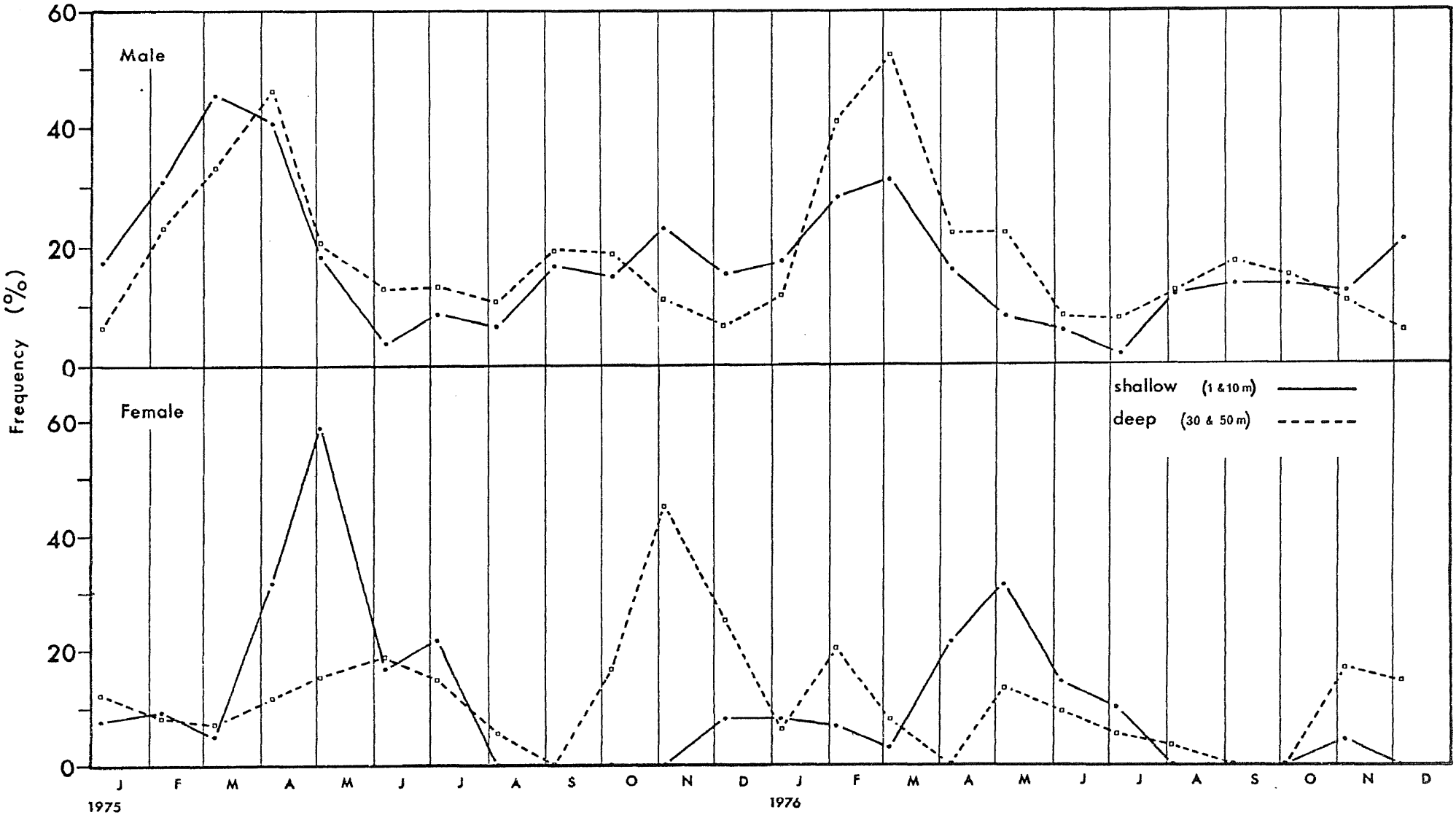


Table 45: Comparison of temperatures at 1-10 m depth and 20-30 m depth over 1975 and 1976 in L. Rotoiti. For January-May 1975, November 1975 - March 1976 and December 1976, the temperatures at 1 m depth intervals within these 2 depth ranges were averaged. For May-October 1975 and April - November 1976 the average of temperatures at 1 m and 10 m depths were compared to the average of temperatures at 20 m and 30 m depths.

Date	Mean temperature (°C) 1-10 m	20-30 m	t	p	n
1975 Jan.	23.1	13.0	23.813	***	21
Feb.	21.0	13.9	18.159	***	21
Mar.	21.3	15.5	12.822	***	21
Apr.	17.7	14.7	8.920	***	21
May-Oct	12.2	11.5	1.081	ns	24
Nov.	15.3	12.2	19.074	***	21
Dec.	18.5	13.9	13.988	***	17
1976 Jan.	18.9	13.7	12.890	***	21
Feb.	19.1	14.6	9.477	***	21
Mar.	18.6	15.3	7.946	***	21
Apr-Nov	12.7	11.9	1.046	ns	32
Dec.	17.4	13.0	15.473	***	17

not as great as in 1975 (refer to values in table 45). This was most probably because of the significantly milder summer in 1975-76 [cf. mean air temperatures at Rotorua airport for November 1974 - May 1975 (20.6°C) and November 1975 - May 1976 (19.4°C): t = 3.684, p = ***, n = 423]. Hence, the duration of the delay in moulting in the deeper waters would have been less than a month and since crayfish were collected at monthly intervals, this delay did not show in the results.

With possible exceptions in November 1975 and December 1976, the timing of male moult activity with depth was similar for the remainder of both years. Over these periods the lake was more or less homothermal at any given time (refer to t values from May - October 1975 and August - November 1976 in table 45), and may explain the results obtained.

Figure 39 shows that the female pattern of moulting activity varied widely with depth, consequently it was not possible to determine whether similar differences in timing existed from the data available. However, it was mentioned on page 111 that females underwent diel vertical migrations to a greater extent than males throughout the warmer months. Therefore the timing of moult activity by females in deep and shallow water would have tended to be similar.

c) Postmoult activity patterns

Since the catches in traps set at different depths largely reflect night-time movement and feeding activity, the data shown in Figure 39 can also be used to show such

behaviour in recently moulted animals. There was a highly significant relationship between the percentages of recently moulted males in shallow and deep water ($r = 0.758^{***}$, $n = 25$), which suggested that their feeding activity was spread fairly evenly over the lake floor. By contrast, there were large annual variations in the depth distribution of recently moulted females, as indicated by the low correlation value ($r = 0.084^{ns}$, $n = 25$). This variation was most pronounced at the two major annual moulting periods, that is, from April - May and around November. During the former period many recently moulted females migrated from the high density band at dusk to feed in the rich, littoral feeding ground, but in November almost all remained and fed at 20-50 m depths, where food abundance was some 80% less concentrated.

d) Relationship with temperature

A comparison of the number of females trapped from January - April with those trapped from July - November for 1975 and 1976, revealed that feeding activity was significantly reduced over the latter period ($t = 5.038$, $p = ***$, $n = 18$) (derived from data in table 46). This may have been caused by the colder temperatures, for a strong positive correlation was found between female feeding activity and temperature (see table 46). By contrast, the feeding activity pattern of males showed a significant negative correlation with temperature (see table 46), such that feeding activity was greatest during the colder months. However, the apparent greater feeding activity by males during the colder periods may not necessarily occur, for

Table 46: Number of females and males trapped each month in L. Rotoiti from January 1975 - November 1976. Mean monthly temperatures between 1 and 30 m depths are included for this period.

Date	Females	Males	Temp. (°C)
1975 Jan.	93	103	17.4
Feb.	113	81	16.7
Mar.	77	60	19.0
Apr.	71	85	16.1
May	30	147	14.8
June	46	163	12.1
July	43	128	11.2
Aug.	45	133	11.7
Sept.	55	154	11.0
Oct.	62	169	11.5
Nov.	48	116	13.7
Dec.	53	117	16.2
1976 Jan.	79	125	16.3
Feb.	54	75	17.1
Mar.	87	100	17.3
Apr.	72	94	16.9
May	71	157	14.2
June	28	210	11.2
July	45	129	10.4
Aug.	48	110	10.2
Sept.	64	141	10.9
Oct.	35	109	12.3
Nov.	42	84	13.6

Females vs temp.: $r = 0.645^{***}$, $n = 23$

Males vs temp: $r = -0.685^{***}$, $n = 23$

the obtained result could be more a function of reduced feeding activity by females at these times enabling more males to enter traps.

The regression equations for numbers trapped versus temperature (figure 40) were compared using the method of Zar (1974 p. 229) and found to differ significantly from each other ($t = 2.810$, $p = **$, $n = 46$). This suggested that males and females differed in their physiological response to temperature, whereby males retained a high level of activity at low temperatures compared to a marked reduction in females. This may at least partially explain why the incidence of moulting in males was higher than for females over the colder months. However, the difference may be somewhat exaggerated, since many females carried eggs over this period and could not moult. The results may also imply that growth in females is restricted to a far greater extent over winter than it is for males (earlier male maturation may relate to this also). In his study on *P. planifrons*, Hopkins (1966; 1967b) found that growth was greatest through spring and early summer and was checked markedly during winter.

e) Diel moulting activity pattern

Of the 40 crayfish that moulted in the laboratory, 36 (90%) did so at night, while 4 (10%) moulted during the day. Therefore, moulting activity in situ presumably occurs mainly at night. Penn (1943) found that *Cambarus clarkii* moulted at night.

f) Depth and location at moulting

It was mentioned earlier that low temperatures

Figure 40. The relationships between number of males and females trapped and temperature. The regression equations were derived from the data in Table 46 and found to differ significantly from each other (see text).

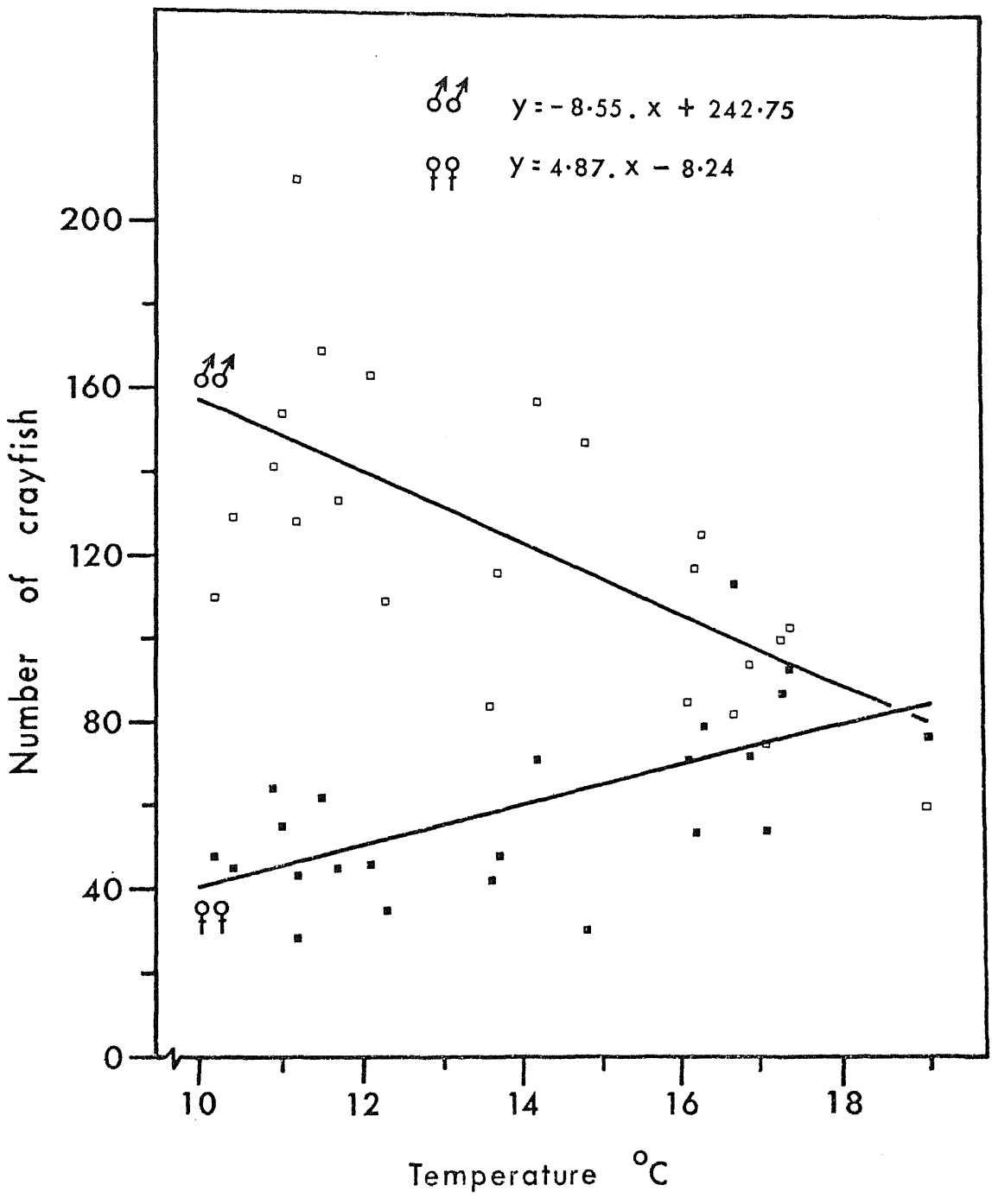


Figure 40
The relationships between
number of males ...
Between pp 164,165

generally inhibit moulting in crayfish, in which case crayfish may need to migrate into shallower, warmer water to moult. However, in L. Rotoiti temperature probably did not restrict the depth at which *P. planifrons* moulted, since moulting occurred at 10°C (during winter homothermy) in the lake, and at temperatures of 10-20°C in the laboratory. This was within the yearly temperature range over the whole lake bottom.

The distribution of suitable shelters seemed to be a more important factor determining spatial distribution of moulting activity. At ecdysis, crayfish are most vulnerable to predation and seek the seclusion of burrows and shelters within which to moult (Hazlett, Rittschoff and Rubenstein 1974).

g) Shelter distribution

In L. Rotoiti suitable shelters occurred mainly above 20 m depth and included rocky areas, piles of allochthonous debris, empty *Hyridella menziesi* shells and objects inadvertently left by man. Below this depth occasional rock outcrops provided the main form of shelter. Consequently, most moulting activity presumably occurred above 20 m depth. The size of shelters chosen was generally directly related to crayfish size and usually one crayfish occupied a shelter. Shelters varied in shape from cylindrical (cans and bottles), to low profile cracks and irregularly shaped recesses with one or more entrances. This variability contrasts with the greater selectivity shown by *Homarus americanus*, which selects shelters that are typically small and flat and with 2 entrances (Cobb 1971).

Riek (1972) classifies *P. planifrons* as a moderate

burrower and Hopkins (1967b) found that it burrowed into the banks of streams. Such burrows were probably utilised as a refuge for moulting. True burrows were never found in any of the lakes examined by diving in this study, possibly because of the generally soft and loose nature of the sand and mud substrates. Instead, adult crayfish would often excavate furrows or pan shaped depressions 6-15 cm in diameter and generally less than 8 cm deep. These excavations were usually formed on low to moderate slopes between 12 and 30 m depths (plate 14) and were most common in Lakes Rotoiti, Rotoma, Okataina and Taupo. In these lakes they were present at densities up to 5 m^{-2}. By day, 5-15% were occupied by adults and of these each usually contained 1 crayfish (plate 15) but occasionally 2 were present.

A few cast exuviae were found either within, or in the near vicinity of excavations below 15 m depth, which suggested their possible role as refuges for moulting. This was surprising since their relative shallowness meant crayfish would gain little, if any, protection from predatory trout. Furthermore, at depths over 20 m, exuviae were occasionally found up to 30 m from the nearest shelter. Unless these were transported from shelters, which seemed unlikely, the implication is that some crayfish moulted without any protection whatsoever.

Plate 15. Adult within an excavation at 22 m depth in L. Rotoma.

0.4x mag.

Plate 14. Excavations formed by crayfish at 23 m depth in L. Taupo. The photograph gives an indication of their density. The area of view is about 20 m^2.

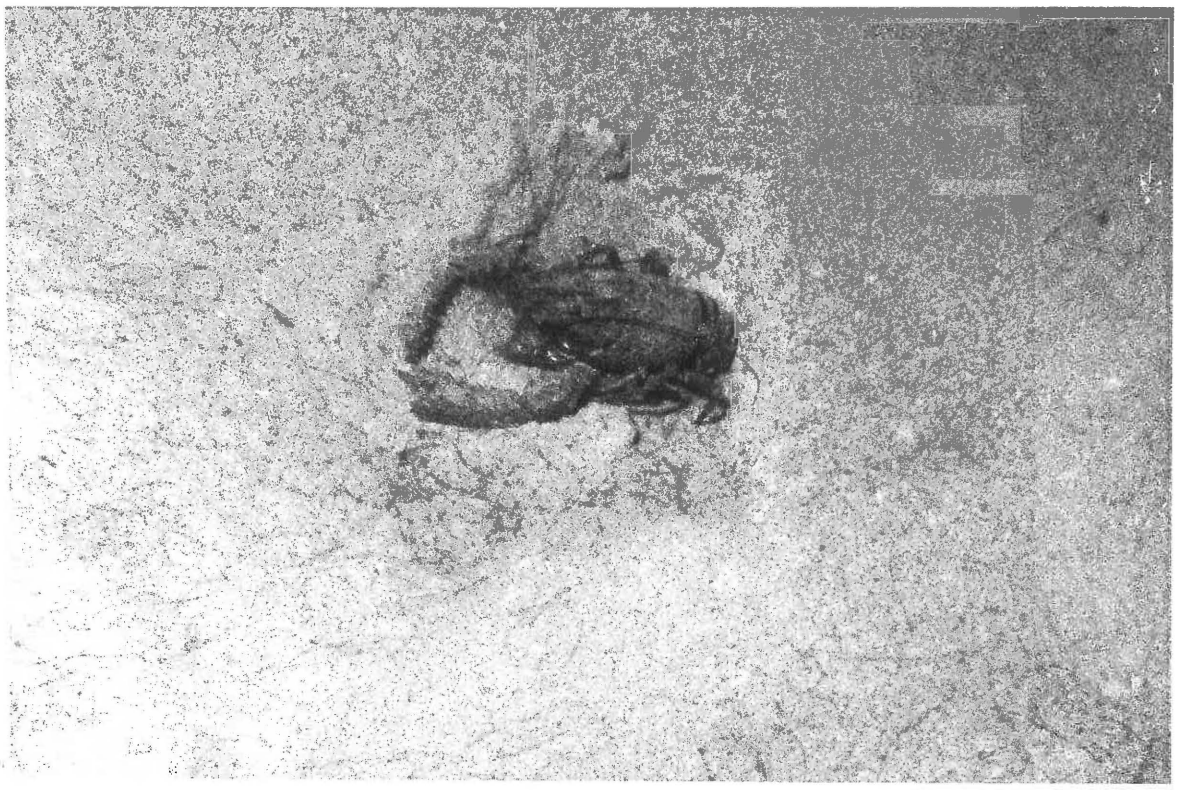


Plate 15
Adult within an excavation ...
Between pp 166,167

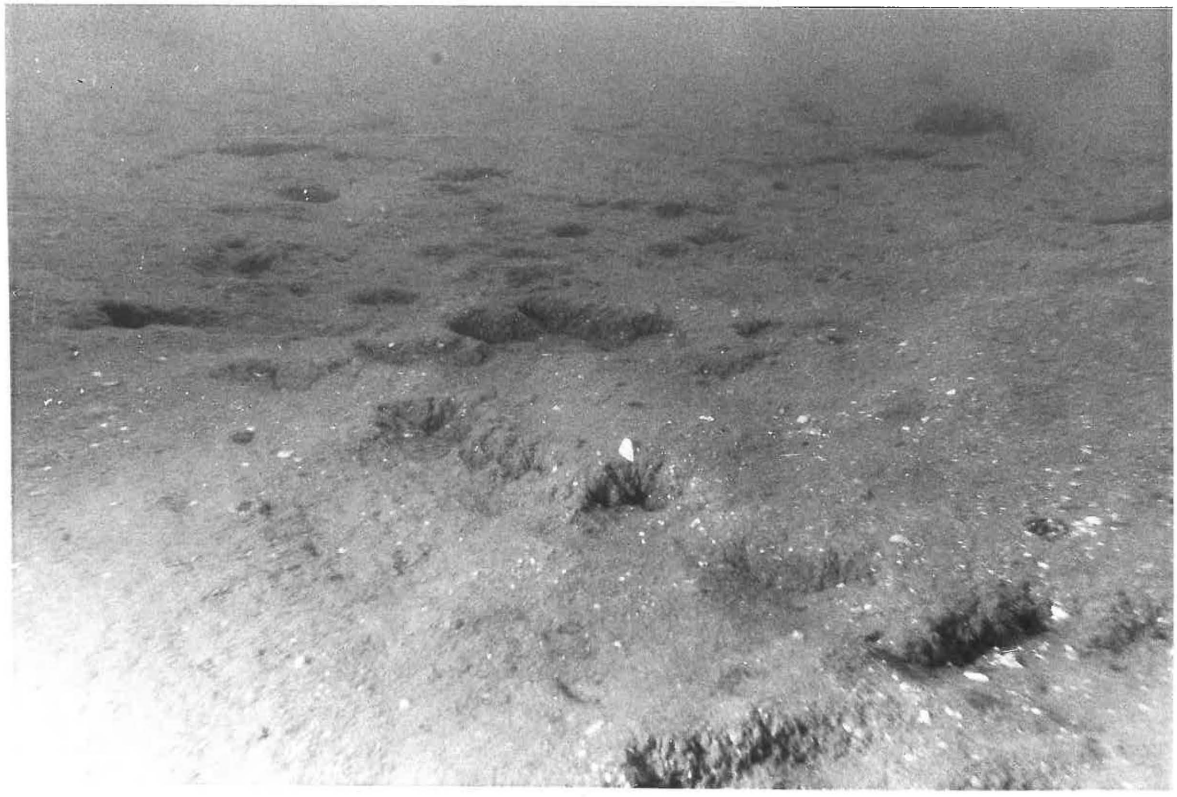


Plate 14
Excavations formed by
crayfish ...
Between pp 166,167

B THE REPRODUCTIVE CYCLE AND ORGAN ANALYSES

1. Introduction

Adiyodi and Adiyodi (1970) state that in decapod crustacea, reproduction and moulting are inseparably integrated events involving cyclic mobilisation of organic reserves from storage organs, to the gonads and epidermis respectively. The hepatopancreas plays a central role in these and other metabolic processes (Vonk 1960) and functions as the principal storage organ (Adiyodi 1969, Adiyodi and Adiyodi 1972). Muscle is another, although less important, store for nutrients (O'Connor and Gilbert 1969). Lipid is generally the predominant organic reserve (O'Connor and Gilbert 1968, Bollenbacher et al 1972).

During periods of relatively low metabolic activity such as intermoult (Passano 1960a) and reproductive quiescence, excess metabolites tend to accumulate within the hepatopancreas especially, to be utilised at times of increased metabolic activity. This may occur during rapid gonadal growth and at ecdysis (Adiyodi 1968, Adiyodi and Adiyodi 1970, Armitage et al 1973). Armitage et al (1972) comment that crayfish in temperate zones tend to store excess food gained during periods of high food production, for example in spring, summer and autumn. These reserves may be utilised during winter dormancy or periods of starvation (Adiyodi 1968, Armitage et al 1972) and when food abundance or the level of feeding activity falls below the requirement for tissue maintenance.

In this part of the study the reproductive cycles of both breeding groups is established and related to seasonal

changes in the distribution pattern. Also, an attempt is made to understand the association of the reproductive and moulting cycles with food held in storage and the seasonal feeding activity patterns. Dependency of the gonads on hepatopancreas and abdominal muscle reserves is gauged in terms of their energy and lipid content. Involvement of the hepatopancreas and muscle as storage organs in association with the moult cycle is briefly considered in terms of seasonal changes in their energy content. Lastly, differences in distribution between each breeding group within L. Rotoiti are outlined and the possible significance of these findings is expressed.

It was also intended to determine the effect of photoperiod and temperature on the reproductive and moulting cycles. [Light, as photoperiod, and temperature, control both the reproductive and moulting cycles of crayfish (eg. Stephens 1952, Travis 1954, Stephens 1955, Word and Hobbs 1958, Passano 1960a; b, Perryman 1969, Armitage et al 1973, Rice and Armitage 1974)]. The method adopted was similar to that applied to *Orconectes nais* by Armitage et al (1973). It required groups of adults to be maintained for up to 1 year under different photoperiod and temperature regimes. However, mortality rates of laboratory maintained *P. planifrons* were such (>95% death rate within 2 months of capture) that insufficient crayfish survived to enable statistical treatment of results.

2. Methods

At approximately mid monthly intervals in 1975, 6 large adults of each sex were collected from L. Rotoiti. 3 crayfish of each sex were taken from shallow water (1-10 m depths) and 3 from deep water (30-50 m depths). In January only 1 deep water female was taken. In March, April and May, deep water numbers were complemented with crayfish trapped at 20 m depth. This was necessary because of the reduction in crayfish numbers in the deeper waters, due to hypolimnetic deoxygenation.

Each crayfish was analysed for carapace water content, gonad and hepatopancreas dry weight, energy, lipid and water content, and also energy, lipid and water content of the abdominal muscle, by the methods described on pages 26-36. A gonad index, similar to that used by Armitage et al (1972) for *O. nais*, was calculated for each individual by dividing the dry weight of the gonad by the length of the cepalothorax. Total lipid content of the gonad was derived by multiplying the gonad's lipid concentration as mg lipid g^{-1} dry weight of gonad by the gonad index. Similarly, the total energy content of the gonad was calculated as kcal g^{-1} ash free dry weight of gonad multiplied by the gonad index. A hepatopancreas index and total lipid and energy contents of the hepatopancreas of each individual were also calculated in the same way.

The 70 females and 72 males analysed were separated into their respective late autumn and early summer breeding groups. This was done in the following way:

In decreasing order of importance the criteria used for separating females were the egg index, presence of empty egg shells attached to pleopods, presence of spermatophores, ovarian size, carapace rigidity and depth captured in association with ovary size. Similarly, males were separated on the basis of sperm extrusion from gonopores following the injection of formalin into the thoracic cavity, testicular size, depth captured in association with testes size and carapace rigidity. 39 females and 39 males were categorised as late autumn breeders and 30 females and 28 males as early summer breeders. 1 female and 5 males were indeterminate and therefore excluded from the results.

3. Results

Results appear in Figures 41-46 in which the results for the early summer breeders are presented as transparent overlays.

a) Females

i) Ovaries

Seasonal trends in gonad development, energy, lipid and water content are shown in Figure 41 along with trends in lake temperature and day length. It is clear from the ovarian development cycles of both breeding groups (figure 41C) that each female bred only once per year. Rapid ovarian growth occurred over a 4-6 month period between December and May in the late autumn breeders and over the 6 months from June to November in early summer breeders. Ovarian growth

Figure 41. Seasonal trends in ovarian cycles of late autumn and early summer (overlay) breeding females during 1975, and also trends in photoperiod and temperature. Numbers heading each month represent crayfish analysed and also apply to Figures 42 and 43. Vertical lines indicate range and means are shown as points and also apply to Figures 42-46. Temperatures were recorded as means from 1-30 m depths.

A Temperature

B Hours of daylight

C Ovarian size

D Energy concentration

E Total energy content

F Lipid concentration

G Total lipid content

H Water content

Figure 41
Seasonal trends ...
Between pp 170,171

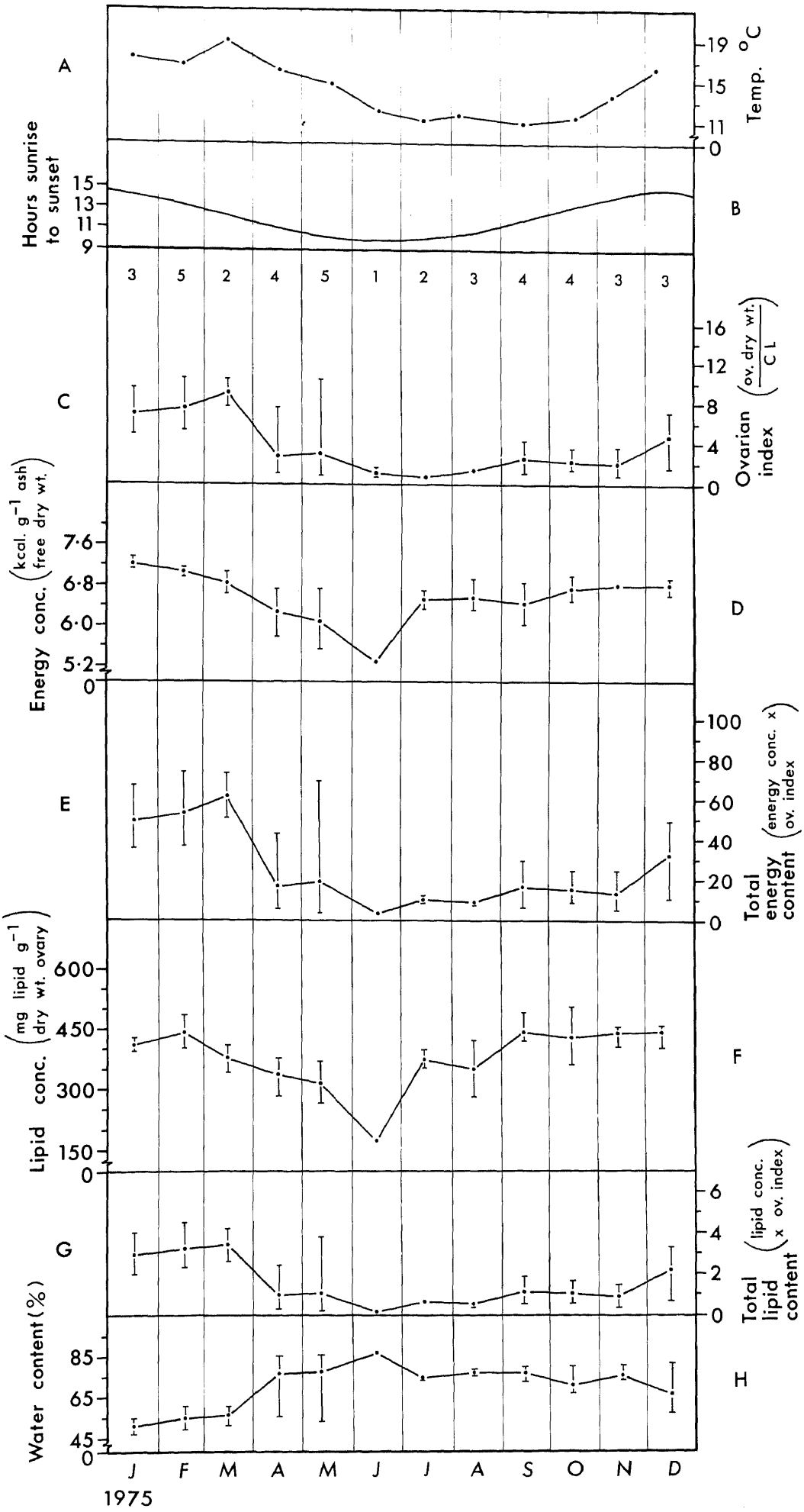
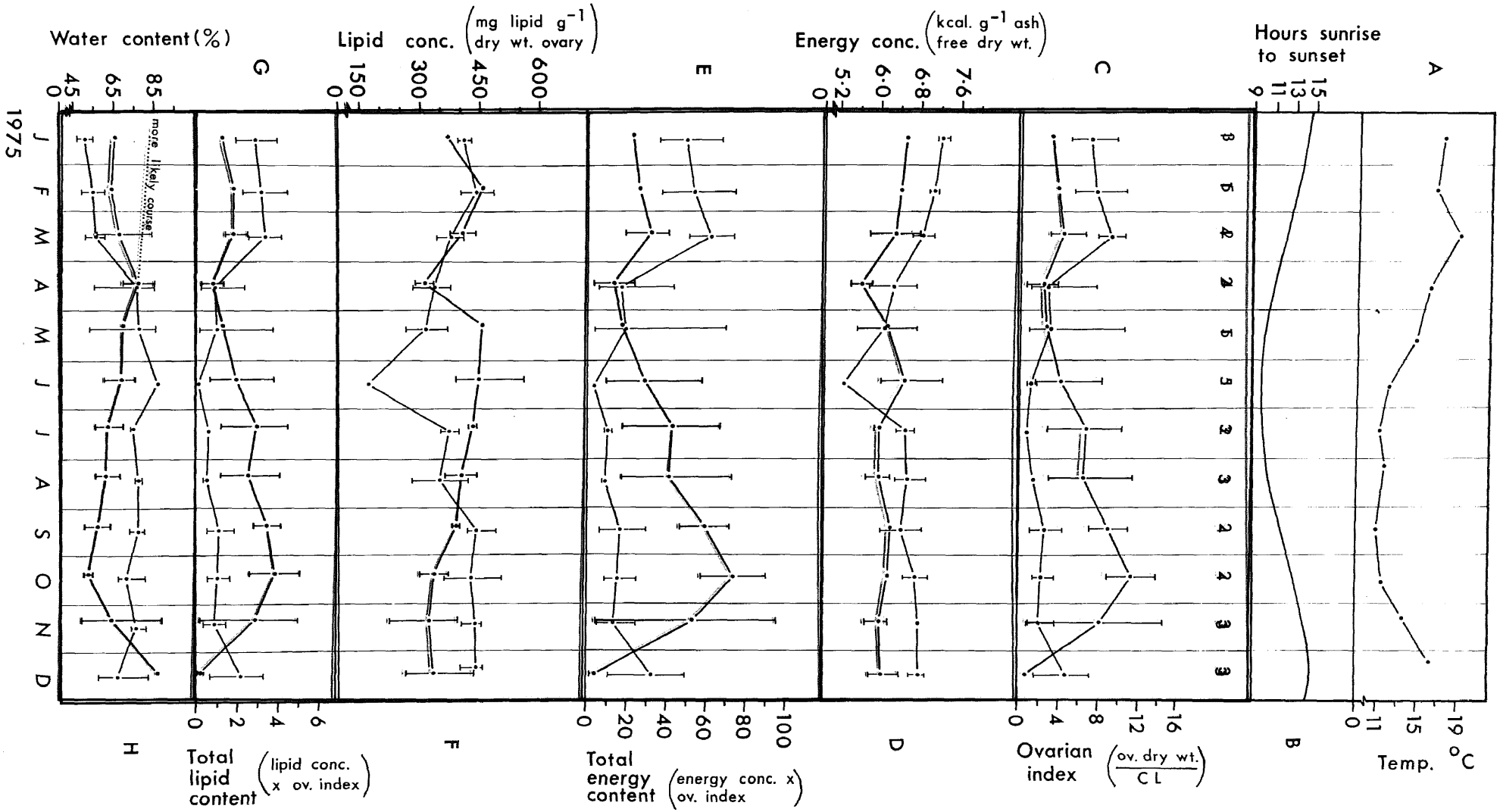


Figure 11
Seasonal trends ...
Between pp 170,171



was negligible for the first 6-8 months and for the first 6 months following egg laying in the late autumn and early summer breeders, respectively. It may be significant that these periods closely corresponded with the time when eggs and hatchlings were attached to the mother.

Ovarian energy concentrations varied between 5.27 and 7.81 kcal g^{-1} ash free dry weight of ovary. Energy concentration in early summer breeders appeared fairly constant throughout the year, while in late autumn breeders it was highest over the summer months and lowest just after egg laying in June (figure 41D). Overall, there was a significant relationship between energy concentration and gonad size ($r = 0.357^{**}$, $n = 69$). The annual cycle of total ovarian energy content for both breeding groups is presented in Figure 41E. As expected, the relationship between total energy content of the ovaries and ovary size was highly significant ($r = 0.997^{***}$, $n = 69$).

Lipid varied from 17.2 - 56.9% (average 39.2%) of the dry weight of the ovary, being somewhat higher than the 5-30% recorded by Armitage et al (1972) for *Orconectes nais*. Ovarian lipid concentration of early summer breeders was maximal in May and June, after which levels slowly decreased as the gonads developed (figure 41F). After the eggs of late autumn breeders were laid in June, there was a rapid increase in ovarian lipid concentration until September, although this period was one in which ovarian growth was

negligible. Lipid levels remained high over spring and summer and following a peak in February, concentrations declined over the next 4 months. The relationship between lipid concentration and gonad size for the whole population was not significant ($r = 0.196^{ns}$, $n = 69$). Seasonal trends in total lipid content of the ovaries of each breeding group (figure 41G) were essentially similar to those for total energy content shown in Figure 41E. The relationship between ovarian total lipid content and gonad size was also highly significant ($r = 0.984^{***}$, $n = 69$).

There were distinct seasonal trends in ovarian water content within both breeding groups (figure 41H). Overall, there existed a strong inverse relationship between ovarian size and water content ($r = 0.893^{***}$, $n = 69$).

ii) Hepatopancreas

Seasonal changes in the size of the hepatopancreas for both breeding groups are presented in Figure 42A. A clear cycle emerged for late autumn breeding females. Here hepatopancreas size decreased from January to April, which corresponded with periods of ovarian growth, then increased slowly to a broad peak during August, September and October, followed by a slight decline. A less obvious trend was apparent for early summer breeders (figure 42A overlay). Although there was much individual variation in hepatopancreas size between May and October in this group, mean

Figure 42. Seasonal trends in hepatopancreas cycles of late autumn and early summer (overlay) breeding females during 1975

A Hepatopancreas size

B Energy concentration

C Total energy content

D Lipid concentration

E Total lipid content

F Water content

Figure 42
Seasonal trends ...
Between pp 172,173

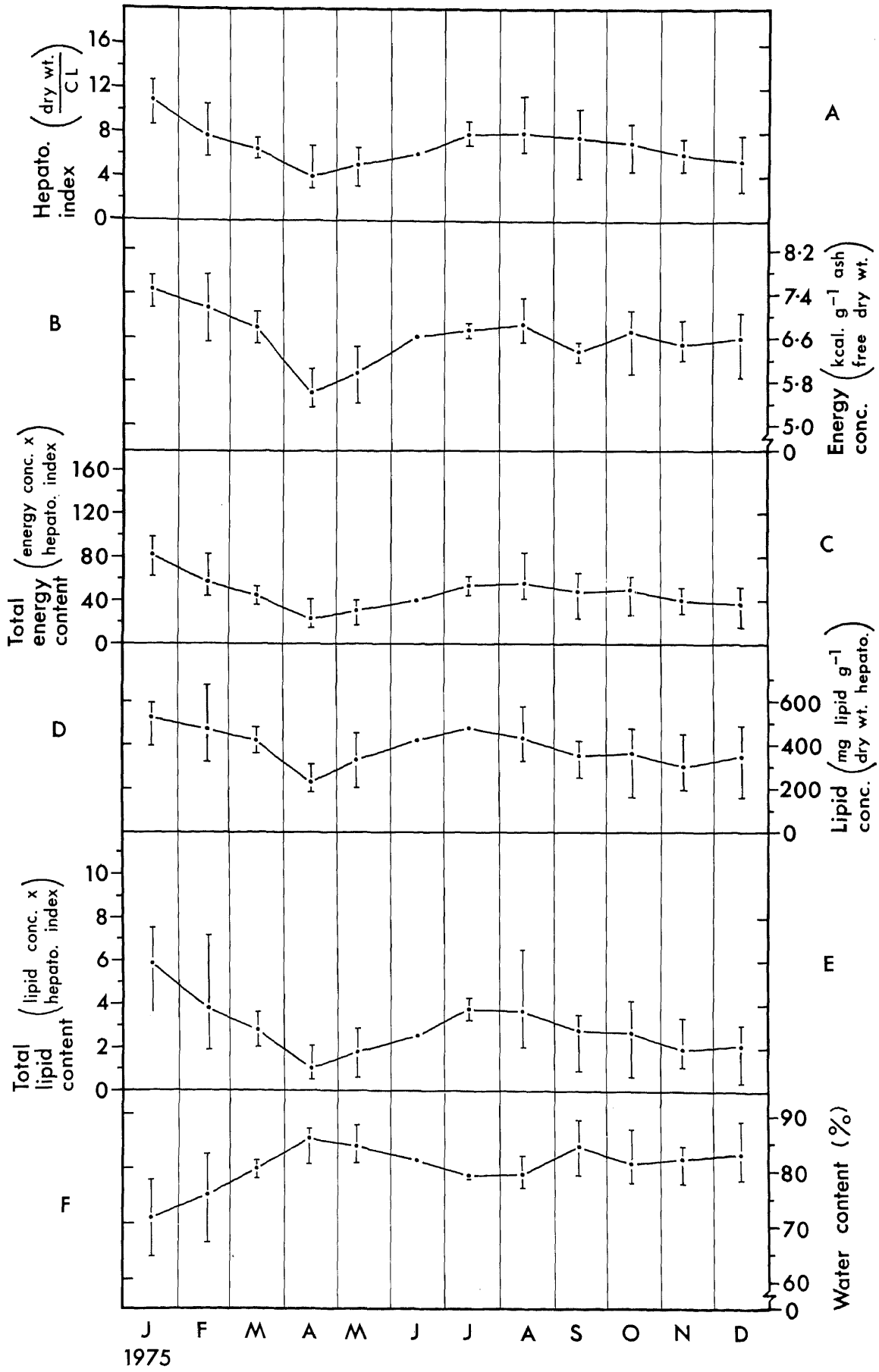
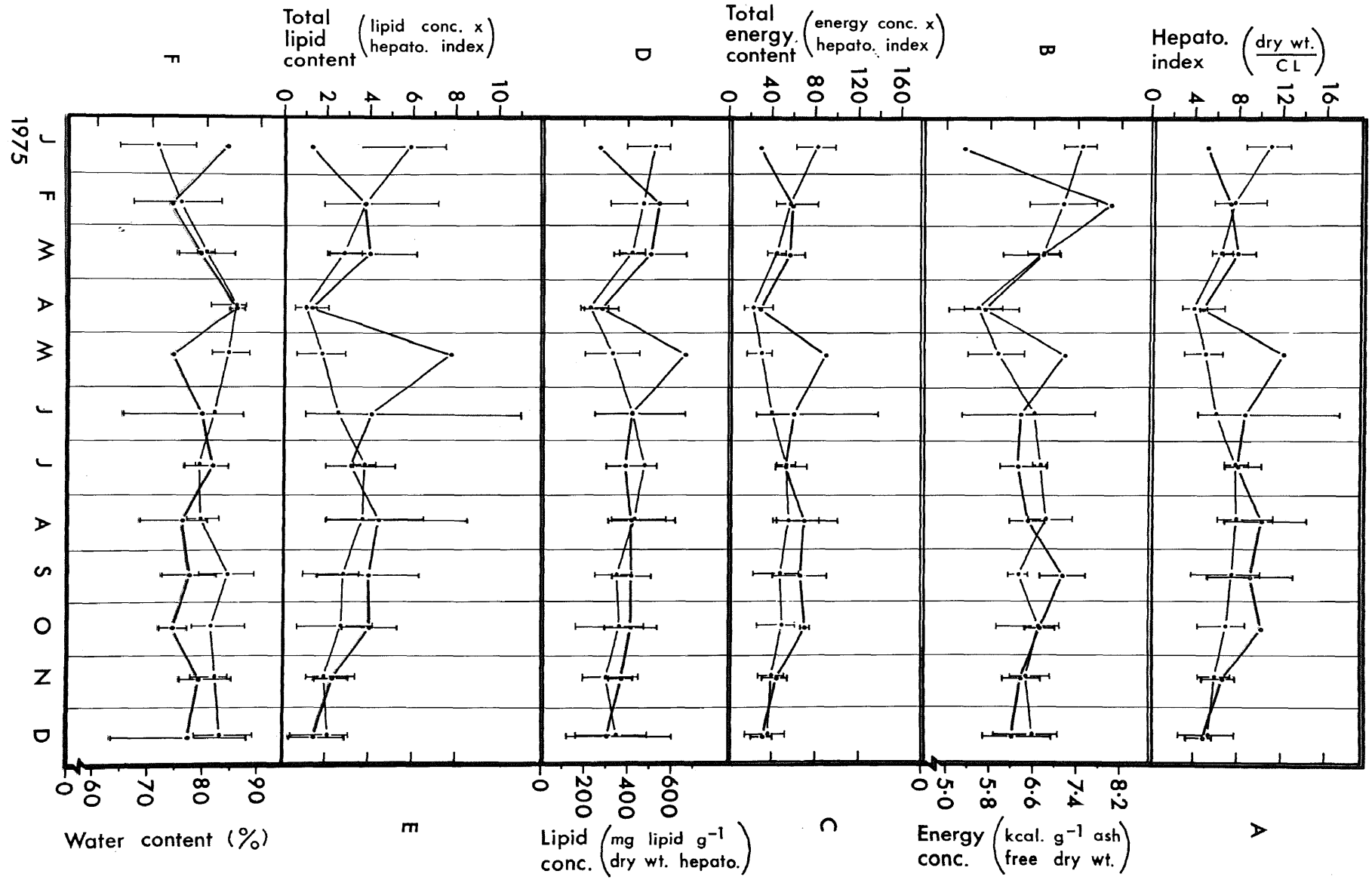


Figure 42
Seasonal trends ...
Between pp 172,173

Figure 42
Seasonal trends ...
Between pp 172,173



monthly sizes tended to remain consistently high over this period. Hepatopancreases were generally smaller throughout the warmer months.

Hepatopancreas energy concentrations varies from 5.22 - 8.20 kcal g^{-1} ash free dry weight of tissue throughout the year. In the late autumn breeders this organ was characterised by a rapid reduction in energy concentration from January to April, followed by an increase until June, after which there were fluctuations within a range of moderate energy concentrations through to December (figure 42B). A clear pattern did not emerge in the earlier part of the year for early summer breeders. From June onwards, energy levels remained fairly steady within a moderate range of concentrations, except for a small increase in September. There was a strong direct relationship between energy concentration and size of hepatopancreas for the female population generally ($r = 0.671^{***}$, $n = 69$).

Trends in total energy content of the hepatopancreas are shown in Figure 42C. Both groups were characterised by large monthly variations between indivisuals but the trends tended to follow those of the hepatopancreas index in Figure 42A. Consequently, there was a strong correlation between hepatopancreas total energy content and size for females as a whole ($r = 0.987^{***}$, $n = 69$).

Lipid constituted 10.3 - 67.2% (average 38.5%) of the dry weight of female hepatopancreases, which was similar to the 25-75% range recorded by Armitage et al

(1972) for *Orconectes nais*. Figure 42D shows seasonal trends in hepatopancreas lipid concentration. For each breeding group the trends resembled those of hepatopancreas size, such that overall there existed a strong correlation between size and lipid concentration ($r = 0.762^{***}$, $n = 69$). Similarly, the trends in total lipid content (figure 42E) and hepatopancreas size were significantly related ($r = 0.932^{***}$, $n = 69$). Trends in hepatopancreas water content for each group are presented in Figure 42F. Overall, there was a strong inverse relationship with hepatopancreas size ($r = -0.749^{***}$, $n = 69$).

iii) Muscle and carapace

The energy concentration of abdominal muscle of females was typically low and varied between 5.07 and 5.80 kcal g^{-1} ash free dry weight of tissue. Figure 43A indicates the seasonal distribution of energy levels of muscle for both breeding groups. There was a close similarity between the two groups, with the highest levels occurring over summer until March, followed by low concentrations during autumn. Concentrations gradually increased over the winter months and moderate levels prevailed through spring and early summer.

The seasonal pattern of muscle lipid concentration was nearly identical for the 2 groups of breeding females (figure 43B). There were 3 distinct peaks in concentration throughout the year; in midsummer, midautumn and midspring. Values were low over winter.

Figure 43. Seasonal trends in abdominal muscle energy (A) and lipid (B) concentration and water content (C), as well as carapace water content (D) for late autumn and early summer (overlay) breeding females during 1975.

Figure 43
Seasonal trends ...
Between pp 174,175

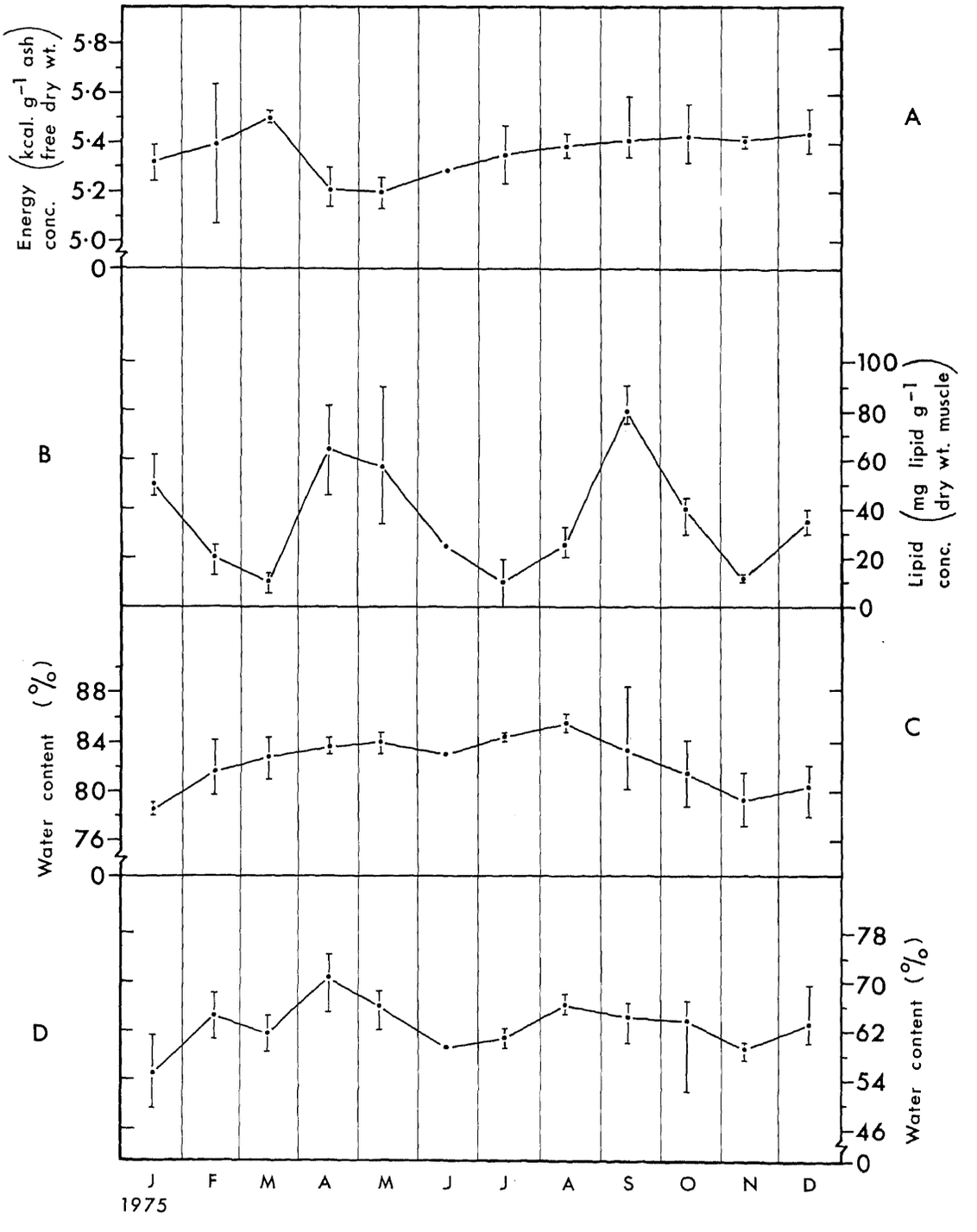
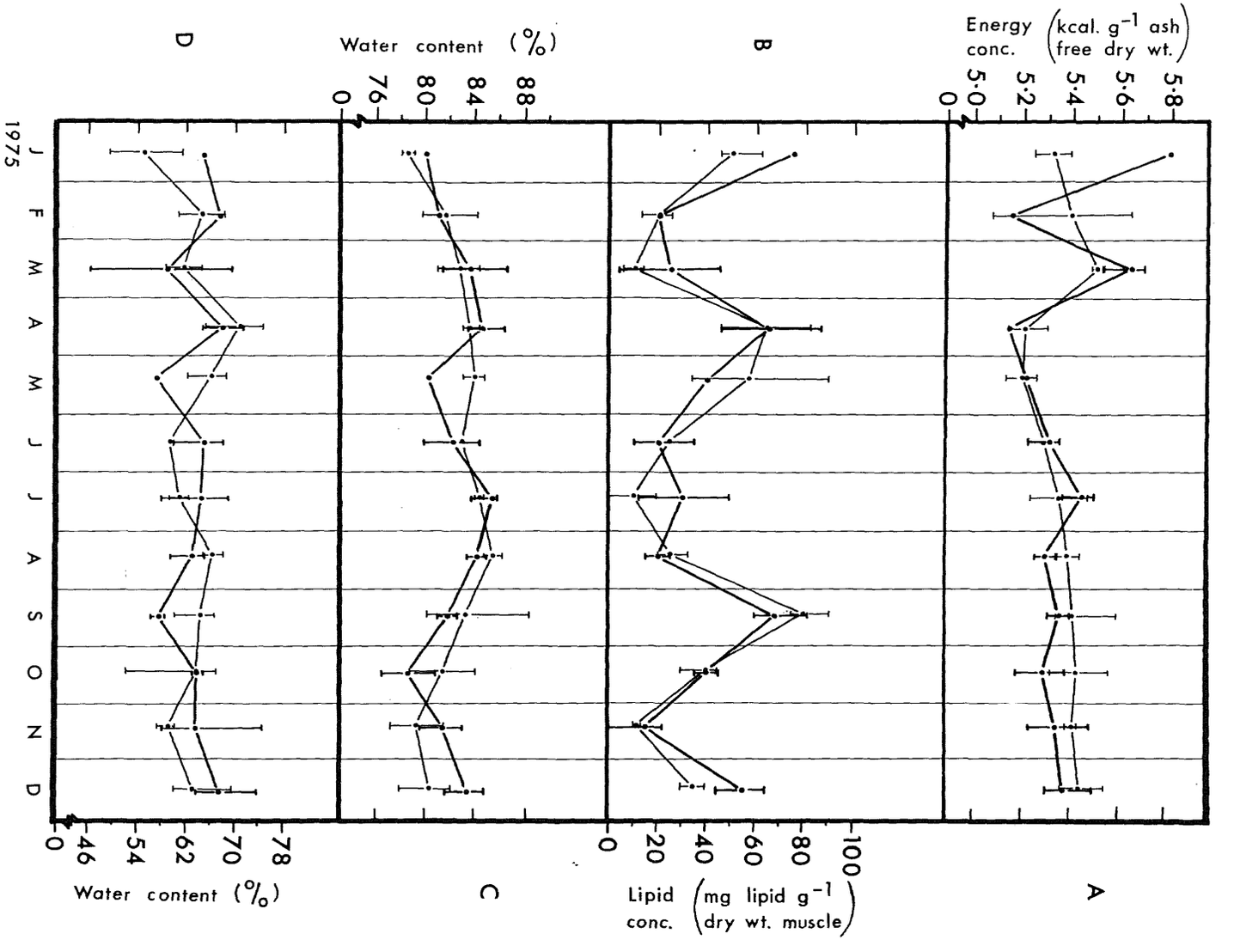


Figure 43
Seasonal trends ...
Between pp 174,175

Figure 43
Seasonal trends ...
Between pp 174,175



The lipid concentration of muscle was generally low and ranged from 0 - 8.9% (average 3.7%) of its dry weight.

There also appeared to be a close similarity in seasonal trends of muscle water content between each group, with the exception that the timing of events was delayed by about a month in late autumn breeders (figure 43C). Generally, muscle water content was high during autumn and late winter and lowest in late spring and summer.

Apart from a possible exception from January through to April for late autumn breeders, there were no apparent seasonal trends in carapace water content for both breeding groups (figure 43D). High values in April for late autumn breeders and in November and December for early summer breeders probably indicated periods of prebreeding moult activity. However, timing of postbreeding moult activity was not clearly evident. Perhaps upper range values in February and December, and in March and April, and possibly also June and July, indicate postbreeding moults of late autumn and early summer breeders respectively.

Any mobilisation of organic reserves into the ovaries was most likely to have occurred during rapid ovarian growth, rather than at any other stage of the reproductive cycle. Of the two breeding groups, the early summer breeders were probably the more likely to have utilised stored reserves. This belief is based on the fact that feeding activity was some 40% lower throughout their

period of rapid ovarian growth compared with the equivalent period for late autumn breeders. (This figure was determined from the difference in the number of females trapped in 1975 throughout periods of ovarian growth of each group; December - April for late autumn breeders, June - November for early summer breeders). Furthermore, early summer breeders did not take advantage of the rich, littoral zone feeding ground to the same extent as late autumn breeders (see later) and consequently may have expended more energy at foraging.

As a means of ascertaining whether the ovaries received nutrients from the hepatopancreas, relationships between each organ's size, energy and lipid contents were tested for significance. Energy and lipid were considered in terms of concentration and total amount. Also, associations between ovaries and abdominal muscle were tested in terms of energy and lipid concentration. Only females with gonads over 25% developed (ie. ovarian index >3.5) were tested. This included 17 late autumn and 18 early summer breeders. The relationships and their associated correlation coefficients are presented in Table 47.

Significant inverse relationships would have implied a transfer of reserves into the ovaries. However, it was evident from the results that neither energy per se nor lipid were transferred in significant quantities from the hepatopancreas or muscle of females within either breeding group. Consequently, it would seem that females generally obtained at least a large proportion of the

Table 47: The relationship between ovarian size and hepatopancreas size, and tests for the redistribution of energy and lipid from the hepatopancreas and abdominal muscle into the ovaries during times of rapid ovarian growth.

Relationship			Late autumn breeders (N=17)	Early summer breeders (N=18)
ovary index	vs	hepato. index	$r = 0.012^{ns}$	$r = 0.427^{ns}$
ovary [energy]	vs	hepato. [energy]	$r = 0.762^{***}$	$r = 0.128^{ns}$
ovary total energy	vs	hepato. total energy	$r = 0.120^{ns}$	$r = 0.428^{ns}$
ovary [energy]	vs	muscle [energy]	$r = 0.048^{ns}$	$r = 0.236^{ns}$
ovary [lipid]	vs	hepato. [lipid]	$r = 0.258^{ns}$	$r = 0.083^{ns}$
ovary total lipid	vs	hepato. total lipid	$r = 0.270^{ns}$	$r = 0.336^{ns}$
ovary [lipid]	vs	muscle [lipid]	$r = -0.197^{ns}$	$r = -0.357^{ns}$

nutrients necessary for ovarian growth directly through feeding with little if any, contribution from stored reserves. However, in both breeding groups ovarian lipid concentrations were very high just before the onset of rapid gonadal growth (November for late autumn breeders and May for early summer breeders, figure 41F) and decreased shortly after. Therefore, it may be that these reserves are utilised during early oocyte production.

In both breeding groups hepatopancreas lipid concentrations declined as the ovaries developed (figures 41C and 42D). Collatz (1969) [cited in Armitage et al (1972)] found a similar relationship for *Orconectes limosus* and suggested that lipid was transferred from the hepatopancreas into the ovaries. However, this was not apparent in *P. planifrons* for there was no reciprocal increase in ovarian lipid concentration (figure 41F and table 47). Armitage et al (loc. cit.) considered that the decline in lipids within the hepatopancreas of *O. nais* during ovarian development, may have been due to an increase in metabolic needs associated with greater summertime activity. This could also apply to *P. planifrons* females over the warmer months, especially the autumn breeders. However, it was also likely that concurrent higher levels of feeding activity served to compensate for any increased energy expenditure.

The seasonal pattern of energy content of the hepatopancreas may be more closely associated with the moult cycle than the reproductive cycle. Passano (1960a) states that reserves stored in the hepatopancreas of decapods are used to meet the special demands for

materials and energy during moulting; a period when feeding ceases. Nearly all of the organic reserves that accumulate throughout intermoult are used up during this fasting period, being utilised for both general tissue maintenance and demands associated with construction of a new exoskeleton.

The possible influence of the moult cycle on energy reserves within the hepatopancreas may be best illustrated in late autumn breeding females. In the underlay of Figure 43D the high carapace water contents in April and December probably indicate pre and postbreeding moults respectively. Figure 42C shows that at these times hepatopancreas energy contents were low but generally higher for the intermoult periods between these dates. Further evidence was obtained by relating carapace water content [a means of staging the moult cycle (Drach 1939)] with hepatopancreas energy concentration for the total female population ($r = -0.434^{***}$, $n = 69$).

To test the extent to which muscle energy reserves were associated with the moult cycle in females, the relationship between carapace water content and muscle energy concentration was determined ($r = -0.208^{ns}$, $n = 69$). Although no significant relationship was found, the negative value of r suggested some reciprocal transfer of metabolites.

According to Armitage et al (1972) crayfish in temperate regions generally store nutrients prior to winter dormancy. Although feeding activity in female *P. planifrons* was markedly suppressed between May and

August in 1975 they never became completely dormant. In April the hepatopancreases of late autumn breeders were small and low in lipid at this time (figure 42E), which suggests that no prewinter storage of lipids occurred within this breeding group. Curiously, lipid levels rose to a maximum in July and August, which showed that storage of food reserves was possible even when conditions were least favourable. By contrast, between April and May, lipid within the hepatopancreases of early summer breeders increased greatly (figure 42E overlay), then slowly decreased over the colder months. Their prewinter increase in hepatopancreas lipid may have been at least partly due to the greater metabolic demands associated with ovarian growth throughout winter and spring.

The seasonal difference in timing of ovarian development was interesting with regard to the nature of the environmental factors controlling this process. Various workers have shown that although ovarian growth in crayfish can occur over a wide range of temperatures and photoperiods, complete maturation (as determined by the laying of eggs) generally requires these factors in a particular combination. For example, Aiken (1969a) found in *Orconectes virilis* that although ovarian maturation occurred under the contrasting conditions of warm water and darkness, cold water and long day photoperiods, and cold water and darkness, egg laying resulted only under the last set of conditions.

Figures 41A, 41B and 41C indicated that ovarian

growth, resulting in egg laying, occurred equally well under the contrasting seasonal conditions of long day photoperiods and high temperatures (late autumn breeders), and short day photoperiods and low temperatures (early summer breeders). Whether or not the ovaries of individuals were able to mature over the full range of temperatures and photoperiods experienced in situ was not determined, however, the results presented in Figure 41C would tend to suggest that this was not so. It seems therefore, that late autumn and early summer breeding *P. planifrons* may differ in their physiological responses to these parameters. If this is correct, then it may be that short day photoperiods and low temperatures, and long day photoperiods and high temperatures do not achieve threshold levels necessary to sustain ovarian growth in late autumn and early summer breeders, respectively.

The ovaries in both breeding groups did not grow appreciably while females carried eggs and young. Since most gonad production was apparently derived directly from feeding activity rather than from stored reserves, this lack of growth could be explained by a similar decrease in feeding activity to that for *Cambarus immunis* (Tack 1941) and *Astacus astacus* (Abrahamsson 1966) females when gravid. However, there was evidence (table 11, p. 44) that female *P. planifrons* do not reduce their feeding activity when gravid, so the timing of negligible ovarian growth and period of motherhood would appear to be somewhat coincidental.

b) Males

i) Testes

Annual changes in size, energy, lipid and water content of the testes are presented in Figure 44. Figure 44A implies that individual males bred during only one of the two breeding periods. Both breeding periods were long. The testes of late autumn breeders remained ripe for 6-7 months, from around February until August, with maximal development between April and June. In the early summer breeders testes were ripe for the 5-6 months between August and February, with peak sperm production occurring in November and December.

Testicular energy concentrations varied between 5.02 and 6.06 kcal g^{-1} ash free dry weight testes (figure 44B) and in late autumn breeders, were highest during summer but decreased rapidly in March. Levels remained low over the period of sperm production, then gradually increased through to December. No distinct seasonal trends were found in early summer breeders. Overall, testicular energy concentrations showed a negative relationship of low significance with gonad size ($r = -0.242^{*}$, $n = 72$). By contrast, the annual cycle of total energy content of the testes within both breeding groups (figure 44C) closely agreed with respective trends in gonad size. The high value of r indicates the strength of this relationship ($r = 0.964^{***}$, $n = 67$).

Lipid comprised 1.4 - 37.5% (average 10.6%) of the testes dry weight. Figure 44D shows that concentrations

Figure 44. Seasonal trends in testicular cycles of late autumn and early summer (overlay) breeding males during 1975.

A Testicular size

B Energy concentration

C Total energy content

D Lipid concentration

E Total lipid content

F Water content

The number of late autumn and early summer breeders analysed each month is given as follows and applies also to Figures 45 and 46.

	J	F	M	A	M	J	J	A	S	O	N	D
LAB	3	3	3	3	6	5	4	3	2	3	2	2
ESB	2	3	2	3	0	1	2	3	4	3	2	3

Figure 44
Seasonal trends ...
Between pp 182,183

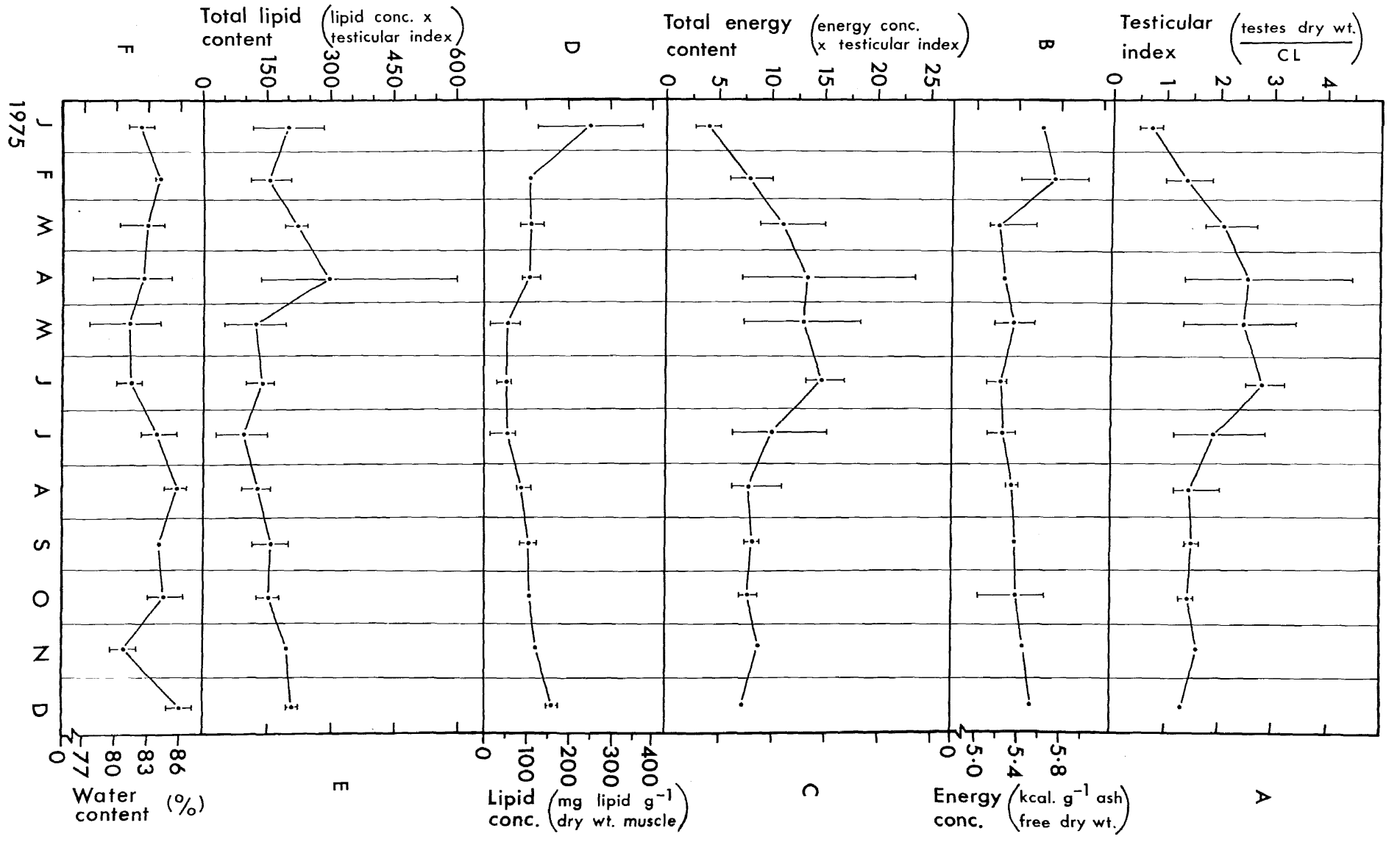
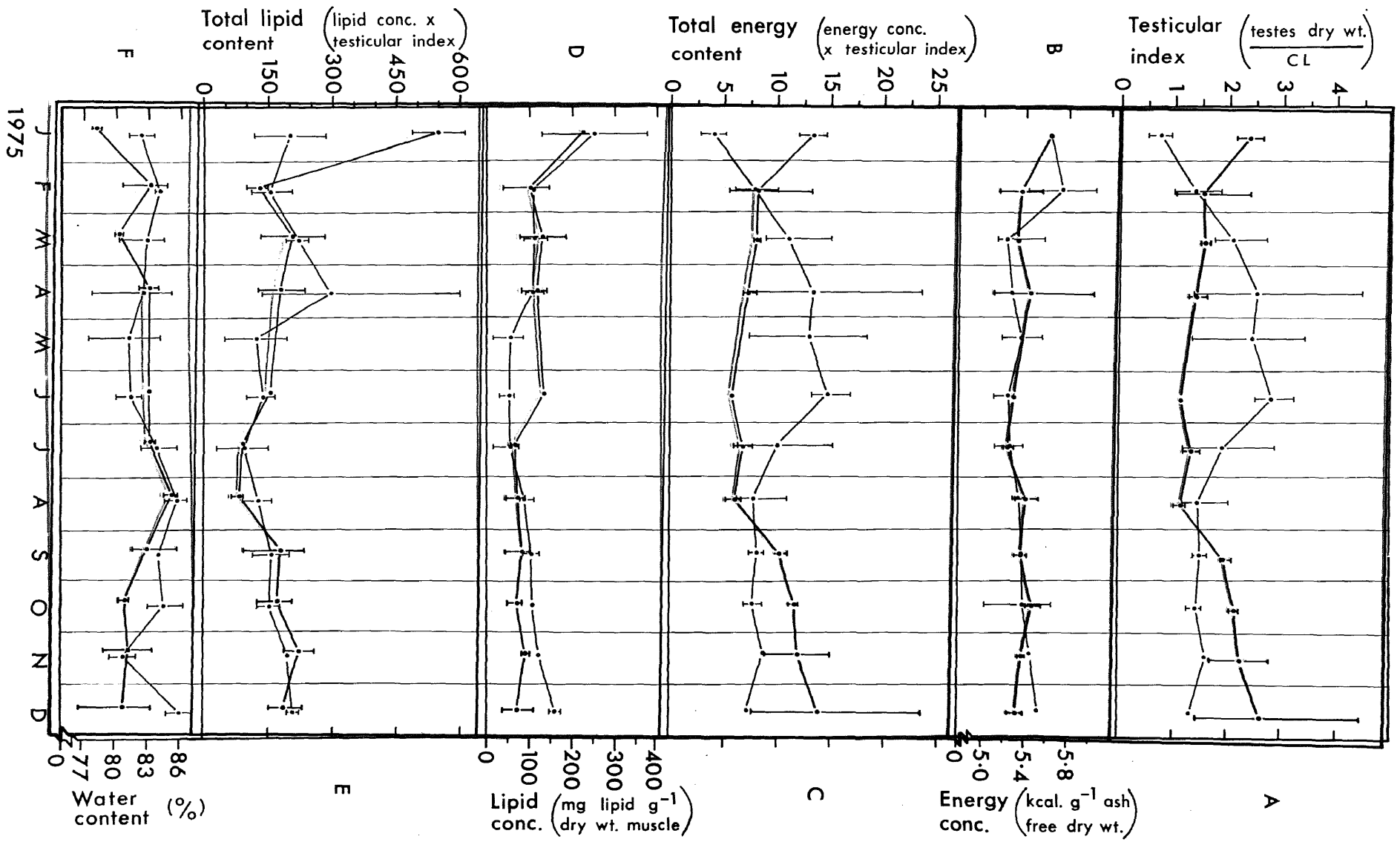


Figure 44
Seasonal trends ...
Between pp 182,183

Figure 44
Seasonal trends ...
Between pp 182,183



were highest in January but had dropped abruptly by February for both groups. Values remained low during the breeding period of late autumn breeders, then slowly increased between August and December. The relationship between testicular lipid concentrations and gonad size for the whole population was inverse and of moderate significance ($r = -0.347^{**}$, $n = 71$).

Total lipid content of the testes was generally a little lower in winter than during other seasons (figure 44E). There was, however, an exception in January for early summer breeders, when values were considerably higher. Since the testes increased in size over the breeding periods, their total lipid contents were expected to be somewhat higher than indicated by Figure 44E. This may have been at least partly due to the inclusion of individuals who had mated shortly before capture and so had empty or near empty testes. Even so, there did exist a direct relationship of moderate significance between gonad size and total lipid content overall ($r = 0.354^{**}$, $n = 66$).

Water occupied between 77% and 87% of the testes wet weight. Generally, water content was highest over the periods of greatest gonad development (figure 44F). In consequence, the relationship between testicular size and water content was inverse and strongly significant ($r = -0.639^{***}$, $n = 72$).

ii) Hepatopancreas

Seasonal changes in hepatopancreas size within each breeding group are illustrated in Figure 45A. Despite large monthly variations between individual late autumn breeders there existed a definite trend. On average, hepatopancreases were large from late spring until midautumn and small over winter. This pattern was in contrast to the generally large hepatopancreases within early summer breeders from June - October and a reduction in size between November and April.

Within each breeding group the seasonal fluctuations in hepatopancreas energy concentration (figure 45B), total energy content (figure 45C), lipid concentration (figure 45D) and total lipid content (figure 45E), were essentially in accord with trends in hepatopancreas size. For the total male population the relationships between each of these parameters and hepatopancreas size were all direct and strongly significant. They are as follows: energy concentration ($r = 0.695^{***}$, $n = 72$), total energy content ($r = 0.987^{***}$, $n = 67$), lipid concentration ($r = 0.753^{***}$, $n = 72$), total lipid content ($r = 0.938^{***}$, $n = 67$). Hepatopancreas energy content varied between 5.11 and 8.05 kcal g^{-1} ash free dry weight of organ. Lipid constituted 8.1 - 65.7% (average 36.1%) of the hepatopancreas' dry weight.

Monthly changes in hepatopancreas water content

Figure 45. Seasonal trends in hepatopancreas cycles of late autumn and early summer (overlay) breeding males throughout 1975.

A Hepatopancreas size

B Energy concentration

C Total energy content

D Lipid concentration

E Total lipid content

F Water content

Figure 45
Seasonal trends ...
Between pp 184,185

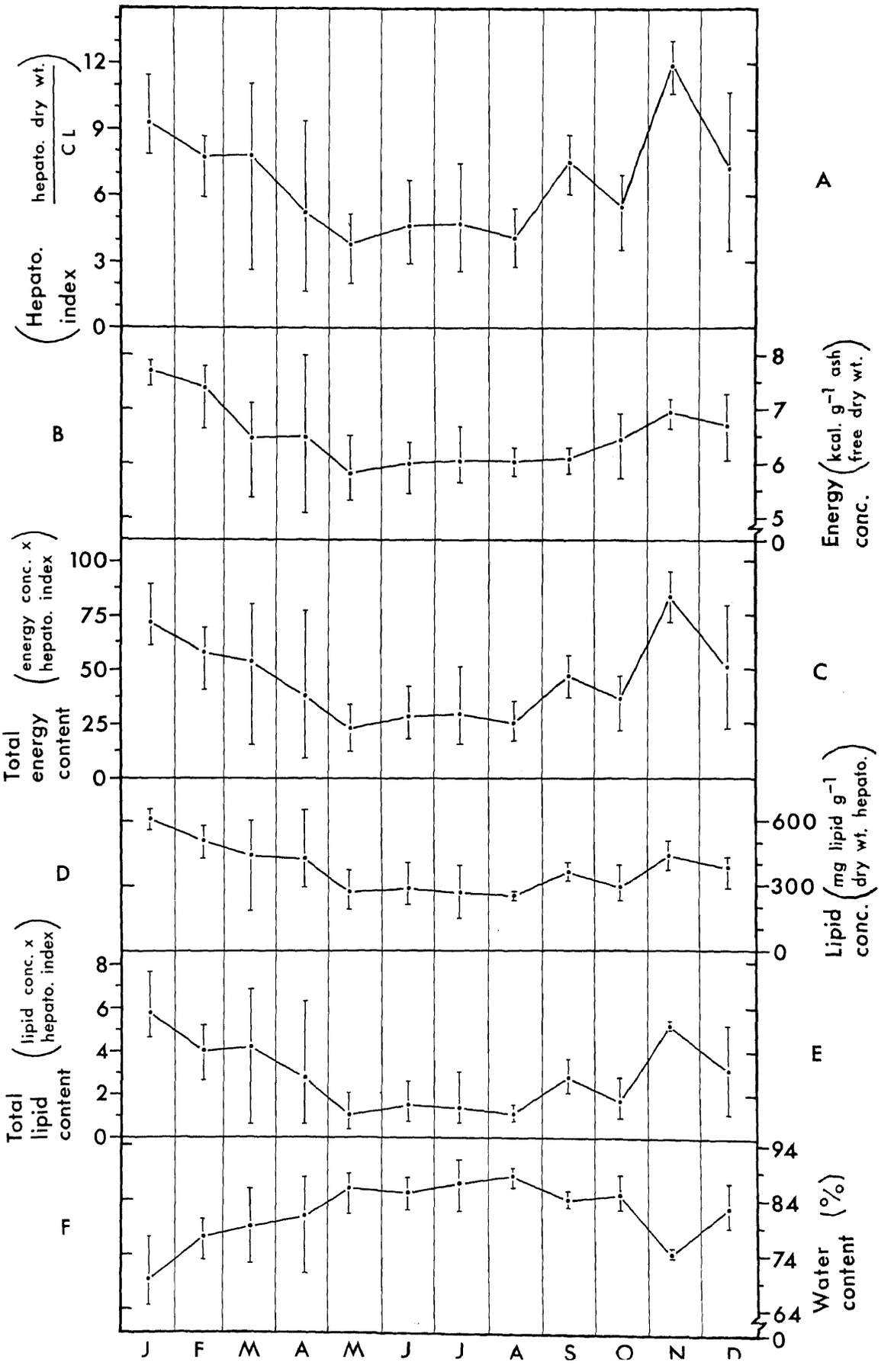
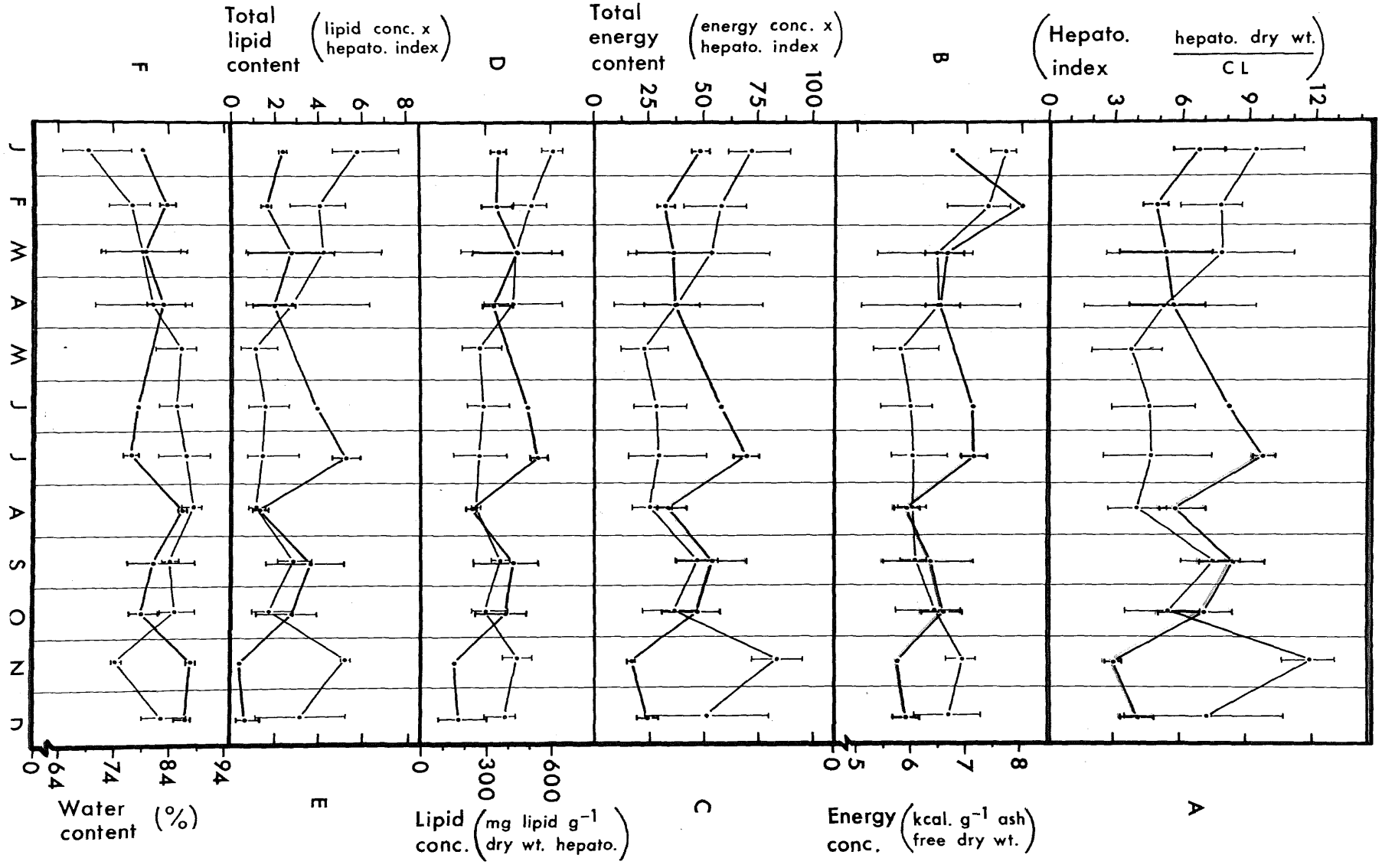


Figure 45
Seasonal trends ...
Between pp 184,185

Figure 45
Seasonal trends ...
Between pp 184,185



for each breeding group are shown in Figure 45F. Overall, hepatopancreas water content showed a strongly significant inverse relationship with hepatopancreas size ($r = -0.814^{***}$, $n = 72$).

iii) Muscle and carapace

The energy concentration of muscle varied from 5.00 - 5.92 kcal g^{-1} ash free dry weight of muscle tissue. Figure 46A indicates that for early summer breeders the muscle concentrations were high in autumn and the late spring/early summer period. Values were fairly low over the colder months. No seasonal trend was apparent for late autumn breeders.

Muscle lipid concentrations were typically low, constituting 0 - 12.7% (average 4.8%) of the dry weight. Seasonal trends in lipid concentration are shown in Figure 46B and indicate an overall similarity between the two breeding groups. There were 3 more or less distinct peaks in lipid concentration; in midsummer, late autumn and spring.

Seasonal patterns in muscle water content were also similar for both breeding groups (figure 46C). Water contents were typically low over summer and highest in midwinter.

There was no obvious seasonal variation in water content of the carapace in late autumn breeders (figure 46D underlay). However, upper range values in February, April, June, August, October and December may indicate moulting of individuals. The generally high carapace water contents in early summer breeders

Figure 46. Seasonal trends in abdominal muscle energy (A) and lipid (B) concentration and water content (C), as well as carapace water content (D) for late autumn and early summer (overlay) breeding males during 1975.

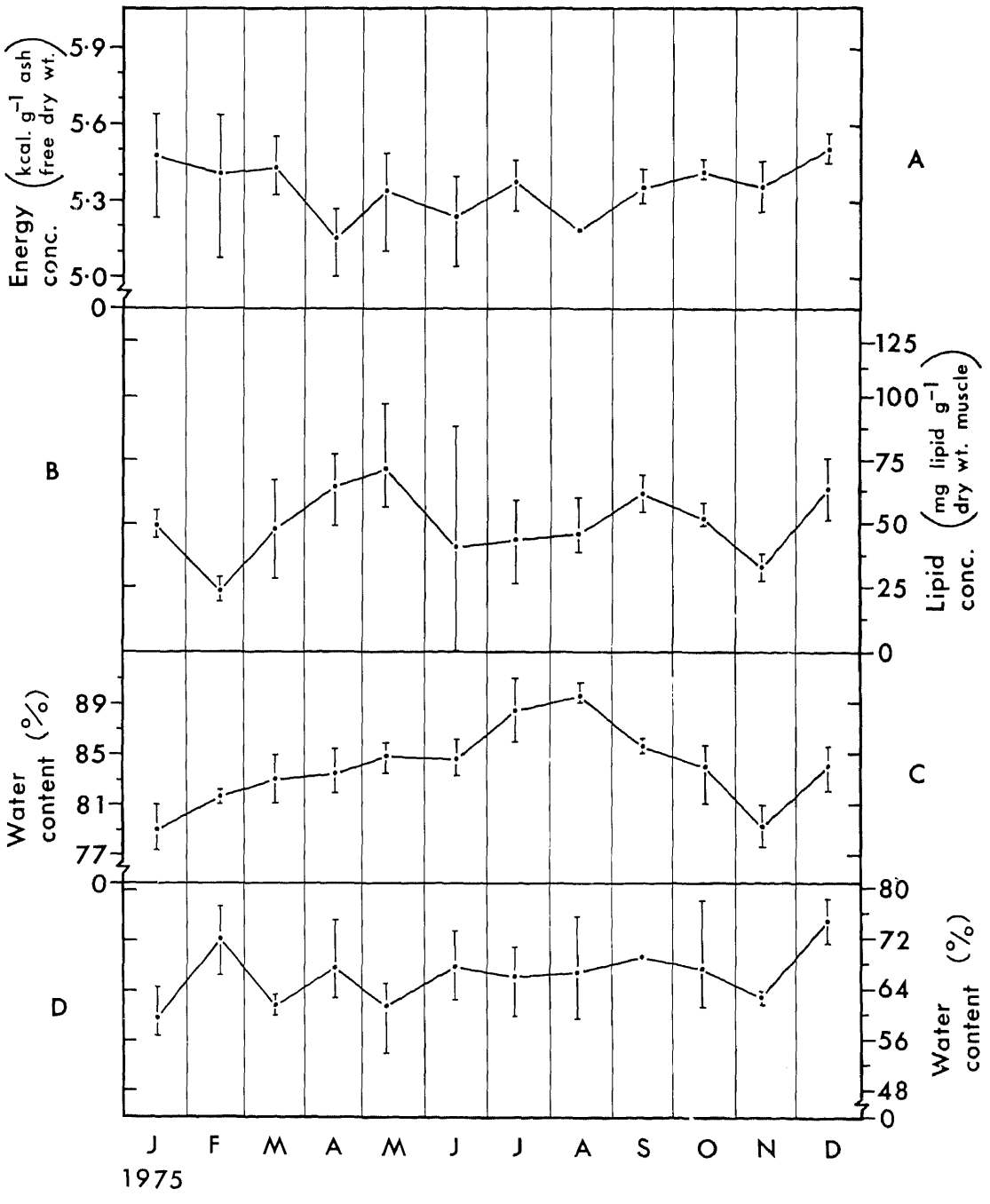


Figure 46
Seasonal trends ...
Between pp 185,186

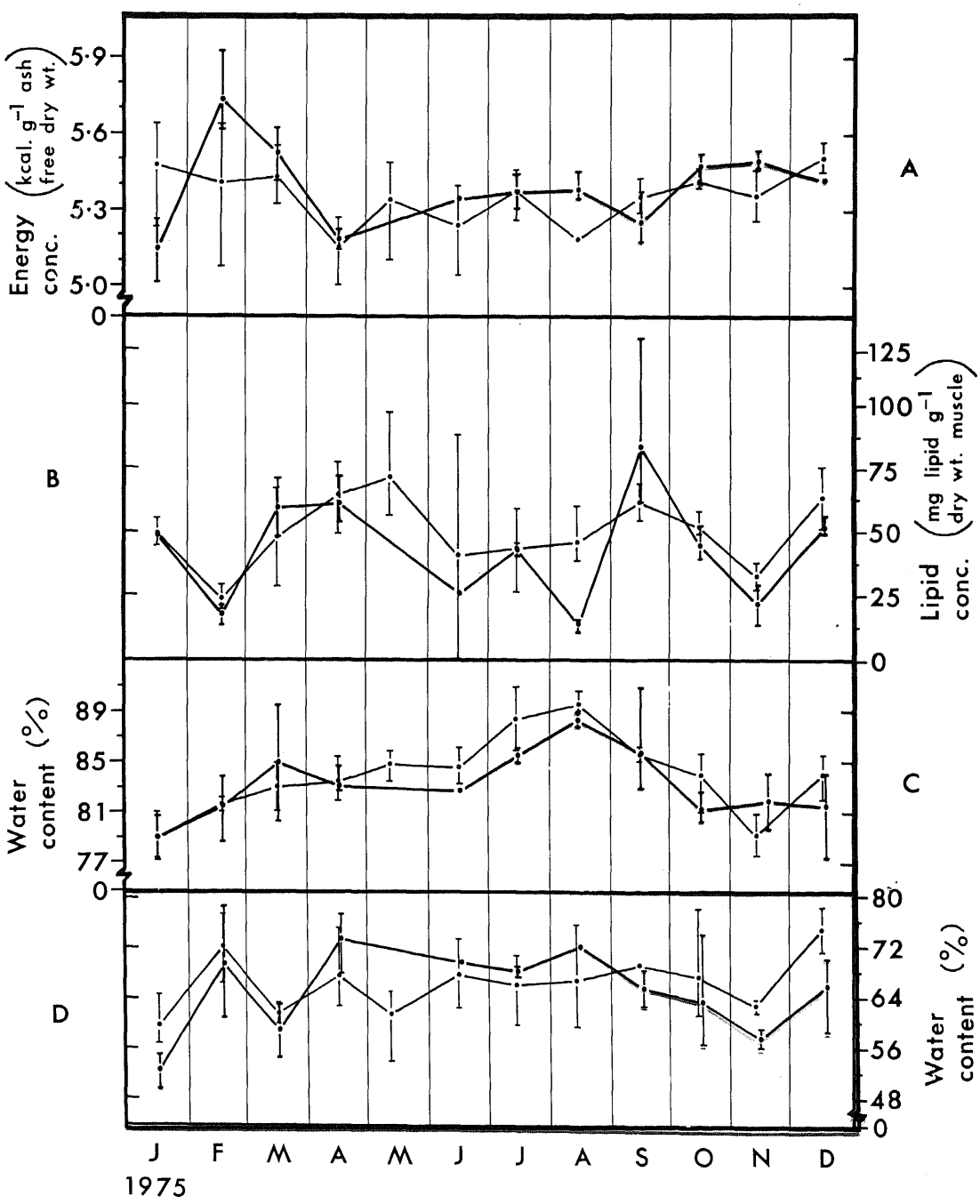


Figure 46
Seasonal trends ...
Between pp 185,186

Figure 46
Seasonal trends ...
Between pp 185,186

from April - August and in February, October and December suggested that moulting occurred at all seasons.

By applying the technique already described for females to males (table 47), the relative importance of the hepatopancreas and abdominal muscle as sources of nutrient supply to the testes was assessed (table 48). This was done during periods of sperm production and included 23 late autumn and 15 early summer breeding males. As with females no significant inverse relationships were found. Therefore, it would seem there was no great reliance on storage organs to furnish maturing testes with either energy generally, or more specifically, with lipid.

The higher negative value of r for gonad size and hepatopancreas size by early summer breeders, suggested that this group made greater use of the hepatopancreas for gonad development than did the late autumn breeders. In early summer breeders the total energy contents of these organs were inversely related but not their total lipid contents. This implied that nutrients other than lipids may have been mobilised from the hepatopancreas. If so, these were likely to be proteins, since Armitage et al (1972) found that proteins constitute a significant part of the testes of *Orconectes nais* during spawning.

The possible regulatory effect of the moult cycle on seasonal changes within the hepatopancreas of males was tested by relating energy concentration of the hepatopancreas with carapace water content ($r = -0.060^{ns}$,

Table 48: The relationship between testis size and hepatopancreas size, and tests for the transfer of energy and lipid from the hepatopancreas and abdominal muscle into the testes during periods of sperm production.

Relationship			Late autumn breeders (N=23)	Early summer breeders (N=15)
testes index	vs	hepato. index	$r= -0.050^{ns}$	$r= -0.222^{ns}$
testes [energy]	vs	hepato. [energy]	$r= -0.045^{ns}$	$r= 0.555^{*}$
testes total energy	vs	hepato. total energy	$r=-0.009^{ns}$	$r= -0.209^{ns}$
testes [energy]	vs	muscle [energy]	$r= -0.063^{ns}$	$r= 0.019^{ns}$
testes [lipid]	vs	hepato. [lipid]	$r= 0.626^{**}$	$r= 0.077^{ns}$
testes total lipid	vs	hepato. total lipid	$r= 0.591^{**}$	$r= 0.055^{ns}$
testes [lipid]	vs	muscle [lipid]	$r= -0.238^{ns}$	$r= 0.065^{ns}$

n = 72). The association with abdominal muscle was similarly tested ($r = 0.002^{ns}$, n = 72). Both relationships were statistically insignificant, which may indicate that the moult cycle had very little influence on the mobilisation of nutrients to and from either of these storage organs.

Unlike females, males did not reduce their feeding activity over the colder months. These findings were based on the number of crayfish trapped per month and actually indicated that male feeding activity was some 37% higher from May - October than between November and April. However, this value was probably somewhat exaggerated because of the reduced feeding activity of females over this period, which meant that relatively more males could enter traps. Furthermore, the longer scotoperiod in winter meant a longer feeding and hence trapping time compared to summer. Consequently, it appeared unlikely that males needed to store nutrients prior to winter. Evidence in support of this comes from the fact that in April and May the size, energy and lipid contents of the hepatopancreas for the male population (figure 46) were generally low.

Overall, it would seem that for each sex of both breeding groups the gonads do not rely on nutrients stored in the hepatopancreas or abdominal muscle to furnish their growth, but more probably obtain the necessary materials directly from the food consumed. This is possible since feeding activity is continuous throughout the year, although somewhat reduced in females over the colder months. It may be because of this decrease

in feeding activity that cyclic changes in energy within the hepatopancreas especially, and to a far lesser extent muscle, are associated with the moult cycle in females. Meanwhile males do not show the same reduction in feeding activity over winter, which may explain why their storage organs do not share a similar relationship with the moult cycle.

c) The two breeding groups

Late autumn and early summer breeding *P. planifrons* within L. Rotoiti were separable not only temporally, as evidenced above by the difference in timing of events associated with their reproductive cycles especially, but also spatially (table 49). Table 49 shows that for both sexes the late autumn breeders dominated waters above 10 m depth and the early summer breeders occurred almost exclusively below 20 m depth at night, throughout the year. The results illustrate differences in the feeding habits of individuals between each breeding group: late autumn breeders tended to feed within the rich littoral zone feeding ground, whereas early summer breeders fed mainly below 20 m depth, where food was some 80% less concentrated. Reasons for the difference are not clearly evident, however, one possibility is that overall energy requirements differed for each breeding group.

Since *P. planifrons* appeared to make little use of its stored energy supply to furnish the various metabolic processes (with a possible exception at ecdysis), it

Table 49: Overall annual depth distribution at night of crayfish comprising the 2 breeding groups. The upper set of values was derived from crayfish collected for the analyses already presented in this section and the lower set of values was determined from females trapped between January 1975 and December 1976. Here the 2 breeding groups were separated by relating the egg index of eggs carried by females and females with empty egg shells attached to pleopods, to the time of year.

Depth range (m)	Sex	Late autumn breeders N	%	Early summer breeders N	%
1-10	M	25	64.1	7	25.0
"	F	29	74.4	6	20.0
30-50	M	14	35.9	21	75.0
	F	10	25.6	24	80.0
1-10	F	158	70.5	14	10.8
20-50	F	66	29.5	116	89.2

was reasonable to assume that most of the necessary energy came directly from food consumed. Furthermore, considering that food was about 80% more concentrated within the littoral zone, it seemed feasible that crayfish would tend to feed within this zone during periods of high energy requirement. These periods were most likely to occur when major metabolic processes such as reproductive growth, general body growth and tissue maintenance were operating at maximum levels. Hopkins (1966; 1967b) showed that general body growth occurred mainly during the warmer months, especially for female *P. planifrons* and Whittle (1973) indirectly demonstrated that energy expenditure for tissue maintenance increased as temperature increased. Therefore, for late autumn breeding females, all three metabolic processes would have operated maximally during the warm period between December and April. As a result the overall energy demands were likely to be very high during this period and may account for their pronounced feeding activity within the littoral zone during that period. In contrast, these metabolic processes never operated at maximum levels in the early summer breeding females, for reproductive growth occurred when temperatures were low. As a result a similar peak in energy needs did not occur, so there was possibly less need for such females to make the post dusk migration into the littoral zone to feed.

However, this argument does not explain the differences in distribution between the males of the two groups. Since

testicular growth occurred within similar temperature ranges for both breeding groups and as energy requirements for general body growth and tissue maintenance were probably more or less standard for each group, it follows that each group's peak energy demand and hence feeding distribution pattern, was unlikely to have differed significantly.

A more general explanation could centre around the existence of certain behavioural differences causing the physical isolation of the two breeding groups. Early summer breeders showed little tendency to migrate into the shallows at night, suggesting that the mechanism(s) controlling post dusk migratory activity was (were) either absent in this group, or operated less effectively than in the late autumn breeding population. It may be that the late autumn breeding population is physiologically adapted to diel migratory activity (according to the diel model of spatial distribution, figure 11, following p. 54), which enables the utilisation of food produced in the littoral zone, while the early summer breeding population is better adapted to an existence in deeper zones. One consequence of differing adaptations such as these, would be to enable the total crayfish population to fully utilise the whole lake floor as a feeding ground.

PREDATORS

Known predators of *P. planifrons* include shags (Falla and Stokell 1945, Dickinson 1951, Duncan 1968, Potts 1972), trout (Smith 1959), eels (*Anguilla dieffenbachii* and *A. australis schmidtii*; Cairns 1950), the kingfisher *Halcyon sanctus* (Oliver 1974) and man. This list may also include the scaup (*Aythya novaeseelandiae*) which feeds on crustacea (Oliver loc. cit.). In decreasing order of importance the 3 major predators within the study area appear to be shags and trout (plates 16 and 17 respectively) and man.

The shag is believed to be the only endemic predator of any consequence. Three species reside in the Rotorua lakes district and, in decreasing order of abundance, are *Phalocrocorax melanoleucos* (=*P. brevirostris*), *P. sulcirostris* and *P. carbo* (Potts 1972). Shags are excellent divers and Potts comments that *P. melanoleucos* dives most efficiently above 3 m depth but also forages at greater depths. Supportive evidence was obtained by the present author who found a shag (possibly *P. melanoleucos*) enmeshed in a net set at a depth of 10 m off the Coromandel Coast of the North Island in 1972.

According to Potts (loc. cit.) shags do not feed at night and Falla and Stokell (1945) comment that feeding occurs at irregular intervals throughout the day. Unless shags actually dislodge the shelters containing crayfish, it would appear unlikely that significant numbers of crayfish are taken during the daytime. However, shags

Plate 16. Shags. *Phalocrocorax carbo*

Plate 17. Trout. *Salmo gairdnerii*

Plate 16
Shags
Between pp 193,194

Plate 17
Trout
Between pp 193,194

were observed foraging up to 1 hour after dusk, by which time many crayfish within the shallows have emerged from shelters and the littoral zone has received its first arrivals from the high density band. Thus, it seems more likely that the greatest predatory impact by shags occurs around this time and similarly in the hour before dawn.

Seasonal predatory pressures by shags appeared to be relatively constant, for during nearly every monthly visit to L. Rotoiti in 1975 and 1976, as well as on other occasions, regurgitated shag pellets composed almost entirely of crayfish parts were found on the University Field Station jetty. Further evidence comes from Potts (1972) who analysed the stomach contents of 255 shags collected from nearby Lakes Rotorua and Rotoehu. He found no apparent seasonal difference in the quantity of crayfish consumed, even though fewer shags occupied L. Rotoehu during the winter months. One of those individuals contained 13 crayfish. Dickinson (1951) reported that large quantities of *P. planifrons* were taken from Lakes Rotoiti and Rotorua in July and that shags would often feed solely on crayfish for a period.

Based on the size of gastroliths collected at the nesting sites of *Phalocrocorax carbo*, Scott and Duncan (1967) deduced that this species consumed *Paranephrops zealandicus* up to 12 cm in length. This was near the maximum size attained by *P. planifrons* in L. Rotoiti, therefore shags probably preyed on all size classes within the population. Gastroliths are most fully developed at ecdysis (Numanoi 1939, Maluf 1941, Kyer 1942, Scudamore 1947) and increase in maximum size with age (Scott and

Duncan 1967). Since large gastroliths, of up to 1 cm diameter, occurred in regurgitated pellets on the jetty, it appears that large *P. planifrons* were consumed at this stage of the moult cycle. At ecdysis the exoskeleton is soft and crayfish are almost totally defenceless (Hazlett, Rittschoff and Rubenstein 1974). Scott and Duncan (1967) found that larger crayfish were consumed after ecdysis, while juveniles were taken at any stage of the moult cycle. They considered that this was because shags would have little difficulty swallowing the smaller individuals.

Rainbow trout (*Salmo gairdnerii*) and brown trout (*S. trutta*) inhabit L. Rotoiti. The diel feeding activity pattern of *S. gairdnerii* has yet to be established but is probably similar to that of *S. trutta*, which according to Tusa (1969), feeds mainly during the day. In his study on *S. trutta* in the Horokiwi stream, Allen (1951) related feeding activity to the amount of food in their stomachs between 9 am. and midnight and found that it was fairly uniform over this period. However, since trout fishermen are more likely to be successful at dusk and dawn (pers. obs.), there may be an upsurge in trout feeding activity at these times.

Smith's (1959) study on *S. gairdnerii* in the lakes of the Rotorua district revealed that only trout larger than 35 cm consumed *P. planifrons* and that the proportion of fish eating crayfish increased with increasing size of trout. Only crayfish above 5 cm total length were consumed, which corresponds to crayfish older than about 1.5 years (Hopkins 1967b) (refer to Appendix II, p. 222) and

includes large juveniles and adults. It is uncertain why the smaller juveniles were not eaten. If trout rely on vision to a large extent to detect prey, the population of small crayfish would tend to be selectively exempt from attack during the day, as they are hidden within shallow water shelters. Also, at dusk and dawn they may go unnoticed in the low ambient light conditions. Another possibility is that it may be uneconomic for trout to feed on crayfish below 5 cm length. Smith (1959) found that crayfish were regularly consumed in small numbers throughout the year, although in L. Okataina there was an increase in the quantity eaten by *S. gairdnerii* in June and July. He did not determine whether trout selected crayfish with soft exoskeletons only, or took crayfish in any stage of the moult cycle.

By contrast, Momot (1965; 1967b) found that brook trout (*Salvelinus fontinalis*) fed only on *Orconectes virilis* in their first year, at less than 2.1 cm long. Only trout longer than 22.9 cm fed extensively on crayfish while maximum feeding activity occurred in midwinter and late summer, and was least in early spring and late autumn. Momot concluded that predation by *S. fontinalis* on *O. virilis* was insignificant as a population control mechanism, even though crayfish formed a significant part of the diet.

Smith (1959) found that *P. planifrons* was the third most important food item of *S. gairdnerii*, though quantities consumed were comparatively small. It seems that predatory pressures by trout on *P. planifrons* may

also be insignificant. Firstly, a large proportion of the adult population especially, resides totally unprotected at all times in each of the lakes studied except L. Rerewhakaaitu. Secondly, since crayfish are certainly most vulnerable at ecdysis, protective measures would be a likely priority if predatory pressures were significant. However, there was evidence that crayfish actually moulted without protection at depths where the only predator would be trout (on p. 166). Further evidence that trout do not act as an important population control mechanism came from L. Taupo, where an adult *P. planifrons* showed no signs of defence toward a trout (*S. gairdnerii*, estimated at 2.5 kg.) which swam to within 1 m of it. (*P. planifrons* could detect divers, as indicated by raised chelae, at distances up to 5 m).

P. planifrons is protected by law and only Arawa and Tuwharetoa Maori people have a special exemption to take koura as a traditional food. Consequently, man theoretically has little predatory impact on the crayfish populations in the Rotorua district. It is interesting to note that up until the early 1900's, koura formed a substantial part of the diet of Maoris in the Rotoiti area and, as a result, vast quantities were regularly taken. However, since that time a change in their dietry habits has meant that relatively fewer koura are taken and at less frequent intervals (Fox pers. comm.).

There was no evidence that eels exist in the Rotorua lakes and very few *Halcyon sanctus* occur around L. Rotoiti, so predatory effects by these species would be negligible. Although L. Rotoiti's population of scaup (*Aythya*

novaeseelandiae) is quite large, its effect on the *P. planifrons* population is unknown. This is an efficient diving bird and has been observed foraging on the bottom of L. Wakatipu at a depth of 2.6 m by Soper (1976), though he considers that they probably dive deeper. *A. novaeseelandiae* were often seen diving at dusk (presumably foraging) in water up to 10 m deep in L. Rotoiti. Their predatory habits on crayfish may be similar to those of shags, though their generally smaller size suggests that only juvenile crayfish would be taken.

CONCLUDING DISCUSSION

Paranephrops planifrons is a common inhabitant of Lakes Rotoiti, Rotoma, Okataina, Tarawera and Taupo and, like many other crayfish species, for example *Orconectes immunis* (Goellner 1943, cited in Momot MS.), *O. virilis* (Camougis and Hichar 1959; Hazlett, Rittschoff and Rubenstein 1974) and *Faxonella clypeata* (Mobberly and Pfrimmer 1967), it is highly mobile and displays an extensive home range (Devcich 1974). In these lakes *P. planifrons* occupies the bottom mostly above 40 m depth, although some individuals exist at far greater depths: a female was trapped at a depth of 120 m in L. Taupo (max. depth 165 m) and in the earlier study (Devcich loc. cit.) a male was recorded at 70 m depth in L. Okataina (max. depth 80 m). This tends to suggest that the home range of the species is the whole lake floor. As a comparison, *Pacifastacus leniusculus* occurs to a depth of 200 m in L. Tahoe (max. depth 500 m), although 90% of the population resides above the 40 m contour and greatest densities are at 10-20 m depth (Abrahamsson and Goldman 1970).

The present study revealed that overall the crayfish population in L. Rotoiti displays a complex set of spatial distribution and movement patterns which are repeated every diel period and, in the adult population, this diel pattern undergoes seasonal cyclic changes which differ between males and females.

To recapitulate, juveniles were almost exclusively

confined to substrates above 10 m depth at all times of the year. Inactive and within shelters by day, they emerged at dusk and foraged in the littoral zone until dawn. Two temporally, and to a large extent spatially separate adult groups comprised the breeding population. Of these, the larger and therefore more important group (ca 80% of the adult population) bred in late autumn (April - May) and generally occupied the bottom to a depth of 30 m. During daytime some of these adults resided under cover above the 11 m contour but the majority occurred in the open as a high density band (up to 50 crayfish m^{-2}) between the 11 m and 27 m contours around the lake. Activity levels increased at dusk and most crayfish forming the band migrated up into the weed bed zone to feed. Those at lesser depths emerged from shelters and also fed in this zone. As dawn approached, most adults migrated downwards and reformed the high density band, while the remainder sought shelters in shallower waters. During migratory activity, crayfish locomotor behaviour became less directed as slope angle decreased. Females performed the diel migration to a greater extent throughout summer and autumn but males migrated fairly consistently all year round. The high density band became vertically displaced seasonally, lying at mean depths of 12.8 m throughout the summer/autumn period and at 16.9 m in the winter/early spring period. Males and females were evenly distributed throughout the band at times of nonbreeding activity but during the April breeding period, females concentrated within its lower quartile. During summer and

autumn, adult numbers increased within shelters above the high density band. A smaller group of adults (ca 20% of the adult population) bred in early summer (November - December) and occurred mainly at depths below 30 m. They generally remained in the open at all times and fed continually, though mainly at night. Usually in December this group especially was involved in a mass migration of all crayfish from the deeper regions of the lake to around the 30 m contour by February. Crayfish then slowly remigrated downwards to fully recolonise the lower lake floor by the end of May.

The distribution and activity patterns shown by *Paranephrops planifrons* were in response to certain extrinsic and intrinsic factors including light, food, substrate type, temperature, shelter abundance, slope angle, oxygen, reproductive condition, moulting activity and predators. Thus, through these factors the L. Rotoiti population is adapted to its environment. As a means of better understanding the adaptive significance of these behavioural patterns it would be helpful to know something of the environmental conditions during the early evolutionary history of lake dwelling *P. planifrons*. Such information is, of course, unavailable. However, it is reasonable to assume that the main food source was confined to the littoral zone, as it is at present and that an avoidance response to endemic shags probably became inherent at an early evolutionary stage.

In evaluating the significance of the findings in this study and comparing them to those obtained for other

species, it is convenient to begin at the stage when crayfish become independent juveniles.

A feature common to lake inhabiting crayfish populations is the migration of females carrying mature eggs and hatchlings, into the littoral zone, where the young are released. Momot (1967a) and Capelli and Magnuson (1975) have reported this sequence for *Orconectes virilis* in West Lost Lake, Michigan, and *O. propinquus* in Trout Lake, Wisconsin, respectively. The L. Rotoiti population shows a similar pattern, whereby over 82% of all *P. planifrons* offspring began their independent existence above the 10 m contour. Similar distribution patterns for juveniles were observed in Lakes Okataina and Rotoma and probably also occurred in Lakes Tarawera, Tikitapu and Rerewhakaaitu, as well as the more protected bays of L. Taupo.

It is probably strategically important that offspring attain sexual maturity in the shortest time possible. Crayfish within a population generally mature at a certain size (Hopkins 1967a, Woodland 1967), (31.0 mm CL for females and 27.0 mm CL for males in L. Rotoiti) and the time taken to reach this size is determined by growth rate. The littoral zone in L. Rotoiti affords optimal conditions for growth due to its abundant food supply and higher mean annual temperatures. (The effect of temperature on the growth rate of juveniles is presented in Appendix I, p. 221.). Consequently, the migration of gravid females into this zone and the subsequent release of young are very possibly mechanisms by which growth rates are maximised and hence sexual maturity is achieved in the shortest time possible.

However, the littoral zone down to about 10 m depth is also the habitat of predatory shags, against which *P. planifrons* has developed a number of defensive strategies. Of these, nocturnalism is probably the most important, for shags rely on vision, subject to water clarity, to detect prey (Oliver 1974) and consequently do not feed at night (Potts 1972). Hayes (1977) states that nocturnalism is used by prey species as a strategy against predators that rely on vision whilst foraging. This generality is exemplified by Flint (1977), who suggests that the nocturnal feeding habits of *Pacifastacus leniusculus* in L. Tahoe may be an adaptive mechanism to avoid predation by fish during daylight hours. Reduced predatory pressure at night is thought to also explain nocturnal locomotor and feeding activity in the marine crayfish *Jasus lalandei* (Fielder 1965). The reduction in predatory pressure at night may also largely explain the nocturnal moulting habits of *Paranephrops planifrons* and crayfish generally (eg. *Cambarus clarkii*, Penn 1943).

A second strategy is the use of shelters. In all the study lakes utilisable shelters were numerous within their littoral zones, especially the rocky areas. Shelters ranged widely in type and shape but the size selected was generally related to the size of the normally single occupant. In contrast, *Homarus americanus* selects shelters on the bases of type and shape, as well as size (Cobb 1971). Mason (1970a) found that newly released *Pacifastacus trowbridgii* could discriminate between light and dark as related to artificial shelters, background colour and

pebbles. He comments that this ability to detect light intensity has survival value in their natural habitat. Juvenile *Paranephrops planifrons* are almost certainly able to also detect light, whereby light would serve as a mechanism for distinguishing protective shelters. Welsh (1934) suggested that the caudal photoreceptor, lodged in the sixth abdominal ganglion of crayfish, could act to warn crayfish that their palatable tail end is exposed and hence vulnerable to attack. In adult *P. planifrons* the caudal photorecptor does not respond to light intensities experienced in L. Rotoiti below 1 m depth (ie. $\leq$1500 lux) but the eyes are sensitive to intensities above the 150-205 lux range. This implies that the eyes are the major photodetectors and further evidence for this is that *P. planifrons* generally position themselves within shelters such that the eyes are directed toward the entrance.

Crypsis was a third strategy and adopted mainly by juveniles. The exoskeleton of juveniles in L. Rotoiti typically displayed a range of light brown and yellow colourations, which made detection difficult on the similarly coloured substrates. The generally darker exoskeletons of adults produced much stronger contrasts with bottom sediments, indicating a far lesser reliance on camouflage as a means of avoiding detection.

During daytime most adults in L. Rotoiti occupied depths below the foraging range of shags and were therefore less vulnerable than juveniles. However, these adults occurred mainly in the open and consequently were potentially susceptible to predation by trout. Although

fish predation is a common source of stress on crayfish populations (Momot and Gowing 1977a), the fact that *P. planifrons* did not seek shelter may therefore imply that the predatory pressure exerted by trout was low. A possible explanation for this behaviour is implied in the findings of Chapman (1966) and Schutz and Northcote (1972) who observed that predatory fish tend to attack moving prey rather than stationary prey. Furthermore, Stein and Magnuson (1976) argued that because active prey should be more conspicuous and therefore more vulnerable than inactive prey, reduced activity by prey should be advantageous in the presence of a predator. *P. planifrons* is relatively inactive by day, so predation by trout may be low for this reason and may at least partly explain the observed lack of response in a large male crayfish to a trout which swam within less than 1 metre of it in L. Taupo.

Stein and Magnuson (loc. cit.) found that predatory small mouth bass (*Micropterus dolomieui*) induced a quicker response in smaller, more vulnerable *Orconectes propinquus* than in larger, less vulnerable individuals. They also noted that the behaviour of males was modified less than females and concluded that females were more susceptible to predation because of smaller chelae size. The functional importance of chelae in *P. planifrons* as defence aids against attack by trout has been revealed by Mylechreest (pers. comm.), who frequently found one chela only amongst the stomach contents of trout inhabiting L. Waikaremoana. Females in L. Rotoiti possessed smaller chelae relative

to body size than males, were generally smaller in body size (mean CL of 42.9 mm for 1375 females, cf. mean CL of 44.8 mm for 2832 males trapped in 1975 and 1976 ; t = 9.299, p = ***, n = 4207) and displayed less aggression toward potentially predaceous divers. Thus, as in *O. propinquus*, *P. planifrons* females appeared more vulnerable to predation, which may at least partly explain the sex ratio of 1.34:1 in favour of males. Supposing females were more prone to predation, it would be strategically advantageous to occupy shelters during daytime more so than males. Under this circumstance the above ratio would be inaccurate, for females would have less readily been included in the 'random' collections by hand which was the method used to obtain this ratio. However, the sex ratio of crayfish trapped also favoured males, by 2.07:1 (N = 4207), which tends to verify that fewer females than males occupied L. Rotoiti.

There are other possible explanations for the lower number of adult females. There may be a preponderance of presumptive males in the eggs, as well as a greater mortality of mature females than males at moulting (Devcich 1974). Abrahamsson (1966) found that when *Astacus astacus* reached sexual maturity, males outnumbered females but not as juveniles. He found that as males increase in size their chelae become accentuated, a phenomenon not occurring in females and considered that the more territorially aggressive males caused a greater mortality of less well equipped females. Although *P. planifrons* males possess larger chelae, this species appears to be

relatively passive and there was no evidence of strong territoriality or sexual domination by adult males in situ.

The redistribution of *P. planifrons* to deeper waters was accompanied by an increase in body size. A number of factors contribute to this change in distribution. Diving observations suggested that there were a greater number of shelters of a small size available within the littoral zone of L. Rotoiti and hence there were fewer shallow water shelters for adult crayfish in this zone. It is believed that this feature, in association with a large adult population (Devcich 1974) and the need to avoid predatory shags, are factors explaining the preponderance of adults below the littoral zone during daytime. As a result, the adult population is effectively isolated from its primary feeding ground and this consequently necessitates the development of diel migratory behaviour.

According to Mayr (1961), food is an ultimate or inherent causative factor affecting distribution patterns generally and is therefore believed to have effected the upward migration at dusk of crayfish adults inhabiting the bottom from immediately below the weed to around 30 m depth. Meanwhile the dawn migration was probably influenced by the factors mentioned in the preceeding paragraph. These dual diel migrations were part of a circadian activity rhythm, the timing of which was modified vertically throughout the lake by changing light intensities at dusk and dawn, as well as seasonally, by daylength. By these means, upward migratory activity always began at sunset and was initiated

in the deepest waters, whilst downward migratory activity ceased first in the shallows and at one hour before sunrise. These changes in the timing of activity were most probably adaptations serving to minimise losses from shags and trout, both of which utilise light when foraging. Migration locomotor activity appeared to be mediated mainly via mechanoreceptors responsive to gravity. Sandeman (1976) states that mechano-proprioceptor systems such as the one associated with orientation, are less useful in water than statocysts, so it was somewhat surprising to find that statocyst ablation did not significantly suppress postural control and therefore migratory activity in *P. planifrons*. Instead, it seemed that proprioceptors, probably in the legs mainly, played a major role in orientation during the twilight migrations. Crayfish movements were less directed on the flatter slopes because of less stress on proprioceptive mechanisms. Consequently, the angle of bottom slope was important in determining the migration period, as were locomotor rate and the total distance migrated. It is logical that these factors would control the arrival times of individuals at the weed bed zone after dusk and to depths associated with high density band formation before dawn.

Light intensity apparently controlled the minimum depth occupied by migratory crayfish during daytime and gave rise to the boundary or transition zone, above which crayfish were confined to shelters, while below this zone the lower, noninhibitory light levels enabled crayfish to exist out in the open. Since it would have been energetically wasteful for crayfish to have migrated

further from the littoral zone than was necessary, it follows that migratory activity should cease once crayfish passed beyond the boundary zone. This does in fact happen and results in the formation of a high density band of crayfish immediately below the boundary zone.

It is interesting to note that crayfish comprising the high density band ceased migrating downwards at a time when ambient light was barely detectable on the photometer. Since this suggested that crayfish were able to distinguish the shallowest depth affording protection from midday light intensities by some means other than light, the question that may be asked is 'what determines the depth at which crayfish cease moving down bottom slopes?' A direct answer lay beyond the scope of this study. However as this depth appeared to be predetermined, endogenous factors were probably important, although the possibility of exogenous influences (eg. pressure) cannot be discounted. According to Crisp (1976), pressure is theoretically the most consistent and reliable indicator of depth.

The high density band phenomenon within Lakes Rotoiti, Rotoma, Okataina, Tikitapu, Tarawera and Taupo is an interesting behavioural feature of *P. planifrons* that appears to be unique to this species. The band contains the majority of the adult population (mainly late autumn breeders) and may be envisaged as a daytime concentration of unprotected and relatively inactive adult crayfish, occupying a relatively narrow depth range around a lake. Its shape or concentration patterning typically resembles a bell-shaped distribution curve between its upper and

lower depth limits. It may not necessarily extend continuously around the entire lake and is absent where slope angles are too steep (>ca 35°), or the substrate is extremely soft or too unstable to support crayfish.

In laboratory experiments, Crawshaw (1974) found that *Orconectes immunis* selected cooler water for its daytime inactivity period and comments that apart from serving to lower metabolic expenditure, this adaptation would also serve to increase predator avoidance in the natural environment, as it would of necessity lead crayfish into deeper water. Throughout the early summer - late autumn thermal stratification period, all but the upper quartile of the density band in L. Rotoiti lay within the thermocline. Therefore, migrating *P. planifrons* would have received the added advantage of a daytime lowering in metabolic expenditure at that time of year.

During this period hypolimnetic deoxygenation induced the migration of all crayfish inhabiting the deeper regions of L. Rotoiti to above the 30 m contour and was believed to be at least partly responsible for the upward displacement of the high density band from its winter mean depth of 21.6 m to 18.3 m during that time. A contributing factor here may be heat which enters the lake through its bottom sediments (Evison and Calhaem 1972). During the thermal stratification period, this geothermal heat source is thought to produce convection currents that transport reducing substances from the bottom sediments and deoxygenated bottom waters to the upper limit of the hypolimnion at around 30 m depth (Fish 1975).

McColl (1974) considers that L. Rotoiti was oligotrophic before the influence of man. If this is true, then the migration from deeper waters in summer would be a relatively recent environmental adaptation. In fact, marked deoxygenation may be a very recent event, for when oxygen readings were first taken within its hypolimnion on 14 April 1957, a low of 3.2 g m^{-3} was recorded (Jolly 1968) but by April 1970 this figure had fallen to zero (Fish 1975). Increased nutrient input from farming and housing is probably responsible for this trend. It appears to have stabilised since 1973 but if it does continue, one effect would be to force the high density band into increasingly shallow water and, as a result, crayfish could conceivably lie unprotected within the diving range of shags. Under these circumstances lake oxygen content would effectively serve as a control mechanism on population size.

Hypolimnetic deoxygenation and subsequent reoxygenation only partly explains the seasonal vertical displacement of the high density band. Devcich (1974) found that *P. planifrons* comprising the high density band began to move up into a transect (extending from the shoreline to 16 m depth) lined with beer cans serving as shelters, in September 1973, while lake deoxygenation did not trigger the movement of deep water inhabitants into the high density band until December. This discrepancy in timing implied that another mechanism operated to trigger the upward shift of the high density band. Evidence for a possible mechanism came from a study by Nosaki (1969) on the spectral sensitivity of *Procambarus clarkii*. He found

that this species was more sensitive to longer wavelengths between June and October (summer and autumn) than from December to March (winter and early spring). Since longer wavelengths generally penetrate to lesser depths than shorter wavelengths (James and Birge 1938, Hutchinson 1957), a similar seasonal change in spectral sensitivity in *Paranephrops planifrons* could feasibly serve to reduce the depth of the boundary zone and its associated high density band over the warmer periods.

Such a change in retinal sensitivity would also serve to increase shelter availability above the boundary zone, for crayfish would necessarily show an increased tolerance to higher light intensities. This may at least partly explain the 4.25 fold increase in adult members within the littoral zone during daytime between late spring and late autumn. As well, an increased incidence of sharing shelters also contributes to the increase in numbers. This appears to be related to an increase in mean population density above a depth of 30 m, due to the migration of deep water inhabitants from the anoxic hypolimnion in December. Density related changes in crayfish behaviour have been recorded by both Cobb (1971) and Bovbjerg and Stephen (1978) who found that under normal density conditions *Homarus americanus* and *Orconectes virilis* respectively, display solitary behaviour but under crowded conditions,aggregative behaviour is common.

The general movement of adults into shallower waters in September and their continuance until April of the following year, is believed to be an adaptation designed

primarily to satisfy increased energy needs during this period. Energy was required mainly for body growth which is maximal in spring and summer (Hopkins 1966; 1967b), for reproductive growth (of late autumn breeders) in summer and autumn, for mating in autumn and for higher maintenance levels associated with increased temperatures. It is conceivable that the savings in energy loss accruing from reductions in diel migration distances, assist in satisfying these energy demands throughout this period.

Greater numbers of females fed within the littoral zone from January to April than males and considering that the female population was comparatively smaller, it would seem that a pronounced difference in energy demands existed between the sexes at this time. In explanation, it appeared that females had a shorter seasonal growing period than males. This was partly because of attached young delaying the postbreeding moult until late spring [female *Cambarus immunis* have a shortened period of growth for the same reason (Tack 1941)] and because female feeding activity was directly related to temperature. Consequently, female growth was most significant during the warmer months. By contrast, male feeding activity did not decrease in winter and moulting was only partly suppressed. Therefore, growth was likely to occur at all seasons. However, it is not known whether males grew significantly over the cooler months. The other contributing factor was that female crayfish have higher energy requirements associated with gonadal development than do males (Woodland 1967).

From laboratory experiments conducted during this

period it was found that females selected warmer water at night, whereas males showed no distinct temperature preference. Therefore, it would seem that temperature affected not only the seasonal activity rhythm of late autumn breeding females but may also have operated on this migratory mechanism in summer and autumn. An adaptation to warm temperature such as this would help to satisfy their higher energy requirements at the time, by directing females into the weed beds at night. Coincident energy needs of males were not as great, consequently there would have been less emphasis placed on the littoral feeding ground and thus may explain the absence of a similar adaptation to warmer temperatures.

Lake dwelling crayfish species commonly migrate into warm, shallow water for the summer and autumn period. [(eg. *Orconectes virilis* (Momot 1967a, Momot and Gowing 1972, Fast and Momot 1973), *O. propinquus* (Capelli and Magnuson 1975), *Pacifastacus leniusculus* (Flint 1977)]. This behaviour is generally associated with the release of attached young, as it is with *Paranephrops planifrons* (mentioned earlier). Additional reasons have also been suggested. Flint (loc. cit.) implied that an abundance of periphyton in the shallows and suitable conditions for gonad maturation and mating, were influential factors in determining the shallow water distribution of *Pacifastacus leniusculus* during the warmer months. Fast and Momot (1973) suggested that both male and female *O. virilis* had a warm water preference but the social aggression of the large males tended to force the females down into the less preferred

colder waters during summer, leaving males only in the shallow warmer waters. Male *Paranephrops planifrons* do not show similar behaviour towards females.

Fast and Momot (loc. cit.) found that *O. virilis* departed from the hypolimnion of both a eutrophic and oligotrophic lake in summer. They concluded that deoxygenation induced the exodus from the hypolimnion of the eutrophic lake while selectivity of temperatures about 10°C caused the absence of crayfish within the hypolimnion of the oligotrophic lake. In contrast, observations made while diving revealed that *P. planifrons* did not migrate from the hypolimnia of oligotrophic Lakes Rotoma, Tarawera, Okataina and Taupo in summer. This tends to imply that these populations did not actively select warmer temperatures, at least during the daytime.

Following lake turnover in May, *P. planifrons* (mainly early summer breeders) of both sexes recolonised the deeper regions. At this time adult numbers decreased within the littoral zone and the high density band shifted downwards. This was possibly in response to the postulated change in retinal sensitivity to shorter wavelengths. Remembering that the late autumn breeders occupied the littoral zone to furnish high energy needs but at the expense of increased risk from predators, the evacuation of adults from this zone may be an adaptation serving to increase predator avoidance during winter, when energy demands are lower. The reduction in energy needs is most pronounced in females (body growth ceases and ovarian growth is negligible in winter), which are now carrying eggs. Consequently females display little diel migratory

activity. However, in males, gonad maturation extends well into winter and this, in conjunction with the possibility of maintained body growth, may explain their continued feeding within the littoral zone during this period.

Other crayfish species also move into deeper waters before winter. Flint (1977) considered that the autumn migration of *Pacifastacus leniusculus* to greater depths in L. Tahoe was an adaptation serving to reduce crayfish mortality from exposure to waves and strong currents during winter storms. The external factors of decreasing light and temperature were believed to have stimulated the migration. Aiken (1969a; b) concluded that the movement of adult *O. virilis* to deeper regions of a stream in late summer and early autumn (Aiken 1968) was related to the sexual cycle. He found that ovarian maturation required 4 months of total darkness of 4°C and these conditions prevailed in deep water during winter. Momot (1967a) and Momot and Gowing (1972) believed that adults of the same species occupied deeper waters of 3 small lakes during winter for the same reason. These lakes and the stream studied by Aiken all freeze over in winter, so crayfish presumably also move from the shallows to avoid freezing.

Crayfish inhabiting temperate regions typically enter a state of torpidity in winter [eg. *Orconectes immunis* (Tack 1941), *Cambarus longulus longulus* (Smart 1962), *O. virilis* (Momot 1967a, Aiken 1968), *O. rusticus* (Prins 1968), *O. nais* (Armitage et al 1972, Rice and Armitage 1974), *Pacifastacus leniusculus* (Flint 1977)],

which necessitates the build up of energy reserves in autumn. Armitage et al (1972) reported the accumulation of nutrients within the hepatopancreas of *O. nais* in autumn and considered that this provided for metabolism during dormancy. *Paranephrops planifrons* did not become torpid in winter, probably because the winter temperature at 10°C was higher than the 0-5°C winter temperature range experienced by the above species. Therefore, there was probably less need for *P. planifrons* to build up energy reserves before winter. Nevertheless, prewinter storage may be important in females, as indicated by the increase in lipid and energy contents of the hepatopancreas between April and June. This was in contrast to the constantly low levels of lipid and energy within male hepatopancreases during this period. Prewinter nutrient storage is likely to be a more important adaptation in *P. planifrons* populations inhabiting latitudes south of the Rotorua district, especially those in the South Island.

The existence of bathymetrically and temporally separate breeding groups within the L. Rotoiti population was perhaps the most intriguing facet of this study. Although individuals belonging to each group were morphologically similar, they appeared to differ physiologically. This was indicated by a difference in the phasing of periods of reproductive growth and by the fact that the early summer breeding group did not perform diel migratory behaviour to nearly the same extent as the main, late autumn breeding group. It is not known how these differences arose or whether they are genetically controlled.

However, it is interesting to speculate on a possible course of events leading to the present day situation.

Assuming that the littoral zone has always provided the best conditions for growth and hence reproduction and population continuance, it follows that the population would have adapted to feed within this zone at an early stage in its evolutionary history. As the population increased in size, intraspecific competition for food may have become increasingly important and could have resulted in the exclusion of weaker individuals from the littoral zone. These individuals may have given rise to the present day early summer breeding population, which now resides almost exclusively in the deeper regions of the lake. Since this group probably had no inherent links with the littoral zone, there would have been no need to develop diel migratory activity. Meanwhile, the present day late autumn breeding group may have evolved from the stronger individuals and consequently were better able to compete for food. They could have developed a diel migratory response enabling them to utilise the littoral zone feeding ground.

It is more difficult to offer a plausible explanation for the differences in timing of breeding activity between these two groups. It was initially thought that early summer breeding females were, in fact, late autumn breeding females whose ovaries had not matured before the rapidly declining temperatures around late May inhibited egg laying activity. Under these circumstances egg laying would have been delayed until temperatures once again rose to the

critical egg laying temperature of around 15°C in the following November. If this was so, then females with large ovaries would have occurred within the samples taken in winter. However, no such females were found which tends to support the suggestion that individuals comprising the adult population were not of the same breeding stock.

The differing periods of reproductive growth may have been ultimately influenced by food availability. In summer and autumn, crayfish comprising the early summer breeding population were confined mainly between the 20 m and 30 m contours and, as a result, their food supply was reduced to low levels. Figure 29 (following p. 121) shows that between February and April food was 67% less abundant at 20 m depth than at other times during 1975. Thus, there may have been insufficient food to support reproductive growth at this time. However, following lake turnover in May, this breeding group was able to take advantage of the higher food concentrations at greater depths. The increased food availability may be significant, for ovarian growth began one month after turnover. By contrast, food in the littoral zone and utilised by the late autumn breeding population, remained continuously high but increased by 16% from December - May, which coincided with their ovarian maturation period.

In conclusion, this study has revealed a little of the ecology of lake dwelling *P. planifrons*. Although the populations inhabiting oligotrophic lakes received little attention, there was, with one exception, no reason to suspect major differences between their diel and seasonal

distribution and movement patterns and biological cycles generally and those of the L. Rotoiti population. That exception was hypolimnetic deoxygenation, which is presently of little consequence in Lakes Rotoma, Okataina, Tarawera and Taupo and so resident crayfish are not forced to migrate from their hypolimnia during summer. If, however, the nutrient loading of these lakes increases dramatically in the future, then the resultant increased levels of deoxygenation may necessitate migratory activity.

P. planifrons is very similar in habit to the closely related *P. zealandicus* (Hopkins 1970). Therefore, at least some of the more general findings in this study could also apply to lake dwelling *P. zealandicus* populations, especially those inhabiting the larger South Island lakes.

At least two areas of this study warrant further investigation. Firstly, by using spectrophotometric techniques the spectral response curve of *P. planifrons* can be determined, and when coupled with a knowledge of the spectral composition of a lake, it should be possible to clarify the relationship between the daytime patterns of distribution and its seasonal changes, and light. The other involves the 2 bathymetrically and temporally separate breeding groups which comprise the L. Rotoiti population and possibly other lake dwelling populations also. An explanation for their coexistence has been attempted above, however the true significance of such a strategy is more likely to be revealed through future physiologically and genetically based studies on both breeding groups.

APPENDICES

Appendix I Effect of temperature on juvenile growth.

The effect of temperature on the growth rate of juveniles was assessed by maintaining newly released young at 10°C and 20°C in aquaria for up to 1 year. They were fed on detritus collected periodically from L. Rotoiti. The results are presented in Plate 18 and show a far greater growth rate by juveniles reared at 20°C.

On this basis, the release of young in the shallower, generally warmer waters will ensure that growth rates are high. High juvenile growth rates are probably advantageous because they would enhance the rapid attainment of sexual maturity and, because with increased size, crayfish become less susceptible to predatory shags.

Plate 18. Effect of temperature on juvenile growth rate.

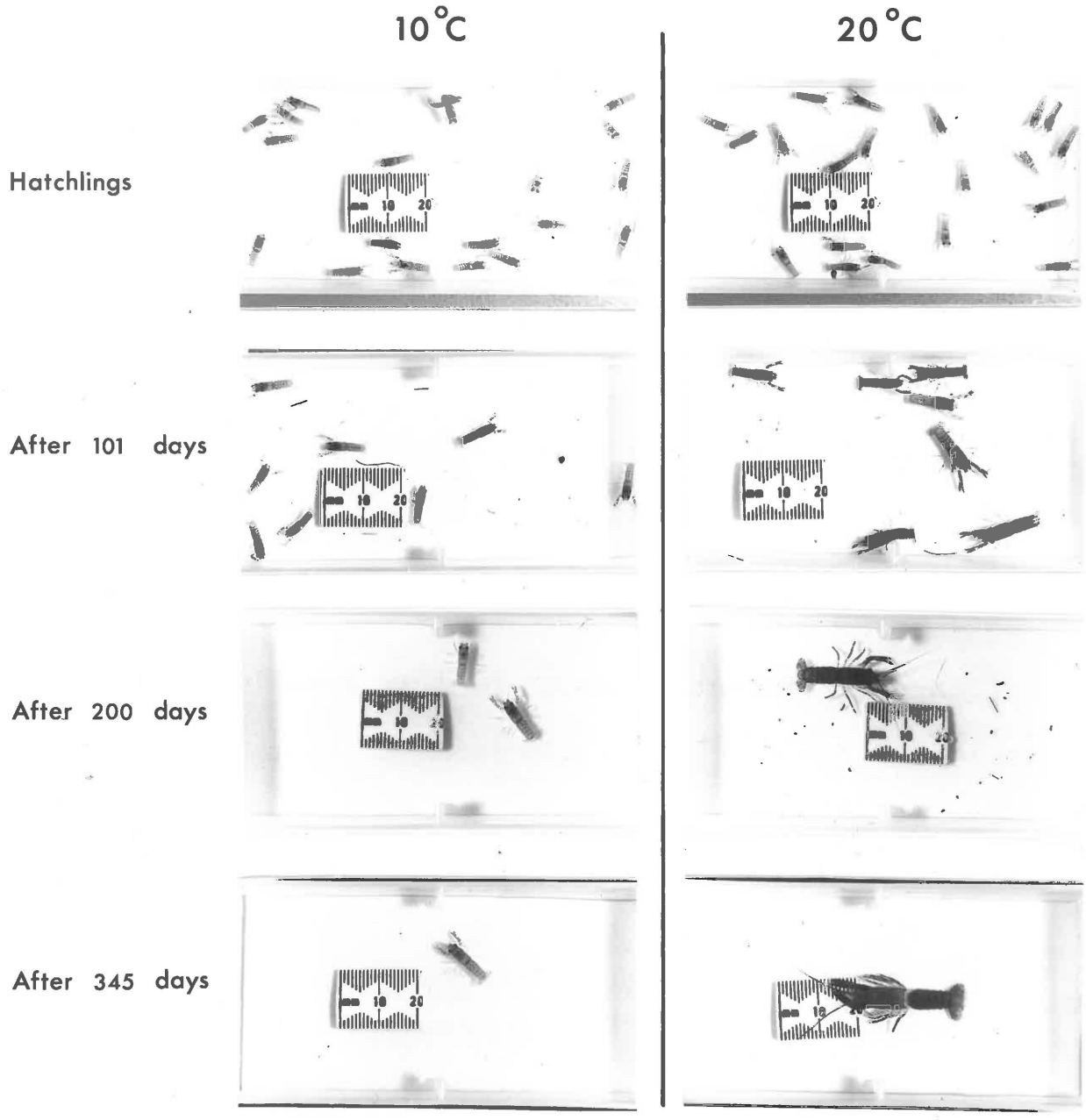


Plate 18
Effect of temperature...
Between pp 221,222

Appendix II Why does *P. planifrons* attain a greater size in lakes than in streams?

Lake dwelling *Paranephrops planifrons* generally attain a greater size than those from stream populations (Chapman and Lewis 1976). Hopkins (1976b) suggested that their greater size may be attributed to either increased growth per moult, increased moult frequency, or to a greater life span. These possibilities were investigated as follows.

Artificial conditions can affect growth increments, so moult data was obtained from crayfish that moulted within 5 days of capture (Hopkins loc. cit., Flint 1975). Growth increments were obtained from 20 adult crayfish within the 28-44 mm premoult CL size range, which was similar to the size range of stream inhabiting adults studied by Hopkins. Results are given in Table 50 and show a mean postmoult increase of 1.7 mm or 4.8% over premoult carapace lengths. Hopkins found that the relative growth per moult decreased as size increased, from about 16% at 13.9 - 15.2 mm premoult CL (rostrum length included) to 8% of premoult CL for crayfish at 41.4 mm CL. This latter perventage increase was higher than the percentage increase in growth per moult recorded for similarly sized L. Rotoiti adults, which indicates that the greater size of lake crayfish is due to factors other than increased growth increments of adults at least.

The life span of crayfish within a population is usually determined from analysis of size classes [eg. by

Van Deventer (1937) for *Cambarus immunis*, by Momot (1967a) and Momot and Gowing (1977b) for *Orconectes virilis* and by Flint (1975) for *Pacifastacus leniusculus*], whereby the total number of distinctly separate size groups represents the maximum attainable age. In annually breeding species the number of groups expresses the total age in years, while for crayfish that breed twice annually, their actual age is half that of the number of obtained size classes. Hopkins (1966; 1967b) was able to separate *P. planifrons* into discrete size classes using arithmetical probability paper analysis (Harding 1949, Cassie 1954) but size classes in the L. Rotoiti population were indistinguishable by this method (Devcich 1974), presumably due to the increased overlap of adjacent cohorts produced by the second annual breeding period. Kurata (1962) states that determining age (and growth) by size class frequency analysis is most inaccurate when applied to species with a short life span but becomes progressively less accurate as the life span increases. It is almost impossible to estimate the age of older individuals of long living species especially, due to variations in growth causing the overlapping of successive year groups and subsequent obliteration of size frequency modes.

From the size at maturity for females, their growth increment per moult and their moult frequency per year, it was possible to estimate the number of years a 70.9 mm CL female (largest crayfish captured in L. Rotoiti) survived as an adult. Female size at maturity was approximately 31.0 mm CL (p. 136) and as there was no significant

difference in the growth increments per moult between males and females (table 50), the total mean growth increment per moult of 1.6 mm CL was used. It was established earlier (p. 158) that adults moult twice annually but probably reduce to a single annual moult once over about 55.0 mm CL. Thus, by adding 3.2 mm CL increments per year between 31.0 and 55.0 mm CL and 1.6 mm CL increments per year thereafter, the adult life span of the 70.9 mm CL female was calculated to be 17 years. With 3 years in the juvenile stage this female was therefore 20 years of age.

Males and females trapped during their main intermoult periods in 1975 (January - March for females, May - August for males) were grouped into year classes using the above method. From the number comprising each year class the survival rate of each class was determined as a percentage of the total number trapped for each sex. The results are presented in Figure 47 which shows that over 50% of the females survived for 6 years and males for 7 years, while less than 10% survived a total of 9 and 10 years respectively. A few females outsurvived males although males generally had a slightly longer life span.

By contrast, Hopkins (1976b) found that crayfish in stream populations survive a maximum of 5 years, of which 2-3 years are spent in the adult stage. These crayfish moult twice in their first year as adults and once annually thereafter. By adding the 3.2 mm CL yearly increments to L. Rotoiti crayfish from the onset of maturity (p. 136) until they reach 55.0 mm CL, it is shown that males moulted twice annually for 9 years and females for 8 years.

Table 50: Growth increment per moult for 20 *P. planifrons* within the 28-44 mm CL size range and for 18 crayfish within the 45-60 mm CL size range.

Sex	Premoult CL (mm)	Postmoult CL (mm)	Growth increment (mm)	% increment
M	28.3	30.8	2.5	8.1
F	28.5	29.3	0.8	2.7
F	28.5	30.3	1.8	5.9
M	29.0	33.3	4.3	12.9
M	30.7	32.6	1.9	5.8
F	31.2	32.4	1.2	3.7
F	32.4	34.2	1.8	5.3
F	37.2	39.6	2.4	6.1
M	37.3	38.6	1.3	3.4
F	38.1	39.9	1.8	4.5
F	39.4	41.4	2.0	4.8
M	40.0	41.6	1.6	3.9
F	41.1	41.6	0.5	1.2
F	42.3	44.2	1.9	4.3
M	42.9	44.2	1.3	2.9
M	43.0	44.6	1.6	3.6
F	43.6	44.3	0.7	1.6
M	43.6	45.0	1.4	3.1
F	43.9	44.8	0.9	2.0
M	44.0	46.0	2.0	4.4
Mean:			1.7	4.8
F	45.0	46.7	1.7	3.7
M	45.6	47.0	1.4	3.0
M	46.2	48.3	2.1	4.4
F	48.4	50.0	1.6	3.2
F	48.5	49.1	0.6	1.2
M	49.2	52.5	3.3	6.3
M	49.8	50.6	0.8	1.6
F	50.7	51.8	1.1	2.1
F	51.0	52.0	1.0	1.9
F	51.4	52.1	0.7	1.3
M	52.3	53.8	1.5	2.8

Cont. over

Sex	Premoult CL (mm)	Postmoult CL (mm)	Growth increment (mm)	% increment
F	54.0	55.0	1.0	1.8
M	54.6	55.2	0.6	1.1
F	54.9	56.1	1.2	2.1
F	55.7	59.0	3.3	5.6
F	56.4	57.5	1.1	1.9
F	58.2	59.9	1.7	2.8
M	60.1	61.6	1.5	2.4
Mean			1.5	2.7
Total Mean			1.6	

$t = 1.624$, p = ns, $n = 38$

Figure 47. The percentage of adult females and males surviving each year class in L. Rotoiti during 1975. Included are crayfish sizes (CL) corresponding to every second year class.

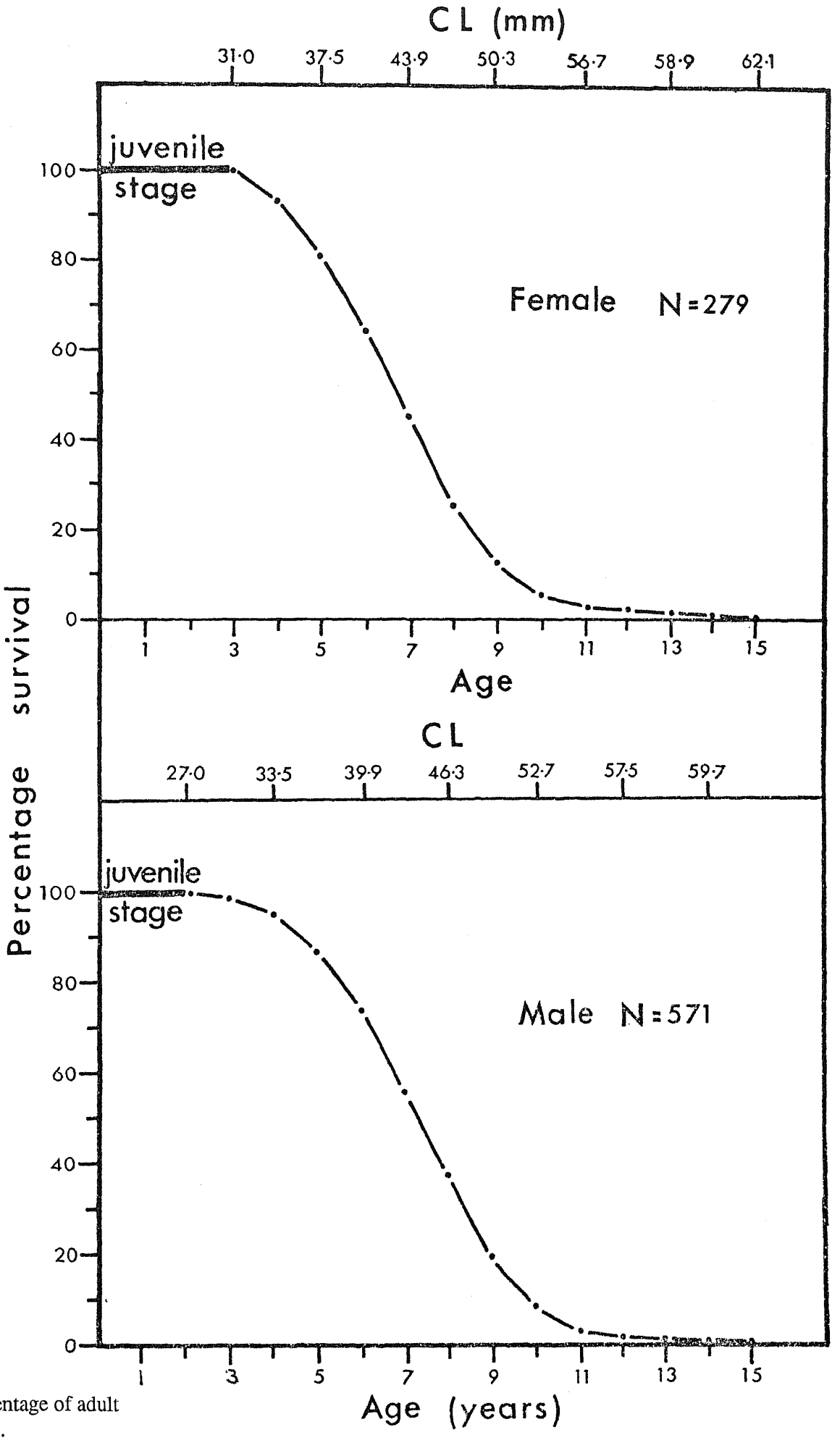


Figure 47
The percentage of adult females ...
Between pp 226-227

Assuming stream and lake crayfish remain in the juvenile stage for similar periods, it follows that the greater size attained by lake crayfish is mainly due to their longer survival as adults and also because adults moult twice annually for a considerably longer period. [The difference in size at maturity between stream and lake females of 25.0 mm CL and 31.0 mm CL respectively, suggests that lake crayfish may remain longer in the juvenile stage. However, Flint (1975) comments that environmental stress induced by current, causes juveniles to expend more energy in maintaining their position and, as a result, they show a smaller growth rate at each moult compared to juveniles inhabiting calmer lake waters. Bearing this in mind the above assumption would appear to be a valid one].

The presence of current is a likely reason for genetic variation between crayfish inhabiting streams and lakes, and may be the ultimate factor determining the smaller size of stream dwelling crayfish. Here, small size is a selective advantage because better use can be made of the lower velocities associated with the boundary layer. Consequently, crayfish are less likely to be swept away. Hopkins (1976b) found that *P. planifrons* in the shallow riffle parts of a stream were generally smaller than those in the deeper pools where current flow was least.

The large disparity in life span between stream and lake crayfish could be induced either environmentally or genetically. Because of the more rigorous environment

associated with the stream habitat, it is conceivable that the adult population in particular is highly susceptible to heavy losses, especially during periodic flooding and, as a result, crayfish may not achieve their normal life expectancy. However, since the reduction to a single annual moult is a characteristic of older animals and occurs in stream dwelling crayfish, it would appear that these crayfish reach old age.

Therefore the disparity in life spans is more probably due to a genetic difference. Such an inherent difference could lie in the mechanism controlling the ageing process of adults. As the reductions in moult frequency may be regarded as indicators of increasing age, it follows that when stream and lake crayfish initially reduce to the same annual moult frequency, their ages are similar in a biological sense although different chronologically, whereby the lake crayfish registers a greater age in years. On this basis, the ageing process of lake crayfish could conceivably occur at a slower rate than for crayfish inhabiting streams.

As *P. planifrons* inhabiting streams has a short life span and small size, it is not surprising that females breed only once on average (Hopkins 1967b). In lakes the same restrictions on size do not exist, so crayfish are free to grow considerably larger and attain a greater age. The greater life span of females in L. Rotoiti enables the majority to breed 4 or 5 times. In fact, a large size in lakes would be advantageous as a protective mechanism against predatory pressures from shags, for large crayfish

tend to occur outside their foraging range (see discussion p. 204).

Crayfish inhabiting lentic waters may generally live longer than the same species in a lotic environment. Flint (1975) isolated 12 year classes of *Pacifastacus leniusculus* within L. Tahoe, while a maximum of 8 year classes was found by Mason (1975) for this species in a coastal stream.

Appendix III

Relationship between cephalothoracic length and total length.

Figure 48. The relationship between cephalothoracic length and total length of *P. planifrons* from L. Rotoiti.

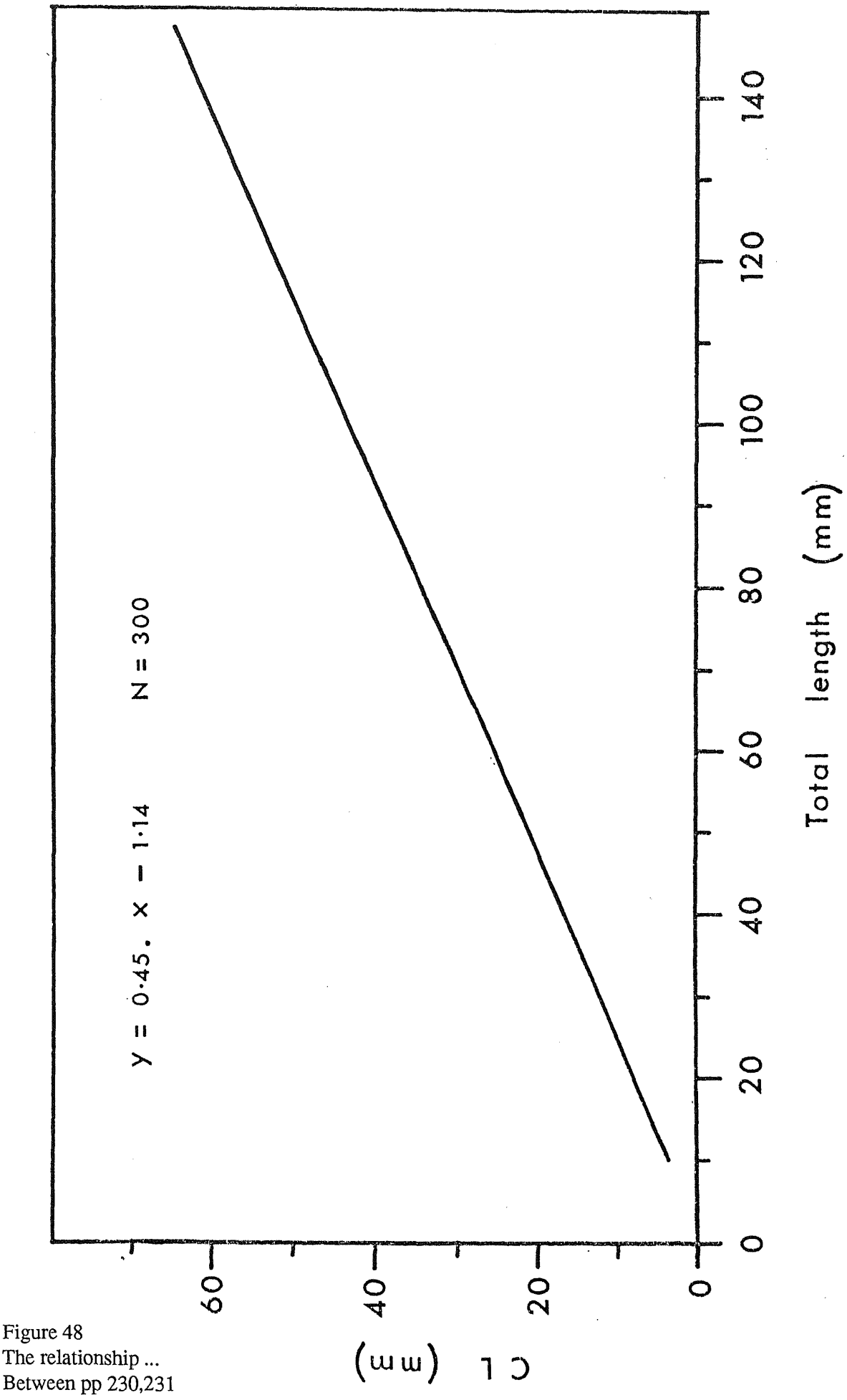


Figure 48
The relationship ...
Between pp 230,231

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