GROWTH, REPRODUCTION, AND SOME ASPECTS OF BEHAVIOUR OF *JASUS LALANDEI* MILNE-EDWARDS.

by

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SUMMARY

The methods used to catch and transport samples of the crayfish Jasus lalandei and to maintain them in aquaria are discussed.

Experiments to determine some aspects of behaviour related to obtaining food and shelter are described. Crayfish tend to occupy shelters that offer a tactile stimulus and a light-gradient. If shelter is limited, the available shelter is occupied and retained according to a dominance order. Such a dominance order was demonstrated in groups of crayfish approximately equal in size and large animals dominated smaller ones. Sex did not play an important role in the establishment of a social hierarchy.

Crayfish feed preferentially, selecting marine types of bait such as fish, shark or squid before terrestrial baits such as horsemeat and rabbit. Fresh baits are taken in preference to stale baits.

The feeding behaviour of crayfish is rhythmic. Captive animals remain dormant in their shelters during most of the hours of daylight. Feeding activity is greatest at dusk, increasing significantly from a low level an hour before and decreasing to a relatively low level two hours following. Little evidence of this pattern of behaviour could be detected in constant light or darkness. During alternating 6 hour periods of light and darkness,

feeding is maintained at a high level during dark periods, decreasing to a low level during light periods. No residuum of this pattern of behaviour was evident in constant light or darkness. The cycle of feeding activity is therefore essentially an exogenous rhythm.

Lack of shelter does not markedly influence the cycle of feeding activity of captive crayfish. The pattern of locomotor activity corresponds quite closely to the pattern of feeding activity under the same conditions of light and darkness.

Measurements of length used by other authors are compared and conversion factors calculated. Weight is proportional to the cube of the carapace-length.

The moulting cycle and physical changes occurring at ecdysis are described. Captive crayfish increase significantly in weight two days before moult and animals 5 to 7 cm. in carapace-length increase by about 13.5 per cent on the day following moult, whilst crayfish 8 to 9 cm. in carapace-length increase by about 5.5 per cent. Weight then increases slowly, becoming stable 35 days following moult. The average percentage of water absorbed at moult by crayfish 5 to 9 cm. in carapace-length is 18.3. The frequency of moulting increases with increasing temperature and small animals moult more frequently than larger ones. An estimate of growth by

length and weight, per moult and per annum for crayfish 4 to 10 cm. in carapace-length is given. Growth at moult is reduced if missing appendages are regenerated. A plastic dart-tag was tested successfully in the laboratory.

Morphological and histological changes are used to describe the ovarian cycle. The development of ovigerous setae is described and their presence is used as an index of sexual maturity in females. A small proportion of female crayfish are mature at 8.5 cm. in carapace-length, but the proportion does not approach 100 per cent until 12 cm. in carapace-length. The number of eggs carried by females, calculated by a volumetric method varies from 85,000 at 9.3 cm. to 362,000 at 13.9 cm. in carapace-length.

The histology and development of the testis is described and compared with the description given for Panulirus penicillatus by Matthews (1951). An attempt is made to describe the method of fertilization from a study of the genital organs.

Some factors influencing the exploitation of crayfish in South Australia are discussed. Past and present protective regulations are analysed and some suggestions made regarding future conservation.

This thesis contains no material which has been accepted for the award of any other degree or diploma in any University, and, to the best of my knowledge, contains no material previously published or written by another person, except when due reference is made in the text of the thesis.

1. Introduction.

Six species of two Genera, Panulirus (White 1847) and Jasus (Parker 1887) of the family Palinuridae have been recorded from Australian waters. Of these, only Panulirus longipes (Milne-Edwards), Jasus lalandei (Milne-Edwards) and Jasus verreaux (Milne-Edwards) are of economic importance. P.longipes occurs between lat. 22°S. and 34°34' S. along the coast of Western Australia. J.verreaux is found between similar latitudes on the east coast of Australia and J.lalandei has a circum-polar distribution between the limits of lat. 21°S. and 48°S. J.lalandei has been recorded doubtfully from Juan Fernandez and is exploited commercially in Tristan da Cunha, South Africa, Australia, New Zealand, St. Paul and New Amsterdam. In Australia J.lalandei is confined to Tasmania and the south coast of Victoria, South Australia and Western Australia. Two forms of J.lalandei have been described (Holthuis 1947), Jasus lalandei lalandei from Australia and South Africa and Jasus lalandei frontalis from all other localities. Local distribution is limited to rocky bottoms and reefs. The fishery extends from inshore reefs to the edge of the continental shelf, but fishing is rarely practised in depths greater than 50 fathoms. The commercial catch of J.lalandei is important in Tasmania, South Australia and Victoria, both for local consumption and in latter years for export.

Members of the Palinuridae, known as crayfish in

Australia are caught almost exclusively by means of baited beehive traps constructed of wire-mesh with entrance-funnels of woven cane. The type of vessel employed in the fishery ranges from open dinghies, operating less than a dozen traps to quite large diesel powered vessels capable of extended cruises and operating more than 60 traps. Fishing is highly selective, extensive use of echo-sounding being employed. Boats that make trips longer than one day are fitted with wells or holding tanks as South Australian health regulations require crayfish to be landed alive. Most professional fishermen employed in the industry fish exclusively for crayfish during the fishing season, but are usually equipped to fish for scale-fish or sharks during close seasons. Occasional fishermen normally employed elsewhere, fishing during holidays or the off-season from other seasonal employment, supplement the ranks of regular crayfishermen in some areas.

Since the end of World War 11 the crayfishing industry has developed rapidly. By 1958 the live weight of crayfish landed at South Australian ports had increased from 771,000 pounds in 1947 to 4,460,000 pounds. During the period 1958-61 catches decreased somewhat on the 1958 maximum to 3,500,000 pounds in 1960 and 3,721,000 pounds in 1961.

Despite the commercial importance of J.lalandei its biology is not well known. The most extensive investigations

were concerned with South African stocks, the results of which were published in a series of reports by Gilchrist and Von Bonde from 1913 to 1936. Bradstock (1950) investigated samples of J.lalandei from New Zealand. Limited investigations have been made by Challenger (1943) and Sheard (1949). Hickman (1946) studied samples of J.lalandei from Tasmanian waters. Hickman's work is the only published report of any length concerning J.lalandei from Australia, but results were based on samples observed from a single locality. Application of these results is therefore difficult and there is little evidence that they have been incorporated in regulations enforced by Australian authorities. It must therefore be assumed that regulations in force at present are more or less arbitrary.

Regulations governing the exploitation of crayfish differ for Australian State and Commonwealth waters. In South Australia regulations specify minimum legal length and closed seasons; berried females may not be taken, and diameter of traps is limited. In Victoria, Tasmania and New South Wales the number of traps per boat is limited in addition to the restrictions already mentioned for South Australia. Western Australian fishermen may fish only one defined area per season, nominated by the fishermen.

In this investigation I have studied the growth-rate of juveniles, the size of crayfish at sexual maturity and

their behaviour in searching for food and shelter because this information is important in exploiting existing stocks and in planning the management of the fishery.

The great distance from the laboratory to crayfishing ports prevented extensive field-work. This meant that observations had to be made on animals maintained in the laboratory. The development of adequate methods of maintenance was therefore a necessary part of this project. Much time was spent at the beginning of this study designing and installing adequate aquaria and associated equipment. The development of a suitable routine for maintaining crayfish in captivity for extended periods required much experimentation as did adapting skin-diving for the collection of small juvenile crayfish. Satisfactory transportation of very small crayfish also presented unforeseen problems, which had to be solved early in the project. A major section of this study was therefore associated with learning how to keep J.lalandei living healthily in the laboratory. Very little reliance can be placed in results obtained from animals maintained under poor conditions in the laboratory.

2. Methods for catching and keeping crayfish.

2.1 Aquarium-equipment.

2.11 Aquaria. Aquaria were constructed of $1\frac{1}{4}$ inch meranti planks with bottoms of $\frac{3}{4}$ inch marine plywood. Initially all aquaria were sealed with bitumen-paint, which proved quite satisfactory, although needing regular upkeep. Later aquaria were provided with fibre-glass linings, which gave good seals and required no maintenance.

Dimensions of aquaria were governed by the size and shape of space available in the laboratory and the purpose for which they were to be used. Aquaria used for keeping stock-animals were 6 ft. by 3 ft. Experiments done with single animals were conducted in aquaria 4 ft. by 3 ft. and aquaria 5 ft. by 2 ft. were divided into compartments 12 inches square for segregation of animals during ecdysis. The depth of water in all tanks was between 10 and 12 inches. A range of smaller glass aquaria was also used for more direct observation.

2.12 Air supply. Air was supplied by a 1 H.P. compressor and piped through clear polythene tubing and porous blocks to aquaria. Air was supplied continuously and concurrently with circulating water.

2.13 Water supply. All aquaria were supplied with circulating sea-water. Water was pumped from an inlet six feet below low water into a wooden storage tank sealed with

bitumen-paint. The pump was a "Davy" deep well, jet pump, manufactured with a cast, gun-metal pedestal and stainless steel shaft. This type of pump was essential as the height required to be pumped was too great for a lift-pump.

The storage-tank was equipped with a "Penn" float-switch, which operated the pump when the tank was half full. Water gravitated from the storage-tank to the laboratory where aquaria were supplied from a glass manifold. Flexible polythene pipes carried water from the manifold to aquaria where it was sprayed into them through glass-jets. All other piping was polythene agricultural and fittings were of glass, plastic or ceramic. All aquaria were fitted with constant-level overflows and after circulating, water overflowed to waste. Incoming water was not filtered in any way.

2.14 Maintenance of water-pipes. Black polythene agricultural pipes required little maintenance, a thorough flushing every six months preventing any blockage. Marine growth was negligible and settling sediment was never enough to restrict flow.

During summer, bacterial slime often sloughed off the clear polythene pipes and blocked the outlet jets. It was therefore necessary to remove bacterial growth as a fortnightly routine.

2.15 Refrigeration. During summer, the water was

cooled by a refrigerator. Water from the main storage-tank gravitated through a plastic ball-cock to a refrigeration-tank, which held 150 gallons. Water was supplied to aquaria from a glass manifold through clear polythene tubing and overflow water was piped to a sump, which held 18 gallons. The sump was fitted with a "Penn" sump-switch, which operated a $\frac{3}{8}$ inch "Jabsco" plastic, self priming pump. This pump returned water from the sump to the refrigeration-tank for recooling and recirculation. The refrigeration unit was a "Werner" 2 H.P. water cooled compressor, controlled by a thermoregulator immersed in the refrigeration-tank, which was insulated with three inches of cork.

The wetted surface of the refrigeration-tank was made of Mo. stainless steel with the refrigerant pipes brazed to the outside. All other fittings to the tank were stainless steel. Pipes were plastic and pipe-fittings were either glass or plastic. A combination overflow, drain was installed in the refrigeration-tank to allow a daily replenishment of at least 60 gallons. A diagram of the system is shown in figure 2.01. This system of refrigeration allowed water in aquaria to be kept at 15 $\pm$ 0.5^{o}C. even though incoming water reached a temperature which would have killed the crayfish.

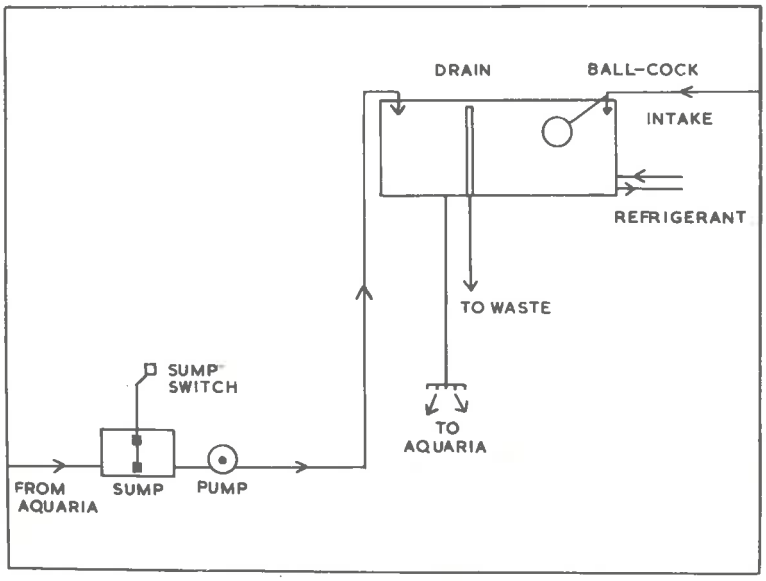


Figure 2.01: A semi-closed system of refrigeration used whenever the temperature of incoming sea-water exceeded 15°C.

2.16 Maintenance of aquaria. Aquaria must be kept clean. Otherwise the water quickly becomes polluted by the finely divided waste from feeding and faeces. Aquaria were cleaned daily by siphoning all waste food and faecal matter from them. All broken shell and other debris, which trapped pollutants was removed weekly.

2.2 Collection of experimental animals. Much use was made of professional fishermen, who provided monthly

samples of undersize animals for examination of gonads and to replenish stocks. All of these animals were caught in baited traps. The size range was limited and animals below 7 cm. total carapace-length were rare. Smaller animals were collected almost exclusively by skin-diving, which proved to be a quick and relatively easy method. It also had the added advantages that animals in all stages of the moult-cycle could be caught and their gut-contents was not contaminated by the bait.

Self-contained breathing apparatus was used on some occasions, but proved to be too cumbersome, preventing the diver from entering many of the smaller caves. This equipment had the added disadvantage of being difficult to recharge in remote areas. These difficulties were overcome by the use of "hooker" equipment. In this apparatus air is supplied from cylinders of compressed air. The cylinder either rests on the bottom or is carried by the diving tender. Air is supplied to the diver through small diameter, thick walled plastic tubes, usually alkathene or polythene, which are buoyant. A reduction valve and normal "aqualung" demand mouth-piece complete the breathing apparatus.

Although the "hooker" apparatus tethers the diver to his supply of air, air-pipes are usually 100 or 200 feet long and the amount of equipment carried about the body

is strictly limited. This allows much more freedom of movement and allows searching under ledges and caves that otherwise would have to be neglected.

Normal skin-diving flippers, weights and face-mask completed the basic equipment and although not essential, rubber diving suits are an advantage, allowing the diver to remain under water for much longer periods. In this case "Pirelli" dry suits were used, although wet suits have the advantage of being more durable and are easier to use.

The technique of collecting by skin-diving was simple as satisfactory catches could be made in shallow water. After the diver had located a source of animals, he herded the crayfish into a corner of the cave or ledge where they were relatively easy to catch. He then either placed the captured animals in a net or surfaced and placed them directly into the diving tender. The success of this method depended on finding crayfish in suitable caves. Many caves containing crayfish were not more than undercut ledges, which the diver could not enter far enough to reach the crayfish. Once driven from their caves into the open, crayfish were rarely caught, but a piece of kelp wrapped around the diver's hand usually offered sufficient disguise to increase the catch-rate significantly.

This method of capture proved satisfactory for

obtaining small animals from 4.0 to 8.0 cm. total carapace-length, in fact larger animals were rarely seen in the areas near to shore where most of the diving was done. Daily catches were stockpiled in wire cages until the required number of crayfish had been obtained. Deaths in holding cages over a period of three or four days were few and little damage to the animals resulted from such enclosure.

Two other methods of capture proved successful. Baited ring-nets placed near caves and pulled at intervals of about half an hour captured small crayfish as did dab-netting. This technique consists of dropping a line baited with fish heads near caves containing crayfish and leaving about fifteen minutes. The line is then carefully drawn up with the feeding crayfish still hanging to the bait. As soon as possible a landing net is moved under the hanging animal, which is caught in the net when it is lifted clear of the water. Although these two methods caught crayfish they were laborious and on occasions much time was wasted before a source of animals was located.

On several occasions baited traps of similar design to those used commercially were placed in holes in the reef where at least forty small crayfish had been observed previously. Although the catch of crabs was large and crayfish were still present in the holes after twelve hours

fishing, no crayfish was caught by this method. Lindberg (1955) could not catch Panulirus interruptus smaller than 7½ inches in overall length in beehive traps.

Methods that depend on a food-bait have several disadvantages: (a) Searching for a good place to fish from the surface often takes a lot of time. (b) Only intermoult stages come to the baits. (c) There is no chance of selecting particular sizes or sexes. Diving is not restricted in this way and has the additional advantage that the animals can be observed living naturally.

2.3 Methods of transportation. Crayfish caught by fishermen based at Port Adelaide were delivered directly from the wells of their boats. These animals had to be transported only a few hundred yards to the laboratory so few precautions were needed. Crayfish obtained from outports had to be transported considerable distances and more elaborate precautions were needed.

Animals longer than 8 inches were the easiest to handle and survived a trip by road of 7 or 8 hours that killed smaller animals. Packing in dry hessian bags or fish boxes was adequate protection during cool weather provided the crayfish were kept out of the wind and packed to prevent them moving in their containers.

When transport by road was not possible, crayfish were packed tightly in damp sea-weed in an aluminium

fish box and the lid wired to prevent movement. The death-rate among animals flown from Mount Gambier and Port Lincoln was less than one per cent.

Initially small animals obtained by diving were difficult to transport. After some poor returns, a heavy packing case was constructed, which contained deck-trays floored with sacking. Crayfish were packed not more than one layer per tray and then packed in damp, washed sea-weed. Care was taken to pack the sea-weed tight enough to prevent the crayfish moving, yet loose enough not to place much pressure on them.

The box was wrapped in hessian to stop the crayfish from drying out. In hot weather they were transported only at night. With practice I learned to keep the death-rate down to about 5 per cent. Intermoult animals survived better than pre- or postmoult animals and were more difficult to damage at capture.

2.4 Selection of experimental animals. Whenever possible damaged animals were rejected. Even when animals lacking appendages were kept, they were not used in growth by weight studies. The crayfish that were used for studying growth were first divided into arbitrary classes according to their size. There were as few as 20 animals in some of the classes because no more could be got from the stocks that were maintained at that time in the aquaria.

An aquarium 6 ft. by 3 ft. usually held a stock of about 10 nine-inch crayfish, but in an emergency double this number could be safely maintained for several weeks provided water and air were kept circulating.

2.5 Tagging in the laboratory. All animals were tagged individually soon after their arrival. Small discs of soft plastic were numbered with a "Marktex" pen and wired to the base of the second antennae with nichrome wire. The nichrome wire was first sheathed in coloured, plastic spaghetti, which served two ends. It increased the diameter of the wire, reducing the tightness of twists and thus reducing wire-fatigue. Different sizes and sexes could be designated easily by using different coloured, plastic spaghetti for each class.

This type of tag was quite satisfactory and durable. Tags were never lost and did not inconvenience even the smallest crayfish used in this study.

2.6 Feeding. Crayfish were fed routinely every second day on chopped fish, tommy ruff (Arripis georgianus) or mullet (Agonostomus forsteri), whichever was available more readily. Squid (Sepioteuthis australis) was used in season and chopped beef or beef-heart was used in emergency. Of these foods, squid appeared to be preferred and had the advantage of keeping well if frozen and did not decompose after several days in aquaria. Chopped beef was not eaten

after a short period of immersion and decomposed quickly, contaminating the water.

A source of living food, cockles (Katelysia scalarina) or mussels (Modiolus spp.) was maintained continuously. These two molluscs lived quite well in aquaria and provided the crayfish with a necessary supplement of calcium. Sand-crabs have been kept in aquaria with crayfish for several months without being eaten, but were eaten immediately they were killed.

Several types of green and brown algae were supplied as a vegetable supplement. Crayfish used it only as shelter and I did not use it after an initial trial.

2.7 Shelter. Short lengths of earthenware pipe placed in the aquaria were occupied by crayfish during the day. Crevices formed by scattered rocks were also soon occupied by crayfish.

2.8 Care of crayfish through moult. From a week before till a week following moult, crayfish are extremely vulnerable and require special care. All experimental animals were tested weekly to detect those about to moult. These animals were segregated in a partitioned aquarium and kept solitary until each animal had hardened completely after ecdysis. Early detection of moult and subsequent segregation was necessary for several reasons:

(a) During the period immediately preceding moult,

crayfish do not feed and tend to isolate themselves. Following moult, the exoskeleton is soft and movement is weak. In this condition they are likely to be damaged by other crayfish. Also they must be handled carefully or they may lose appendages.

(b) If more than one animal moulted in the same aquarium during the same night, identification was difficult as their tags were shed with the exuviae.

(c) Segregation allowed direct observation of individual animals and physical changes during moult could be measured as a routine.

2.9 Death of captive crayfish.

2.91 Lethal temperature. Lethal high temperature was the greatest single cause of death among captive crayfish. In nature crayfish probably never encounter temperatures above 19°C. The maximum temperatures recorded at the surface during 1959 for New Amsterdam and St. Paul by Grua (1960) were 18.5°C. and 17°C. If higher temperatures are encountered in nature, crayfish are able to move into deeper and cooler water. This was impossible for captive animals and temperatures of water in aquaria often reached 30°C. for short periods and remained above 24°C. for longer periods during summer.

Figure 2.02 shows total deaths minus those that could be explained by other factors not including temperature

plotted against the monthly average temperature of water in aquaria. Deaths have been converted to percentages of the total number of animals in stock during each month. Table 2.01 shows the relative figures included in figure 2.02.

Table 2.01: Relationship between death and temperature of water.

Month	1959					1960					1961				
	A	B	C	D	E	A	B	C	D	E	A	B	C	D	E
Jan.						22.8	28	10	9	34.3	23.2	49	29	26	53.0
Feb.						21.8					23.4	20	3	3	15.0
Mar.						21.0					21.1	17	2	2	11.8
Apr.						17.7					19.1	56	7	7	12.5
May.	14.8	40	2	2	5.0	13.5					15.6	50	6	4	8.0
Jun.	13.4	40	3	2	5.0	11.7	58	3	1	1.7					
Jul.	11.7	36	1	1	3.0	10.8	57	9	1	1.8					
Aug.	13.6	35	3	2	5.7	11.7	46	1	0	0.0					
Sep.	15.0	32	1	1	3.1	13.5									
Oct.	16.1	31	1	1	3.2	16.2	45	2	0	0.0					
Nov.	19.5	30	3	3	10.0	17.2	43	3	1	2.3					
Dec.	19.3	28	3	1	3.6	21.3	75	26	5	6.7					

A = Average monthly water-temperature.

B = Number of animals in stock at the beginning of each month.

C = Total number of deaths.

D = Total deaths minus those of known cause.

E = D as a percentage of B.

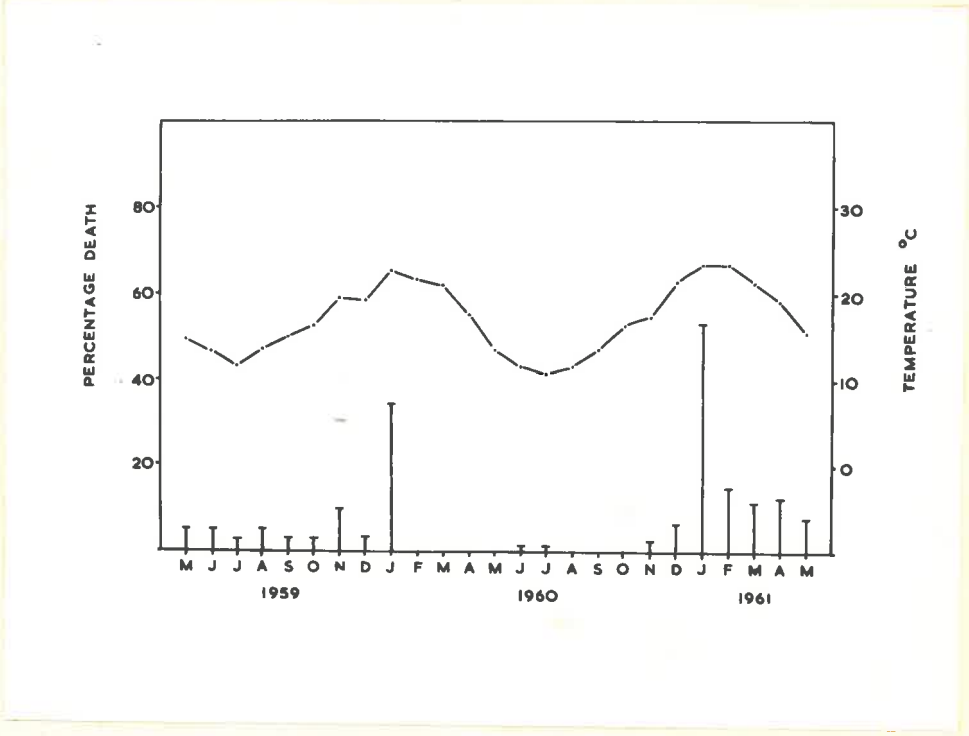


Figure 2.02: Relationship between death and temperature of water.

It can be seen from figure 2.02 and table 2.01 that unexplained deaths increased enormously in January 1960 and 1961. Both these months had average water-temperatures near 23°C., which approached the maximum monthly average recorded for each year. Since temperature was the only environmental factor that had apparently changed from winter months when death-rate was low, it can be assumed that the water-temperature during these months had at least approached the upper lethal limit for J. lalandei. Support

to this estimate of about 23° C. for the upper lethal limit is given by the overnight death of 64 crayfish after the water-temperature had risen to 22.8° C. from 18.2° C. fifteen days previously. These animals were not included in table 2.01 as they had been in the laboratory less than two months.

The above figures are related to normal, rather slow increases in temperature. Sudden increases in water-temperature above 15° C. resulted in mass mortality. In October 1961, water-temperature increased from 16 to 20° C. in three days killing the entire stock of sixty animals within seven days. These crayfish included several that had been maintained for 2½ years and had survived two previous summers.

Signs of death through heat. Intersegmental membranes become enormously distended and fluid is expelled under pressure when a membrane is punctured. Movement becomes progressively weaker, death occurring after a rapid decline in the rate of respiration.

2.92 Anoxia. The entire course of death through lack of oxygen has not been observed as such deaths were usually due to failures in power during the night. Failure in the supply of air or water alone never resulted in many deaths provided the temperature of water was low and aquaria were not crowded. When both systems failed at once.

70 to 80 per cent of the crayfish were likely to die within a few hours.

2.93 Desiccation. Death was rapid if crayfish were kept out of water during hot weather. Animals escaping from aquaria during winter have remained alive more than 24 hours. Death due to desiccation can usually be prevented in the laboratory.

2.94 Death at moult. Of 157 crayfish with carapace shorter than 7 cm. that moulted between May 1959 and April 1960, 17 or 11 per cent died at moult. Table 2.02 shows death-rate at moult recorded for these two years.

Table 2.02: Death of crayfish at moult.

Month	Number of animals moulted	Number of animals died at moult	Percentage
Jan.	22	12	54.5
Feb.	1	0	
Mar.	6	0	
Apr.	8	0	
May.	9	0	
Jun.	15	2	13.2
Jul.	14	0	
Aug.	16	0	
Sep.	11	0	
Oct.	18	1	5.5
Nov.	21	0	
Dec.	16	2	12.5

It can be seen that 12 of the 17 deaths at moult occurred in January, the month during which most deaths attributed to temperature occurred. This indicates that moulting is completed satisfactorily only within an optimum

range of temperature. During the same period used in table 2.02, 27 crayfish with carapace greater than 7 cm. moulted, of which 16 or 59 per cent died at moult. This higher mortality indicates that moulting is more dangerous for larger animals at least in the laboratory.

Signs of death at moult. Crayfish dying at moult during periods of high temperature showed the following signs. Death occurred early during ecdysis. The membrane between carapace and abdomen had split and some of the abdominal skeleton had usually been cast.

Death at moult during winter was rare in animals with carapace less than 7 cm., but was common in larger animals. Prior to ecdysis these animals were usually found near the centre of their aquaria standing well up on their extended legs, their abdomen extended straight behind them. Ecdysis was atypical and often not completed. The abdominal skeleton detached from the thoracic exuvium and was cast separately. Premature loss of the abdominal skeleton prevented the crayfish climbing out of its exuvium through lack of leverage and the animal probably drowned. The carapace-condyles of the new skeleton were usually free, leaving the carapace with no posterior attachment. Intersegmental membranes were distended, releasing much fluid under pressure when punctured. One or both of the fifth walking legs were usually broken and haemorrhage

from an unknown source was common. These signs indicate that ecdysis did not occur quickly enough. The animal increased in size before it was rid of the old skeleton preventing normal ecdysis.

2.95 Poisoning by heavy metals. On one occasion two brass fittings were inadvertently incorporated into pipes supplying the aquaria with sea-water. Heavy metals leaching from these fittings proved highly toxic. The entire stock of 45 crayfish died within four days of admission of the fittings. An analysis showed that water in the aquaria contained 0.24 mg./l. of copper and 0.19 mg./l. of zinc compared with 0.004 mg. /l of copper and 0.07 mg./l. of zinc in the water as it entered the aquaria.

Signs of death due to heavy metals. Autotomy of appendages was common and occurred soon after contamination of the water. Movement and respiration became progressively weaker and paralysis of muscles occurred shortly before death. Post-mortem examination showed that blood in the haemocoele was congealed in a solid jelly-like mass. The heart was hard and distended and contained no free fluid. No oxidation of the blood was apparent.

3. Behaviour.

3.1 Components of shelter.

Introduction. Observation of animals maintained in the laboratory showed that short lengths of earthenware pipe were quickly occupied. When the number of animals exceeded the number of pipes, the remaining animals were almost always found backed into a corner of the aquarium. Crevices formed by broken pieces of pipe or rock were also used as shelters and appeared to be equally effective.

In nature divers rarely observe J.lalandei outside of caves. Lindberg (1955) observed that P.interruptus invariably sought a solid support after foraging. He found lobsters in sea-caves, rock-crevices, on isolated pilings and A frames. Occasionally gorgonians and eel-grass were used as cover, but lobsters were never observed in open, sandy or muddy areas.

These observations indicated that shelter was important during the day and that suitable shelter probably had several components. A light-gradient and probably a tactile stimulus appeared to be two requirements for shelter. The following experiment was done to determine the relative importance of these factors as requirements for shelter.

Materials and methods. Six shelters were constructed of wood at each end of an aquarium 6 ft. by 3 ft.

filled with 10 inches of water. Each shelter was 4 inches wide, 6 inches high and 8 inches deep. Initially the shelters had no roof, which allowed them to be covered with a sheet of glass or plywood, or to remain unroofed. Roofing materials were compared in the following way.

Six intermoult crayfish of the same size were used in each comparison, which was duplicated. Roofs were alternated between shelters daily and the number of animals in each set of shelters was recorded each morning for ten days. The following comparisons were made.

1. One set of uncovered shelters open, the other closed.
2. One set of shelters roofed with glass, the other uncovered.
3. One set of shelters roofed with plywood, the other with glass.
4. One set of shelters roofed with plywood, the other uncovered.

Results were compared by means of a x^2 test.

Results.

Table 3.01: Crayfish occupying unroofed shelter each morning for ten days.

	Sheltered	Unsheltered	P
Observed	45	15	<0.001
Expected	30	30	
Observed	48	12	<0.001
Expected	30	30	

It can be seen from table 3.01 that the crayfish entered the shelters, even though they offered no shelter from above, in preference to remaining in the open part of the aquarium. Since the possible influence of a light-gradient was reduced as much as possible, a natural tendency to back into crevices was indicated. Crayfish at rest in their shelters, almost without exception, attempted to have as much of their bodies in contact with the walls of the shelter. Often they were observed lying diagonally along the shelter with legs extended to the side slightly so they were in contact with three sides of the shelter. These observations suggested that a tactile stimulus was a necessary component of shelter.

Table 3.02: Crayfish occupying shelter covered with a sheet of glass each morning for ten days.

	Glass Roof	No Roof	P
Observed	33	27	$\langle 0.5 \rangle 0.3$
Expected	30	30	
Observed	31	29	$\langle 0.9 \rangle 0.8$
Expected	30	30	

It can be seen from table 3.02 that the two shelters do not differ significantly. Although the roof was low enough to be touched by the antennae it appears that a roof does not need to be sensed mechanically if it is a necessary component of shelter. No attempt was made to keep the antennae in contact with the roof. The antennae of crayfish at rest were either pointed forward through the opening of the shelter or folded along the back of the animal.

Table 3.03: Crayfish occupying shelter covered with plywood, the other with glass, each morning for ten days.

	Plywood Roof	Glass Roof	P
Observed	42	18	$\langle 0.01 \rangle 0.001$
Expected	30	30	
Observed	40	20	$\langle 0.01 \rangle 0.001$
Expected	30	30	

It can be seen from table 3.03 that the two shelters differ significantly. It is therefore apparent that a

light-gradient is necessary for a shelter to be optimal.

Table 3.04: Crayfish occupying shelter covered with a sheet of plywood each morning for ten days

	Plywood Roof	No Roof	P
Observed	49	11	< 0.001
Expected	30	30	
Observed	49	11	< 0.001
Expected	30	30	

This comparison was made merely to complete the series as the result should have been similar to that obtained in the previous comparison. It can be seen from table 3.04 that such is the case. The difference between shelters is slightly more significant however, which is probably due to the formation of a layer of silt from muddy water on the glass roof used in the previous comparison. The glass was not completely clear introducing a weak light-gradient.

Discussion. It is apparent that shelter has at least two components. Crayfish tend to hug the walls of a shelter, which suggests the necessity of a tactile stimulus. The second component and probably the more important of the two is the necessity of a light-gradient. It will be shown later that crayfish are normally nocturnal animals, which would account for their marked preference for dark shelters during the day. It will also be shown that the ability to gain and retain shelter is a very

important factor in the life of crayfish. Whilst searching for shelter crayfish naturally tend to back into crevices. Crevices with a solid roof will be occupied in preference to unroofed crevices. In the absence of these types of shelter crayfish will back into a depression at the base of some massive structure such as a rock and lie so that as much of their body as possible is in contact with the vertical wall. Sutcliffe (1956) also observed that P.argus tended to huddle in groups in the corners of a tank during the day if no shelter was provided. For this reason future experiments concerning shelter were done in aquaria lacking sharp corners.

3.2 A dominance order for shelter.

Introduction. Records of dominance relations among the invertebrates are few, and with the exception of a dominance order described for Polistes wasps by Pardi (1948) and a dominance order for the crayfish Orconectes virilis by Bovbjerg (1953), most are documentary. Allee and Douglis (1945) observed two rank hierarchies in the hermit crab Pagurus longicarpus. Douglis (1946) described dominance relationships for the lobster Homarus americanus and interspecies relationships between a variety of Crustacea. Aggressive actions have been noted in Cambarus virilis by Roberts (1944) and Sepia officinalis by Tinbergen (1939).

Aggressive actions were noted between captive specimens of J.lalandei early in this study. If food or shelter was limited, certain animals in an aquarium were able to obtain the available food or shelter to the exclusion of the others. Olsen (1958), by means of skin-diving, observed that large crayfish entered traps before smaller ones and very small animals did not leave their shelters to enter traps. This observation substantiates observations made by fishermen, who often catch single, large crayfish in a number of traps, indicating a possible size hierarchy.

Previous workers have usually relied on direct

observations of tension-contacts to define dominance orders. This is a laborious method and must tend to be subjective. Since the ability to gain and retain shelter appeared to be a dominance relationship, the following experiments were done, using retention of shelter as a measurable index of dominance.

Materials and methods. Both ends of two aquaria, 6 ft. by 3 ft. were blanked with plywood filler walls constructed of five segments joined at an angle of about 130°, converting the rectangular aquaria to effective ovals. The removal of 90° corners from the aquaria reduced the possibility of corners being used as shelter when experimental shelters were available. Three artificial caves constructed of plywood 5½ inches by 5½ inches by 9 inches were placed in each wall. Each shelter could be closed with a trap-door and running water and air were supplied from two supporting beams across each aquarium.

Seven crayfish were used in each replicate experiment. One shelter was opened on day 1 and an additional shelter opened according to a random series each day following until all were open. Animals occupying shelter were recorded each morning and the order of entry taken as a dominance order for shelter.

Two combinations of animals were observed; females of the same size and females graded in size. Each experiment

was duplicated and done at least twice.

Results.

1. Animals of the same size. Results were obtained from a replicated series of five experiments using the same animals in each replicate.

In each case a dominant animal was apparent from the outset, but the order of dominance below this first animal was difficult to determine. The fact that a straight line dominance order was not apparent from these results was not unexpected as most of the dominance orders cited in the introduction had been associated with differences in size. Two groups of animals ranging in size from 6 cm. to 11.5 cm. total carapace-length were therefore tested before the experimental technique and/or the hypothesis was rejected.

2. Animals graded in size. Results were obtained from a replicated series of four experiments using the same animals in each experiment.

In each case the largest animal was dominant from the outset. The order of entry of the other animals was not constant enough to delineate a straight line dominance order relating size with retention of shelter. Analysis of results were complicated in this experiment by the occurrence of cohabitation. The shelters, large enough for the largest animal in the series, could be occupied by more than one of the smaller animals. Cohabitation of the

smallest and largest animals was observed most frequently. The small animal entered a shelter, which was entered subsequently by one of the largest animals. Almost without exception the larger animal did not appear to be aware of the smaller animal even though it attempted to leave the shelter.

Although the two above experiments had failed to demonstrate a stepwise dominance order for shelter, the hypothesis was not rejected on the following grounds. The experiments had demonstrated that one crayfish was dominant over the others. The difference of one day in the order of entry effectively disrupted a stepwise order, which may have taken some time to develop. Regular observations made during the above experiments also supported the hypothesis of a dominance order.

Once opened, shelter was entered quickly, usually within five minutes and the shelter was either retained or relinquished to other animals according to fixed patterns of behaviour. On entering a shelter the occupying animal remained in the front half of the shelter standing well up on its legs with antennae testing the area immediately facing the shelter. This was considered to be the "alert" position compared with the normal position of rest in which the ventral surface is allowed to rest on the substratum and the legs are tucked into the sides. When shelter was

limited, animals occupying shelter were almost always observed in the "alert" position for some hours after entry. At the approach of another animal the antennae of the sheltered animal were oriented towards the approaching animal. Subsequent behaviour depended on whether the occupying animal defended its shelter or was evicted.

On many occasions the mere approach of another animal was sufficient to evict a sheltered animal. Actual contact was not necessary, the sheltered animal simply leaving the shelter allowing the new arrival to enter it.

In other cases the animal occupying shelter, although not actually defending its shelter, had to be evicted by force. The occupying animal retreated into the shelter still following the approaching crayfish with its antennae. If the new arrival intended to enter the occupied shelter it usually attempted to back into it, but was prevented by the bulk of the occupying animal. After this proceedure had failed the challenger either discontinued its attempt or left the shelter to face the occupant in frontal attack. The challenger grasped the occupant with its first pair of walking legs and pulled it out of its shelter with a series of jerking pulls. Once removed from its shelter the evicted crayfish always moved rapidly away from the shelter and allowed the challenger to enter it.

Defence of shelter by apparently dominant animals

was very vigorous. This pattern of behaviour was observed more frequently than those described previously as available shelter was usually taken by the more dominant animals first. If a crayfish occupying shelter intended to defend its shelter, it quickly oriented its antennae towards approaching animals. Although the flagella of the antennae formed quite an effective barrier, they rarely prevented another crayfish approaching closer. If such animals came within 6 to 8 inches of the shelter without stopping, the occupant came part-way out of its shelter, stood high on its legs and waved its first walking legs in mantid fashion at the challenger. This "threat" attitude often prevented further approach and resulted in immediate retreat of the challenging animal. In other cases the occupying animal made short darts from its shelter striking at the challenger with lowered antennae. In a few cases it actually grasped the challenger with its first walking legs, forcing the captive animal to struggle away. Animals that chose to defend their shelters were never observed to be evicted in over 40 observations of this behaviour.

On the basis of these observations the following simpler experiment was done.

Materials and methods. The equipment was the same as that used initially. Four crayfish were used in each experiment and either two or three shelters opened according

to a random series on alternate days. Animals occupying shelter were recorded each morning for 28 days. If results did not clearly define a dominance order then the following analysis was possible.

The number of times each animal was in or out of shelter when two or three shelters were open was recorded. If no dominance order existed, it could be expected that each animal would find shelter on seven days when two shelters were open. When three shelters were open each animal could expect to find shelter 10.5 times. The sum of $\frac{(\text{observed} - \text{expected})^2}{\text{expected}}$ calculated for ins and outs for two and three shelter-days for each animal equals x^2_3. A significant x^2 would indicate the existence of a dominance order. Twenty eight days was the minimum period before analysis was possible, but a shorter period of 14 days or more was deemed satisfactory if a straight line dominance order was apparent from the beginning.

Three combinations of animals were used in three replicated experiments.

(1) Four animals of the same size and sex.

(2) Two animals of each sex, but the same size.

(3) Four animals graded for size.

Results.

(1) Replicate experiments were done using females between 9.41 and 9.50 cm. total carapace-length (T.C.L.)

in one and between 9.07 and 9.17 cm. T.C.L. in the replicate. Results were recorded for 26 and 14 days respectively.

Table 3.05: Dominance order for shelter in animals of the same size and sex.

			2 Shelter		3 Shelter	
Experiment	Animal	Possible	In	Out	In	Out
1.	A	13	13	0	13	0
	B		13	0	13	0
	C		0	13	13	0
	D		0	13	0	13
1a.	A	7	7	0	7	0
	B		7	0	7	0
	C		0	7	6	1
	D		0	7	1	6

(2) Replicate experiments were done using animals between 9.40 and 9.43 cm. T.C.L. in one and between 9.20 and 9.40 cm. T.C.L. in the replicate. Results were recorded for 23 days in both cases.

Table 3.06: Dominance order for shelter in animals of the same size, but different sex.

			2 Shelter		3 Shelter	
Experiment	Animal	Possible	In	Out	In	Out
2.	A Female	14	14	0	14	0
	B Male		13	1	14	0
	C Male		0	14	13	1
	D Female		1	13	1	13
2a.	A Male	14	14	0	14	0
	B Female		14	0	14	0
	C Male		0	14	11	3
	D Female		0	14	3	11

(3) Replicate experiments were done using animals between 7.70 and 9.47 cm. T.C.L. in one and between 7.44 and 9.04 cm. T.C.L. in the replicate. Results were recorded for 28 days in both cases.

Table 3.07: Dominance order for shelter in animals graded for size.

			2 Shelter		3 Shelter	
Experiment	Animal	Possible	In	Out	In	Out
3.	A 9.47	14	14	0	14	0
	B 9.08		14	0	13	1
	C 8.59		0	14	8	6
	D 7.70		0	14	7	7
3a.	A 9.24	14	14	0	14	0
	B 9.0		14	0	14	0
	C 8.56		0	14	6	8
	D 7.44		0	14	8	6

It can be seen from tables 3.05, 3.06 and 3.07 that the design of the experiment does not allow the first two ranks to be separated, but allows the bottom ranks to be defined. Table 3.05 shows that dominance, subordinance relations are developed in animals of the same size. Similar results are shown in table 3.06, from which it can be seen that sex is not an important factor in the formation of a dominance order. Results shown in table 3.07 do not differentiate the first and second pairs of animals, but show that the two larger animals were dominant over the two smaller.

Some difficulty was encountered in obtaining results for a satisfactory period due to the death of experimental

animals. Replacement of dead animals meant the experiment had to be repeated and results to the time of death deleted. Each of the three replicate experiments had to be started at least twice before results could be collected. Eleven deaths occurred during observation of the six groups of animals. In each case the animal that died was one of the subordinate pair. On nine occasions the lowest ranked animal died and on two occasions the third ranked animal died. Death was sudden or occurred after one or two days of atypical behaviour. No obvious external lesion could be detected. Animals lacking appendages or appearing below normal in any way were not used in the experiments, limiting the possibility of health influencing the ranking order.

In seeking a cause for deaths recorded during this series of experiments, the following facts must be taken into account. As far as could be determined the health of all animals was equivalent at the beginning of an experiment. Only animals in the second ranked pair died during the experiments. Death was sudden and no obvious lesions were found on post-mortem examination.

These observations indicate that stress placed on low ranked crayfish by the failure to obtain shelter is sufficient to kill them.

Conclusions. Available shelter is taken by crayfish in order of dominance. One sex is not dominant over the

other, but large animals dominate small ones.

Discussion. Bovbjerg (1953) showed that a dominance order was established in O.virilis by observing tension-contacts between individuals of the same size and sex, maintained in groups of four and provided with no shelter. Such a dominance order was stable and was usually established on the first day. Moulting of animals, regardless of rank, was followed by a period of complete subordinance. The same ranking was resumed after recovering from moulting. Limited observations indicated that large individuals dominated small ones and males dominated females. Although territoriality was not demonstrated, smaller animals were observed to defend shelters successfully against larger animals.

On the basis of limited observation in the field, Bovbjerg suggested that the dominance order as demonstrated in the laboratory probably does not exist in nature. He postulated a system of random, initial contacts, the outcome of which depends on such factors as size, sex and innate aggressiveness. He also suggested that population-density and size may influence the dominance order and that aggressive behaviour may be controlled by sinus-gland hormones.

The use of tension-contacts to describe a social hierarchy in J.lalandei was difficult as activity during

daylight is minimal, limiting potential contact between individuals. Bovbjerg was able to divide tension-contacts into four easily recognized categories. Such categories could not be recognized easily while observing several individuals of J.lalandei foraging in the same aquarium, although aggressive behaviour occurred when food was placed in the aquarium. Bovbjerg's experiments were done in aquaria lacking shelter of any kind to eliminate the factor of territoriality. Although ability to gain and retain shelter was used as an index of dominance in the above experiments, the possible influence of territoriality on the dominance order was reduced by changing the available shelter daily. This meant that a new shelter had to be occupied and retained each day. The formation of fixed territories defended by the same animals was therefore not possible. The formation of a dominance order depended firstly on occupying available shelter before other animals and secondly on defending it successfully. It is doubtful whether territoriality in its full sense influenced the formation of a dominance order to any marked extent.

It is doubtful whether shelter would be limited so strictly in nature. Animals unable to occupy shelter in one area would be able to search elsewhere, which of course was not possible experimentally. The occurrence of such an absolute dominance order for shelter also appears

doubtful from underwater observation. The majority of shelters occupied by J.lalandei in nature are probably undercut ledges and small caves, quite different in structure to the experimental shelters, which could be occupied by only one animal. Observations made in the field while collecting experimental animals indicated that crayfish between 4 and 9 cm. T.C.L. live in cliques. Crayfish smaller than this were often observed singly, sheltered in small holes at the back of larger caves. Only a small number of crayfish larger than 9 cm. T.C.L. were observed, but observations made by Olsen (personal communication) suggest a tendency for large animals to be solitary. Similar findings were reported for P.interruptus by Lindberg (1955). He found that lobsters below 10 inches were usually located in groups under ledges or in large concentrations in small caves. Large lobsters were usually solitary in shelters just large enough for them, but this may have been caused by the type of shelter available.

The tendency for crayfish to aggregate in large caves indicates that dominance orders for shelter are rare in nature. However the existence of documentary evidence of dominance, subordinance relations regarding feeding behaviour makes it reasonable to assume that social hierarchies are inherent in populations of crayfish.

The formation of a dominance order for shelter in

areas of limited shelter would be an important behaviour pattern. The best shelters would be taken by the more dominant animals forcing subordinate animals to utilize inferior shelter or to move to other areas, making them more prone to predation. The formation of a dominance order as such in nature depends on the maintenance of discreet groups of crayfish for reasonable periods. Whether groups of crayfish function as entities in nature is not known, leaving the question of social hierarchy still in the balance. Future investigation requires underwater observation to determine the importance of territoriality. More extensive documentation of aggregation and types of shelter should be made and the existence of discreet groups or families within a population should be determined.

3.3 Food and feeding.

3.31 Natural food. Von Bonde and Marchand (1935) observed that J.lalandei is a scavenger when food is scarce, but that fresh bait is more efficient than stale bait. They also suggest that the structure of the mouth-parts indicates Molluscs eg. mussels as the chief food and reject fish as a source of food due to their much greater mobility.

Hickman (1946) examined the gastric mills of a large number of J.lalandei and found the remains of Molluscs, other crayfish, crabs, echinoids and sea-weeds. He also correlated a predominance of molluscan material with a peak catch of newly moulted females and suggested preferential feeding on calcareous food for the necessary hardening of the skeleton.

Lindberg (1955) examined the stomachs of a large number of P.interruptus and found a predominance of calcareous food such as worm-tubes, Molluscs, sea-urchins, Crustacea, coralline algae and Bryozoa. Algae and the remains of fish were rarely found. He concluded that P.interruptus was omnivorous and was principally a scavenger. He also indicated that fishermen have larger catches when fresh bait is used in preference to stale.

George (1957) stated that P.longipes is a scavenger from his observation of sea-weeds, fragments of coral,

remains of fish, forams, fragments of shells and particles of sand in gut-contents.

At the beginning of this project the gastric mills from 30 specimens of J.lalandei caught by skin-divers near Cape Jaffa were examined. The stomachs ranged from empty to full and contained similar types of food to that described by other authors above. All species found in the gut-contents were predominant in the area and included Gastropods, Pelecypods, Crustacea, including other crayfish, prawns and crabs, sea-urchins, Bryozoa and algae with some particles of sand. No remains of fish were found, but few were observed in the area. With the exception of the Crustacea all other species were sessile or slow moving. However, the Crustacea, especially the prawns are capable of relatively fast movement and would have to be eaten dead if crayfish are scavengers. It is difficult to determine whether the Crustacea were taken alive, but several species of crabs and shrimps, including Leander intermedius, Paguristes frontalis, Naxia aurita, Ozius truncatus, Helice haswellianus and Ovalipes bipustulatus were maintained in aquaria containing crayfish and were not killed and eaten. On the other hand dead crabs and crayfish, especially their freshly cast exuviae were eaten. Food left in aquaria longer than one day when it had begun to putrefy was never eaten.

From these observations it is apparent that crayfish are normally scavengers, the capture of motile prey playing a minor role in the feeding behaviour of J.lalandei.

3.32 Mechanism of feeding. J.lalandei in aquaria feed according to a fixed pattern. When a foraging animal finds some potential food it is grasped by the first walking legs and maxillipeds. The animal then attempts to back into a shelter before actually eating the food. If shelter is not available near by, a corner of the aquarium is sought and only then does the animal begin to feed.

The mechanism of feeding is not efficient and much potential food is lost. The food is gripped firmly by the mandibles and the first walking legs are then used to pull the food away from the mandibles, tearing a small piece from the mass of food. The maxillipeds manipulate the food in a circular fashion and aid the first walking legs in tearing pieces from the food. This treatment tends to disintegrate a mass of food and a feeding crayfish is always surrounded by a cloud of small particles of food, which is lost and tends to pollute water in aquaria.

3.33 Detection of food. Lindberg (1955) stated that spiny lobsters detect their food by sight and smell, and that animals from which he had removed the antennules were less able to find food. He also found that blind animals exhibited normal foraging behaviour, but their

ability to catch moving prey was impaired. He found sensory hairs on all appendages and observed that detection of food by the legs was common.

Crawford and De Smidt (1922) found that the sense of smell was located primarily on the antennules of P.argus.

Visual and chemical detection of food appear to be complementary in J.lalandei, although visual detection does not appear to be very efficient. The antennules of foraging animals are constantly active, testing the arc of water preceding the advancing animal. Fish-blood introduced into an aquarium stimulates the activity of antennules and orientation towards the point of distribution. The bifid segments of the antennules, which have a thick fringe of sensory hairs, become active, and after testing the water, orient towards the stimulant. A piece of fish dropped into an aquarium in view of a crayfish is also followed by the antennules as it sinks. The antennules finally orient towards the particle of food and if it is close enough to the crayfish it is eaten.

Sensory hairs are present on the base of the walking legs and probably inside the branchial chamber. Often food is not detected until the crayfish walks over it. Similarly food placed to one side or behind a foraging crayfish is located probably by these sensory hairs. It will be shown later that crayfish normally feed during the hours of

darkness and that they can feed quite adequately in total darkness. It would therefore seem that location of food by chemical means is more important than visual detection.

Visual detection of food was demonstrated by the following observations. A glass aquarium, 24 inches by 16 inches by 12 inches was divided into two compartments by a glass partition. Animals starved for a week and placed in one of the compartments almost always attempted to obtain a piece of food or some other object dropped into the other compartment. The compartments were quite separate eliminating the possibility of chemical detection.

3.34 General patterns of feeding. Segregated animals were rarely observed to feed during the day unless food was placed within a few inches of them. During intermoult, animals occupying a shelter were rarely observed to leave it completely during the day to search for food. Crayfish would often forage quite actively whenever food was placed in an aquarium during late post-moult.

Observations made of animals feeding actively after dusk indicated that feeding was accompanied by aggressive behaviour. The larger animals in the group often obtained food to the exclusion of smaller animals. Smaller animals often relinquished food at the approach of larger ones, but more often the larger animal obtained the food by force.

It was not unusual to find almost all the animals in an aquarium fighting for food during a period of active feeding.

3.35 Preferential feeding.

Introduction. It has been suggested previously that crayfish are normally scavengers, but it is difficult to determine whether they feed selectively from the study of stomach-contents. The following experiment was done to determine whether crayfish feed selectively and to compare the catching power of some of the baits used by commercial fishermen.

Materials and methods. The experiment was done in an aquarium 3 ft. 6 inches by 3 ft. filled with 10 inches of water. A piece of earthenware pipe 9 inches long and 5 inches in diameter was placed in each corner of the aquarium as shelter. Four baits, tommy ruff, shark, rabbit and horseflesh, all used commercially were compared. A comparison was also made between fresh and stale fish and squid was compared with one of the best of the initial four baits. Three intermoult crayfish of the same sex and between 8 and 9 cm. T.C.L. were used in each experiment. Each animal was offered the same combination of foods for two consecutive periods of 24 hours, while the other two crayfish were segregated. Segregated animals were not fed during this period so that each animal was allowed to feed on only two days in every six.

A feeding recorder was built, which recorded the time and period of feeding at two baits. The recorder consisted of two baits hung from rods, which closed an electrical circuit when displaced from vertical. Completion of the circuit actuated a relay, which marked the displacement on a smoked drum. The baits had to be displaced at least two inches before the circuit was closed, reducing chance displacements by antennae or movements of the water.

The two baits were placed as near as possible the same distance from any shelter and baits were alternated between rods daily to reduce positional effects. All combinations of the initial four baits were compared and fresh baits were used each day.

Each crayfish was allowed to find its own shelter and the time spent at each bait for each period of 24 hours was calculated. Activity was scored by measuring the width of marks on the smoked drum to the nearest tenth of a millimeter. The sum of these measurements during a period of 24 hours was taken as the time spent feeding during that period. Linear measurements were not converted to measurements of time. Results from the three animals used in each comparison were totalled, thus results for each combination of food represent the time spent feeding at each bait for a period of six days. The time spent at each bait was then converted to a percentage of the time spent at both.

Results. Since the position of the baits was alternated daily, any positional feeding opposed to selective feeding could be easily detected. On only one occasion out of 24 trials did the crayfish go only to the bait nearest its shelter. On this occasion rabbit and horseflesh were being compared and results showed little difference in preference between these two. On all other occasions the crayfish either sampled both baits or followed one bait from one recorder to the other on the two days of comparison.

Table 3.08 Comparison of baits used commercially to catch crayfish.

Bait	Feeding Activity	Percentage	x^2
Tommy-ruff	17.8	81.6	8.7-0.01⟩P⟩0.001
Horse-meat	4.0	18.4	
Tommy-ruff	12.6	88.7	8.5-0.01⟩P⟩0.001
Rabbit	1.6	11.3	
Tommy-ruff	11.5	53.0	0.039-0.9⟩P⟩0.8
Shark	10.2	47.0	
Rabbit	4.7	47.9	
Horse-meat	5.1	52.1	
Rabbit	12.7	33.9	3.92-0.05⟩P⟩0.02
Shark	24.8	66.1	
Horse-meat	3.9	18.9	9.1-0.01⟩P⟩0.001
Shark	18.0	82.1	
Fresh fish	11.7	79.6	5.16-0.05⟩P⟩0.02
Stale fish	3.0	20.4	
Shark	10.6	45.0	0.22-0.7⟩P⟩0.5
Squid	13.0	55.0	

It can be seen from table 3.08 that tommy ruff is significantly different to horseflesh and rabbit but not to shark. Similarly shark is significantly different to rabbit and horseflesh. Rabbit and horseflesh do not differ significantly. Fresh fish is significantly different to stale fish, but the difference between squid and shark is non-significant.

Conclusions.

(1) Crayfish will feed selectively if given a choice of foods.

(2) Marine baits such as fish and shark are preferred to terrestrial baits such as horseflesh and rabbit.

(3) Fresh baits are preferred to stale baits.

(4) It is unlikely that crayfish would discriminate between a range of fish or terrestrial baits.

(5) Squid should be as efficient a bait as fish.

Discussion. The animals used in this experiment were smaller than the minimum legal size for crayfish in South Australia, but animals of this size are often caught by fishermen. It is therefore reasonable to assume that the feeding behaviour of undersize crayfish is similar to that of crayfish of legal size.

Although quite large differences in efficiency of various baits was apparent experimentally, it is often not feasible to use the bait with the greatest catching

power in practice. Soft types of bait such as fish and shark are eaten quickly by "sea-lice", which are prevalent on some South Australian grounds. This short-coming can be remedied to some extent by using two baits per trap, a bait of high catching power such as shark or fish and another that will not be eaten quickly by "sea-lice" such as horse or kangaroo-leg.

The differences observed between marine and terrestrial baits could be explained, firstly by the fact that terrestrial baits soon become stale when immersed in water, i.e. they lose their colour and become flaccid, and secondly, they would normally never be encountered. Fish on the other hand remains in good condition for several days.

3.36 Feeding rhythms.

3.360 Introduction. The rhythmic nature of biological processes is well known and many such rhythms have been documented. Recent reviews of the literature have been published by Pittendrigh (1958), Harker (1958) and Brown (1958, 1959). Rhythmic processes can be classified into two groups; those which occur as immediate responses to environmental changes, but do not persist when environmental conditions are kept constant, deemed exogenous and those which do persist in constant environmental conditions, deemed endogenous.

Observations made in the field and in the laboratory

indicated that J.lalandei is most active and feeds most at night. Fishermen expect larger catches from traps set overnight than they do from the same traps set during the day. Captive crayfish forage for food during the day only under exceptional circumstances such as during postmoult. Allen (1916) and Crawford and De Smidt (1922) claimed that larger catches of P.interruptus and P.argus are obtained on dark nights than on moonlight ones, although a correlation between feeding activity and the tides was suggested in the latter case.

Sutcliffe (1951) showed that catches of P.argus were greater on dark nights than on moonlight nights and preliminary experiments indicated that activity was controlled in the main by light-intensity.

The following experiment was done to detect a feeding rhythm and to erect an hypothesis concerning its control.

Materials and methods. A single feeding recorder similar to that used previously to describe preferential feeding was constructed. The apparatus consisted of a fish-bait wired to a rod with nichrome wire, which closed a low voltage circuit when displaced two to three inches from vertical. Completion of the circuit activated a relay, which recorded the displacement on a smoked drum. An alternating current was used so feeding was recorded as a solid block marked on the kymograph, which rotated once

every 24 hours. Each record for 24 hours was then divided into divisions of two centimeters, each division equivalent to one hour. Feeding activity was measured for each hour by measuring the width of each mark on the kymograph to the nearest tenth of a millimeter and summing them. Since this measurement was related directly to time the conversion was not calculated.

Experiments were done in aquaria 3 ft. 6 inches by 3 ft. filled with 10 inches of water. A piece of earthenware pipe 9 inches long and 5 inches in diameter was placed in each corner of the aquaria as shelter. Single animals were used for each record of seven days. Only intermoult animals of the same size were used. Continuous records for seven days were obtained for each animal and ten animals were used in each treatment. Day-length was changed by means of 20 watt fluorescent tubes mounted inside light tight cabinets erected above the aquaria and controlled by "Venner" time-switches. Normal feeding behaviour was recorded using diffuse light from windows in the laboratory.

Feeding activity was recorded for the following conditions of illumination.

(1) Normal diurnal period of light and dark.

(2) Reciprocal of normal diurnal period of light and dark.

(3) Acclimatization to normal diurnal period of

light and dark followed by constant light.

(4) Acclimatization to normal diurnal period of light and dark followed by constant darkness.

(5) Acclimatization to normal diurnal period of light and dark followed by alternating periods of 6 hours light and darkness.

(6) Acclimatization to alternating periods of 6 hours light and darkness followed by constant light.

(7) Acclimatization to alternating periods of 6 hours light and darkness followed by constant darkness.

3.361 Normal diurnal period of light and dark.

Table 3.09: The hourly feeding activity of ten crayfish, each observed for seven days. Figures for hourly activity are totals for seventy days.

P.M.				A.M.			
Time	Activity	Time	Activity	Time	Activity	Time	Activity
12	0.1	6	33.2	12	7.1	6	0.7
1	0.1	7	19.6	1	4.5	7	0.2
2	4.8	8	10.1	2	4.3	8	0.0
3	5.3	9	9.1	3	1.4	9	0.0
4	20.7	10	5.7	4	3.0	10	0.0
5	39.5	11	7.6	5	1.5	11	0.0

These records were obtained during June and July when it was quite dark by 6.30 p.m.

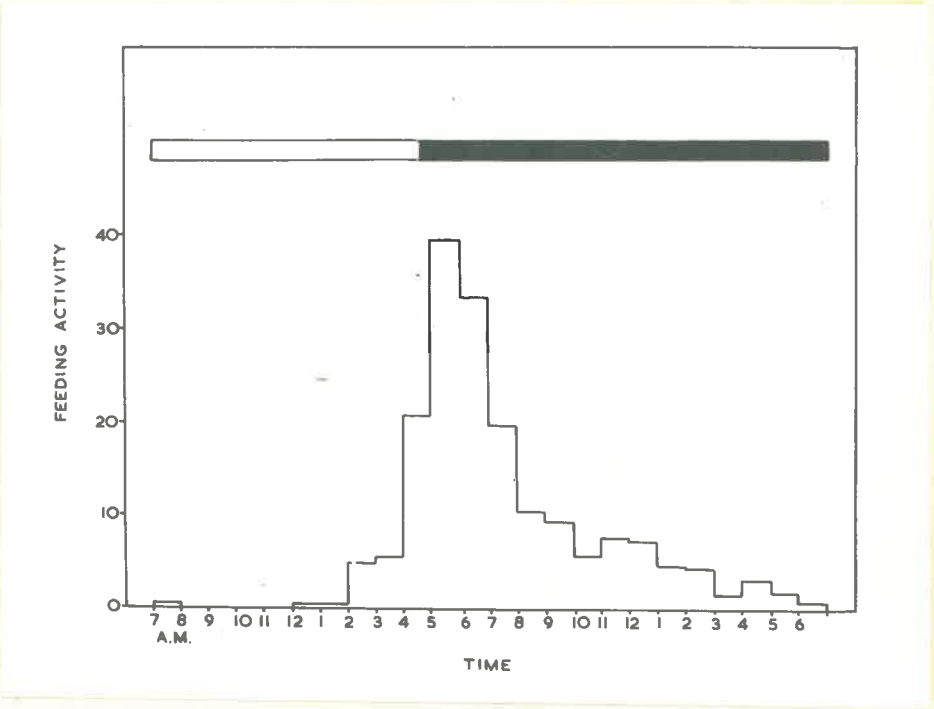


Figure 3.01: Feeding activity for normal diurnal period of light and dark.

From figure 3.01 it can be seen that no feeding occurred between 8 a.m. and 12 noon. A gradual rise in activity took place from 2 p.m. to 4 p.m. and between 4 p.m. and 5 p.m. the level of activity rose sharply, reaching a maximum between 5 p.m. and 6 p.m. Between 6 p.m. and 8 p.m. feeding activity declined rapidly, remaining at a low level between 8 p.m. and 8 a.m. and diminishing to zero activity between 8 a.m. and 12 noon.

Feeding activity is greatest at dusk, increasing significantly from a low level during the hour preceding and decreasing to a relatively low level two hours following. During this period of four hours, 63.3 per cent of feeding activity for the 24 hours occurred.

Harker (1960) defined six stages for the locomotor activity of Periplaneta americana during a period of 24 hours. Similar stages can be identified in the feeding activity of J.lalandei.

Stage A. Feeding activity increases from a low level two to three hours before the onset of darkness.

Stage B. Feeding activity reaches a maximum at dusk, i.e. activity is greatest during a period of rapidly decreasing light-intensity.

Stage C. A relatively high level of activity is maintained for a period of about two hours.

Stage D. Feeding activity decreases over a period of five hours.

Stage E. Feeding activity remains at a fairly low level until dawn.

Stage F. Feeding activity is minimal during a period from dawn to mid-afternoon.

3.362 Reciprocal of normal diurnal period of light and dark.

Darkness was maintained between 7 a.m. and 6 p.m. Uniform illumination was maintained during the remaining

period.

Table 3.10: The hourly feeding activity of ten crayfish, each observed for seven days. Figures for hourly activity are totals for seventy days.

P.M.				A.M.			
Time	Activity	Time	Activity	Time	Activity	Time	Activity
12	35.5	6	1.4	12	0.4	6	2.9
1	25.5	7	0.5	1	0.8	7	24.8
2	25.2	8	1.3	2	0.5	8	15.3
3	30.9	9	1.0	3	1.9	9	11.0
4	30.4	10	2.1	4	6.5	10	31.5
5	14.2	11	1.4	5	2.2	11	35.2

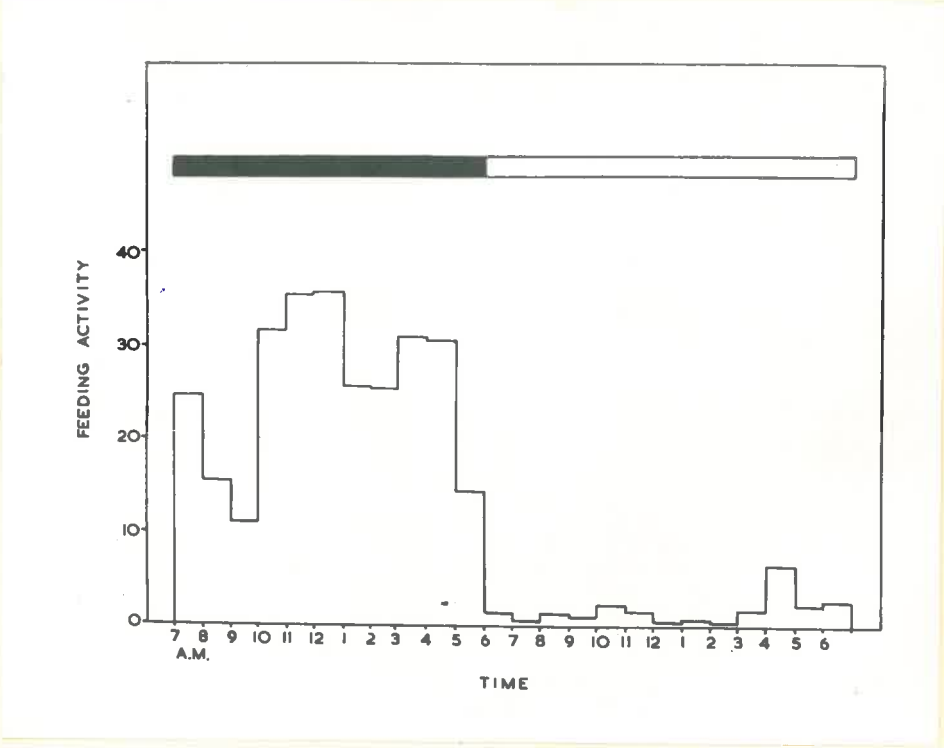


FIgure 3.02: Feeding activity for reciprocal of normal diurnal period of light and dark.

It can be seen from figure 3.02 that feeding activity increased sharply from a very low level at the onset of darkness. Feeding activity was maintained at a high level during darkness, decreasing sharply to a low level at the onset of the light period. Feeding activity remained at a fairly constant low level during the light period.

In every case the above feeding pattern was apparent from the first day of observation. No residuum was apparent during this experiment. During the period of darkness 92.4 per cent of feeding activity occurred.

3.363 Acclimatization to normal period of light and dark followed by constant light.

Table 3.11: The hourly feeding activity of five crayfish, each observed for fourteen days. Figures for hourly activity are totals for seventy days.

P.M.				A.M.			
Time	Activity	Time	Activity	Time	Activity	Time	Activity
12	45.8	6	7.5	12	5.2	6	3.3
1	9.2	7	9.8	1	6.2	7	3.7
2	12.3	8	5.0	2	3.5	8	2.7
3	15.6	9	5.2	3	4.0	9	4.6
4	7.5	10	6.7	4	4.1	10	26.4
5	11.1	11	2.3	5	4.8	11	22.5

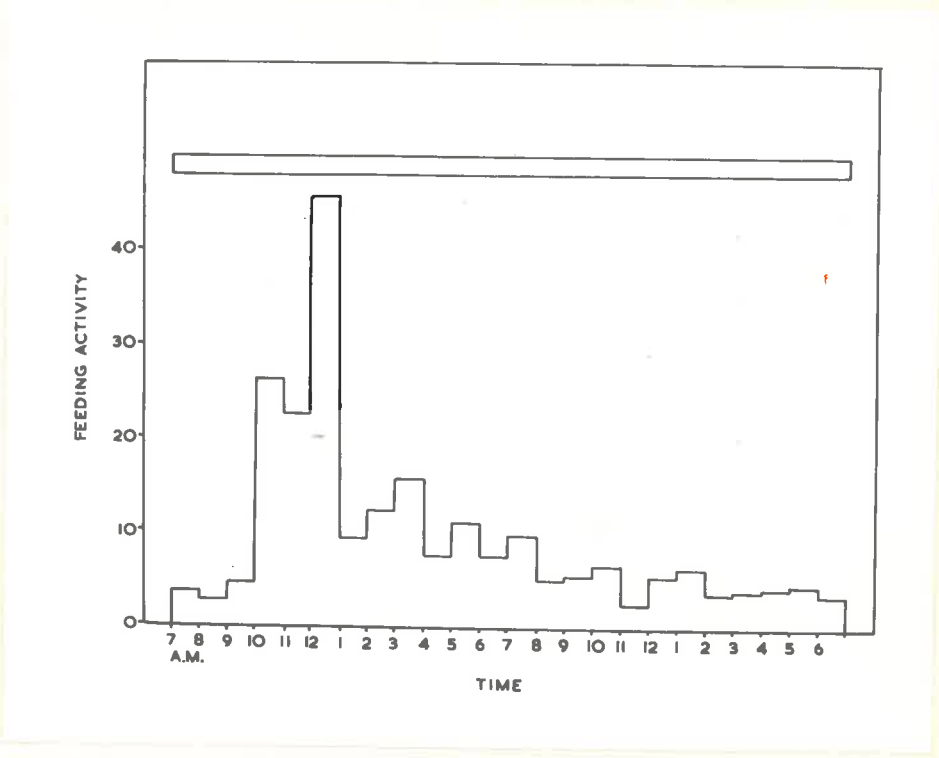


Figure 3.03: Feeding activity in constant light after acclimatization to normal diurnal period of light and dark.

It can be seen from figure 3.03 that with the exception of the period of three hours between 9 a.m. and 1 p.m. feeding activity remained at a fairly constant low level. The period of increased feeding activity immediately followed admission of fresh food, which probably resulted in increased activity. No residuum of the normal diurnal feeding pattern was apparent, nor was it developed after periods of up to five weeks.

3.364 Acclimatization to normal diurnal period of light and dark followed by constant darkness.

Table 3.12: The hourly feeding activity of five crayfish, each observed for fourteen days. Figures for hourly activity are totals for seventy days.

P.M.				A.M.			
Time	Activity	Time	Activity	Time	Activity	Time	Activity
12	3.8	6	53.7	12	48.0	6	24.0
1	10.2	7	36.6	1	35.4	7	3.8
2	12.5	8	43.0	2	20.6	8	3.9
3	21.1	9	35.1	3	11.9	9	1.1
4	25.1	10	61.2	4	13.0	10	2.9
5	68.7	11	31.5	5	17.8	11	1.0

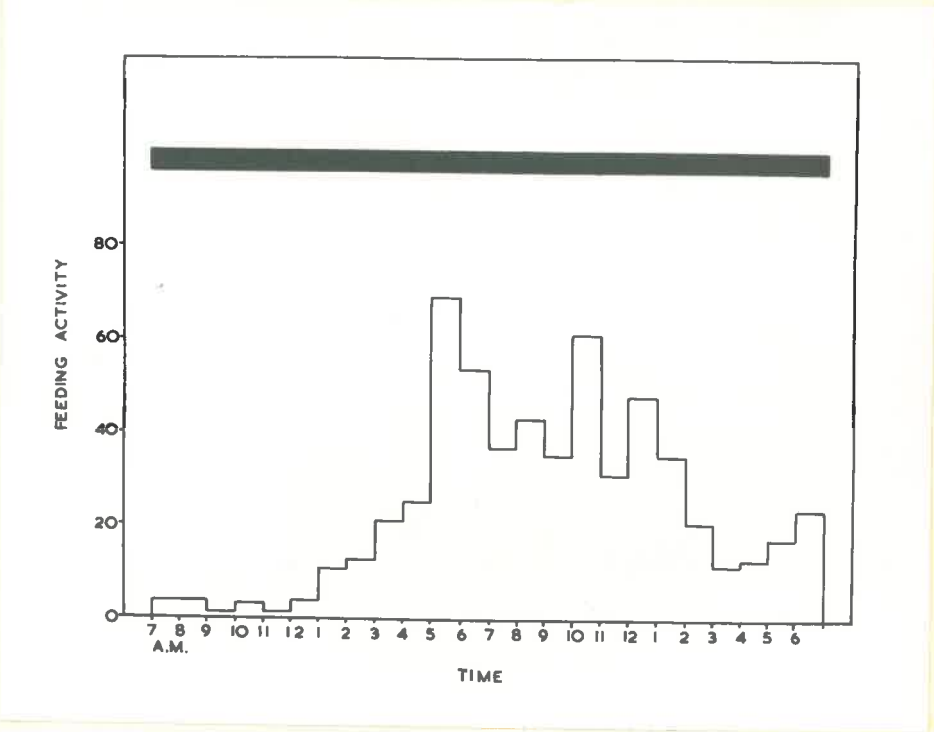


Figure 3.04: Feeding activity in constant darkness after acclimatization to normal diurnal period of light and dark.

It can be seen from figure 3.04 that feeding activity under conditions of constant darkness was maintained at a high level for most of the 24 hours. Although the pattern of feeding activity was similar to the normal pattern between 7 a.m. and 7 p.m., the period following was quite different. The sharp rise in activity at 5 p.m. was not followed by a steady decrease over the next five hours to a steady low level, but feeding was maintained at a fairly high level until 7 a.m. A steady but gradual decrease in activity with intermittent peaks of increased activity replaces the normal pattern. The low level of feeding activity recorded between 9 a.m. and 12 noon can be attributed to disturbance caused by renewing the source of food between 9 a.m. and 10 a.m.

3.365 Acclimatization to normal diurnal period of light and dark followed by alternating 6 hour periods of light and dark.

The alternating periods of light and dark were chosen so that a period of light coincided with the time of dusk. A dark period at dusk would have prevented detection of an endogenous rhythm had a peak of feeding activity occurred during this period as it could have been caused by decreasing light-intensity.

Table 3.13: The hourly feeding activity of ten crayfish, each observed for seven days. Figures for hourly activity are totals for seventy days.

P.M.				A.M.			
Time	Activity	Time	Activity	Time	Activity	Time	Activity
12	64.5	6	4.3	12	44.6	6	8.8
1	37.3	7	7.3	1	32.4	7	7.2
2	37.0	8	4.1	2	29.1	8	2.2
3	35.9	9	3.0	3	26.0	9	1.7
4	30.3	10	5.5	4	26.5	10	3.2
5	9.4	11	50.4	5	23.5	11	75.5

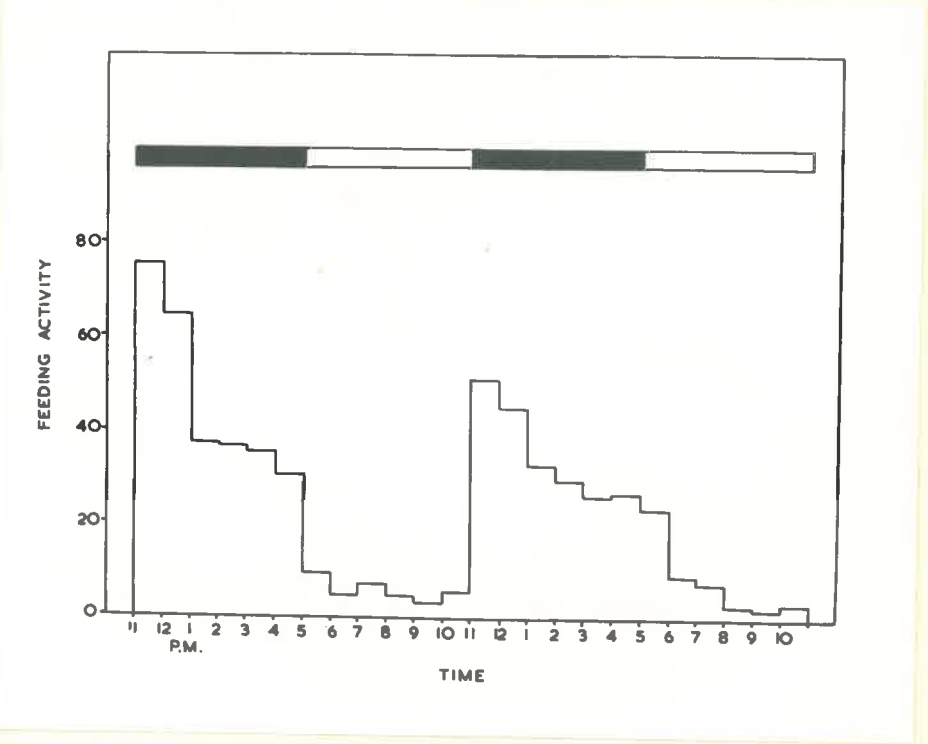


Figure 3.05: Feeding activity during 6 hour periods of light and darkness after acclimatization to normal diurnal period of light and dark.

It can be seen from figure 3.05 that onset of darkness was accompanied by a sudden increase in feeding activity. Feeding was at a maximum during the hour immediately following onset of darkness and gradually decreased during the remaining period. Feeding activity remained at a low level during periods of light.

In each case this feeding pattern was apparent from the first day. Feeding activity during the hours of darkness accounted for 86 per cent of the total feeding activity during the 24 hours.

The time spent feeding between 11 a.m. and 5 p.m. was almost 35 per cent longer than between 11 p.m. and 5 a.m. It has been shown that crayfish feed selectively on fresh fish rather than stale. Fresh fish was introduced between 9 a.m. and 10 a.m., thus it would have lost much of its initial freshness by the second period of darkness and was probably not as attractive to the crayfish.

Comparison of times spent feeding. Experimental animals were the same size and stage of moult and had been in captivity for approximately the same period of time. Direct comparison of results was therefore justified.

Table 3.14 shows the percentage of feeding activity occurring during periods of darkness, between 4 p.m. and 8 p.m. and the total feeding activity for each treatment. The percentage feeding in darkness calculated for constant

conditions of light and dark, represents the feeding activity during the hours of darkness before admission to constant conditions.

Table 3.14: Comparison of feeding activity under various conditions of light and dark.

Treatment	% Feeding in Darkness	% Feeding between 4 and 8 p.m.	Total Feeding
Normal diurnal	93.7	63.3	178.5
Reciprocal of normal diurnal	92.4		302.4
Alternate 6 hours light and dark	85.9		570.2
Normal diurnal then constant light	36.2	15.7	229
Normal diurnal then constant dark	87.1	32.9	575.9

It can be seen that almost all feeding occurred during the hours of darkness. Most feeding occurred during constant darkness and alternating 6 hour periods of light and dark. Almost identical total activity was recorded under these conditions. However the period of darkness in the latter treatment is half that of the former. In the advent of commercial culture, growth-rate could possibly be controlled by regulation of light and dark periods. Reduction of intermittent light and dark periods to values less than six hours may further increase feeding activity per 24 hours.

The most striking feature of feeding under normal conditions of light and dark is the activity between 4 p.m. and 8 p.m., when 63.3 per cent of the total activity occurred. This peak of activity was not apparent in constant light or darkness; 15.7 per cent of the total activity occurring between these hours in constant light and 32.9 per cent in constant darkness.

Records of feeding activity for the first and last two days of each trial of seven days were similar to the summed results. Similar results were also obtained after three weeks in constant light or darkness. However the occurrence of most feeding activity during the hours of darkness when crayfish were placed in constant darkness indicated a weak persistence of the normal feeding pattern.

In an attempt to obtain further evidence of the persistence of a feeding rhythm under constant conditions, records of feeding activity in constant light and darkness were obtained from crayfish which had been kept in alternating 6 hour periods of light and darkness for at least three weeks. Records of feeding activity obtained during the preliminary period of acclimatization showed that each animal was feeding according to the rhythm described for alternating 6 hour periods of light and darkness.

3.366 Acclimatization to alternating 6 hour periods of light and dark followed by constant light.

Table 3.15: The hourly feeding activity of five crayfish, each observed for seven days. Figures for hourly activity are totals for 35 days.

P.M.				A.M.			
Time	Activity	Time	Activity	Time	Activity	Time	Activity
12	2.5	6	2.1	12	0.3	6	0.1
1	1.8	7	0.3	1	0.4	7	0.2
2	2.3	8	0.2	2	0.0	8	0.0
3	4.6	9	0.1	3	0.1	9	0.1
4	2.7	10	0.8	4	0.3	10	0.1
5	2.3	11	0.8	5	0.3	11	0.4

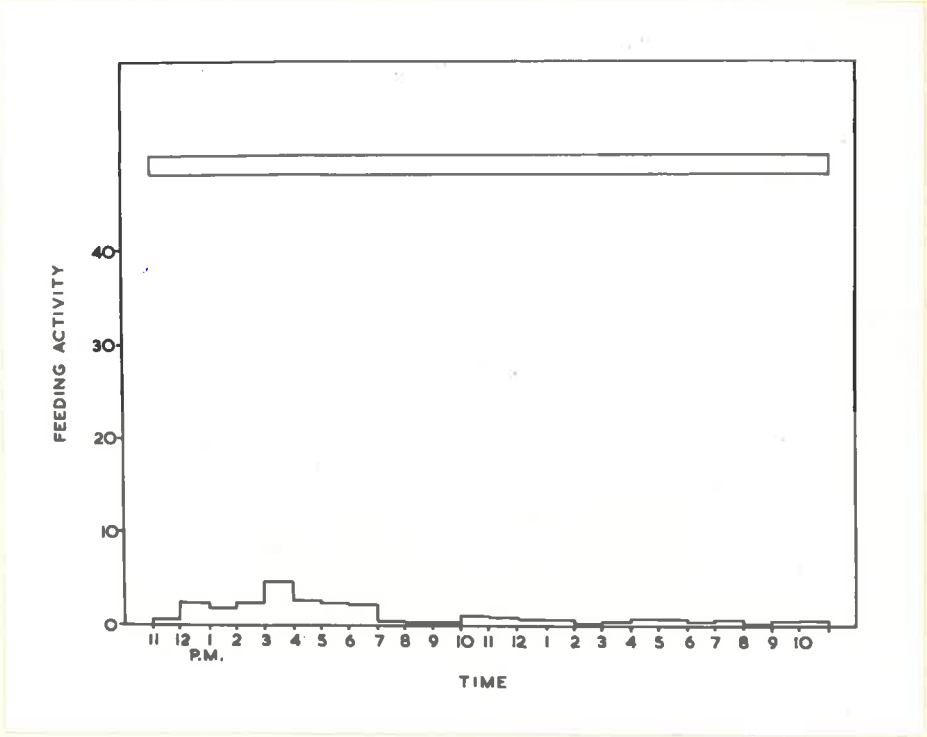


Figure 3.06: Feeding activity in constant light after acclimatization to alternating 6 hour periods of light and darkness.

It can be seen from figure 3.06 that the level of feeding activity was low throughout the 24 hours. Since no evidence of a persisting rhythm was apparent, recording of feeding activity was terminated after five weeks.

3.367 Acclimatization to alternating 6 hour periods of light and dark followed by constant darkness.

Table 3.16: The hourly feeding activity of ten crayfish, each observed for seven days. Figures for hourly activity are totals for seventy days.

P.M.				A.M.			
Time	Activity	Time	Activity	Time	Activity	Time	Activity
12	5.7	6	3.7	12	4.2	6	2.2
1	4.5	7	10.1	1	3.9	7	2.4
2	4.9	8	11.8	2	5.1	8	0.7
3	12.0	9	3.2	3	7.3	9	3.2
4	6.1	10	7.5	4	3.0	10	4.9
5	10.4	11	5.8	5	2.6	11	3.1

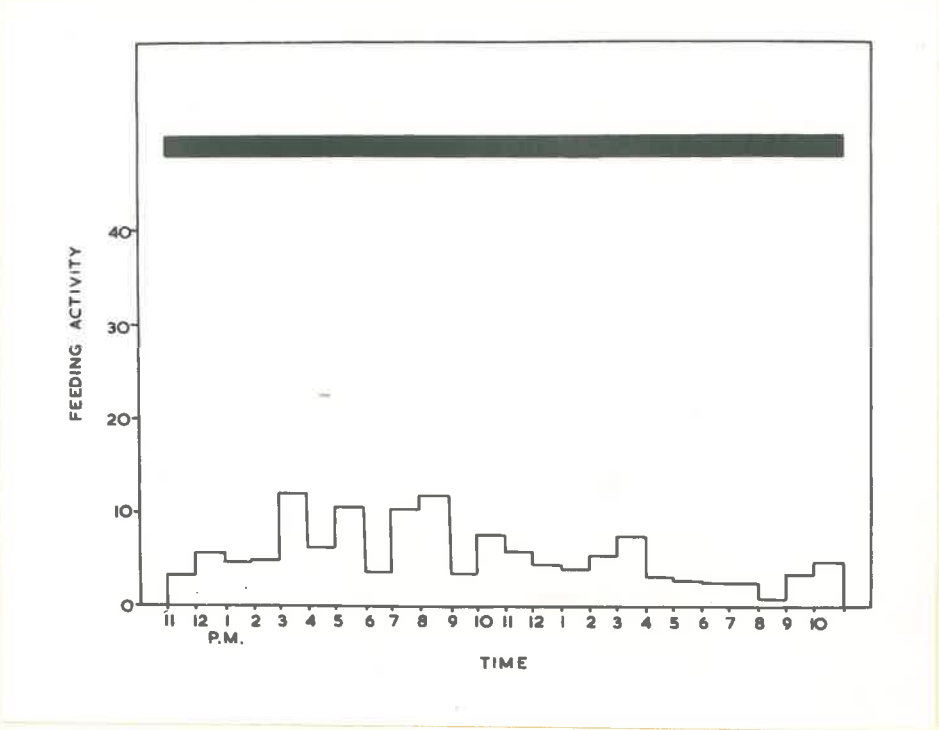


Figure 3.07: Feeding activity in constant darkness after acclimatization to alternating 6 hour periods of light and darkness.

It can be seen from figure 3.07 that feeding activity under conditions of constant darkness was also maintained at a low level throughout the 24 hours. No peaks of activity were apparent.

Table 3.17: Feeding activity under constant conditions of light and dark during the dark periods of previous treatments, and the total feeding activity for the period of observation.

Treatment	Percentage Feeding in Darkness	Total Feeding
Alternate 6 hours light and dark then constant light	71.1 but 62.7% during first period	22.8 for 5 weeks
Alternate 6 hours light and dark then constant dark	55.5	126.3

It can be seen that the total feeding activity in both treatments was low. In constant light, 71 per cent of the feeding occurred during the previous hours of darkness, but 62.7 per cent occurred during the first period. In constant darkness, feeding activity during dark periods did not differ markedly from that during light periods.

Discussion. Twenty-four hour rhythms of locomotor activity and metabolic rate have been described for several Crustacea.

Kalmus (1938) described a 24 hour rhythm of locomotor activity for Astacus astacus, which was more active between 4 p.m. and midnight than at other times.

Roberts (1941, 1944) described a 24 hour rhythm of locomotor activity for Cambarus virilis. He found that locomotor activity was about nine times as great during

darkness as during daylight and fluctuation of the single environmental factor, light, was capable of regulating locomotor activity. He concluded that the locomotor rhythm of C.virilis was partly due to an endogenous tendency to move about at intervals of 24 hours and partly the result of direct influence of a marked change in light-intensity. The response to decreasing light-intensity was more pronounced and constant than the reaction to increasing illumination.

Schallek (1942) studied spontaneous rhythms of locomotor activity in Cambarus virilis, Procambarus clarki and Cambarus diogenes and described three types of animal in each species. One type was most active at midnight, one was most active at noon and the third type was most active at dawn and dusk. Most animals were more active during the night than the day. Rhythmic locomotor activity was observed to persist after five weeks in constant darkness, but was often obscure in the first week. Three animals were placed in a changing environment of alternating light and dark for 48 hours. These animals were about seven times as active during dark periods as light. Four times as much activity was recorded during the dark period occurring at night as that occurring during the day. From these observations, Schallek concluded that crayfish could adapt themselves to changing light and dark periods, but the underlying

24 hour rhythm of activity was still evident.

Edwards (1950) described 24 hour rhythms of metabolic rate and spontaneous locomotor activity for Uca pugilator, Uca pugnax and Uca minax. Brown, Bennett and Webb (1954) described a persistent 24 hour rhythm of oxygen-consumption for U.pugilator and U.pugnax. Fingerman (1955) described 24 hour rhythms of metabolic rate in Cambarus shufeldti and Fingerman and Lago (1957) described endogenous 24 hour rhythms of locomotor activity and consumption of oxygen for Orconectes clypeatus. Naylor (1958, 1960) described spontaneous tidal and diurnal rhythms of locomotor activity in Carcinas maenas. Harker (1956, 1958, 1960) described a persistent diurnal rhythm of locomotor activity for Periplaneta americana, which depended on rhythmic secretion of a hormone from the neurosecretory cells of the sub-oesophageal ganglion.

The normal rhythm of feeding activity for J.lalandei is similar to the rhythm of locomotor activity described by Kalmus for A.astacus, which was most active between 4 p.m. and midnight. Roberts found that C.virilis was about nine times as active during darkness as it was in light. Roberts found that fluctuation of light could regulate the locomotor activity. Similarly the feeding activity of J.lalandei can be regulated by fluctuating light-intensity. Schallek described a persisting rhythm of locomotor activity for

three species of freshwater crayfish. He concluded that they could adapt themselves to changing light and dark periods, but the underlying 24 hour rhythm of activity was still evident. The normal rhythm of feeding activity of J.lalandei was not evident during fluctuating periods of light and dark nor did it persist to any marked extent under constant conditions of light and dark.

Apart from weak persistence in constant darkness, the feeding activity of J.lalandei can be regulated by fluctuating light-intensity. The response to a new cycle of light and dark periods is rapid, no residuum of the previous rhythm being apparent.

3.37 Shelter and feeding activity.

It has been mentioned previously that crayfish were rarely observed to forage away from their shelters during the day. It has also been suggested that failure to obtain shelter has an adverse influence on crayfish. Since shelter was provided in excess during experiments 3.361 to 3.367, records of feeding activity were obtained when potential shelter was reduced to a minimum.

Materials and methods. The recording equipment and method were the same as those used previously. No pipes were provided as shelter and plywood filler walls were placed across each corner of the aquaria, eliminating corners of 90°. The aquaria were almost circular, presenting

a monotonous environment containing no refuges. A dark period was maintained between 5 p.m. and 7 a.m.

Results.

Table 3.18: The hourly feeding activity of ten crayfish, each observed for seven days. Figures for hourly activity are totals for seventy days.

P.M.				A.M.			
Time	Activity	Time	Activity	Time	Activity	Time	Activity
12	0.3	6	14.2	12	9.2	6	2.0
1	1.7	7	10.8	1	6.9	7	0.4
2	1.9	8	20.1	2	12.1	8	0.6
3	1.3	9	16.0	3	4.4	9	0.2
4	1.7	10	9.0	4	4.0	10	0.2
5	15.4	11	13.8	5	7.2	11	0.6

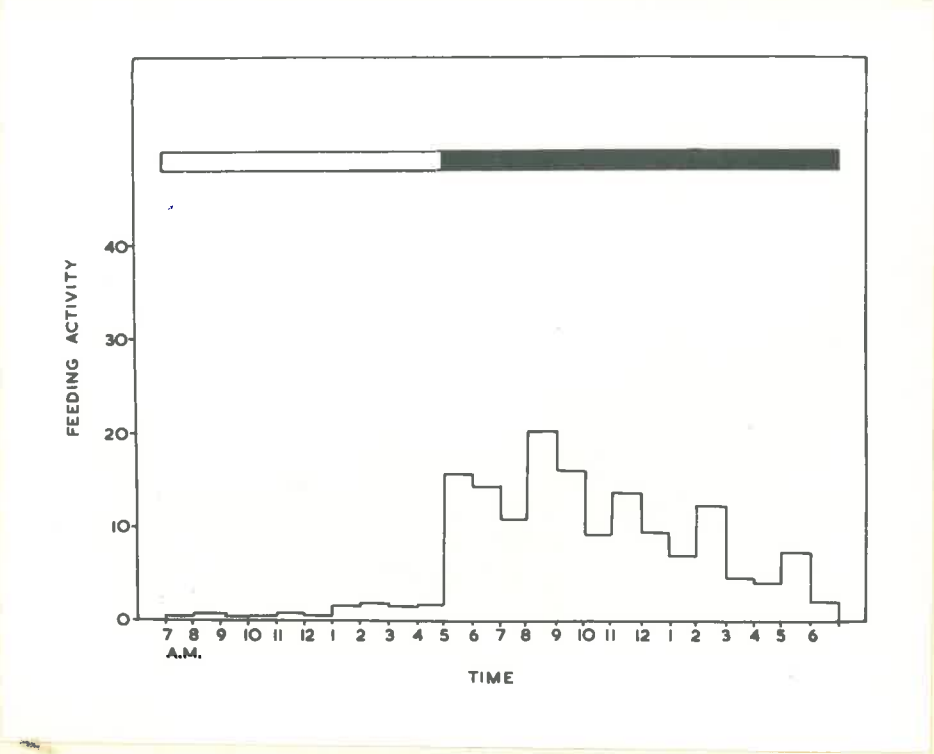


Figure 3.08: Feeding activity for normal diurnal period of light and dark with shelter restricted to a minimum.

It can be seen from figure 3.08 that feeding activity remained at a fairly low level during the light period. Onset of darkness resulted in a sharp increase in activity, which reached a peak between 8 p.m. and 9 p.m. and slowly decreased during the remaining dark period. The total feeding activity recorded for the seventy days of observation was 154 mm.

Discussion. The above feeding pattern is comparable to patterns of feeding activity during artificially induced periods of light and dark observed previously. Feeding activity during the light period was low, while 94.2 per cent of the total activity occurred during the dark period.

Strict comparison with the normal feeding pattern is not possible as the change from light to dark in the absence of shelter was sudden, while the change was gradual in the normal pattern. The total feeding activity recorded in the absence of shelter was only 16 per cent less than that recorded with excess shelter. It therefore appears that lack of shelter does not markedly influence the feeding activity of J.lalandei held in captivity.

3.4 Locomotor activity.

Introduction. Roberts (1944) correlated feeding of C.virilis with locomotion that occurred outside of niches and stated that most feeding must therefore occur at night. Locomotor activity was checked to a considerable

extent whilst food was eaten. On the basis of these observations, Roberts postulated that the rhythm of locomotor activity was partly an adaptation to obtain food.

Most of the literature cited previously concerning rhythmic processes occurring in the Crustacea dealt with rhythms of locomotor activity. The following experiment was therefore done to compare the locomotor activity of J.lalandei with that of other Crustacea.

Materials and methods. A length of fine nylon thread was attached to a crayfish by a rubber band stretched across the dorsal surface of the abdomen and looped over two tergal spines. The thread was then passed over the pulley of a radial switch through a ferrule one foot above the centre of the aquarium. A small weight kept the thread taut. The switch consisted of eight radial terminals set into a circular disc attached to a smaller pulley and mounted on needle bearings. A low voltage circuit was closed when a terminal contacted two fine brushes. Movement of the crayfish rotated the switch, making and breaking the circuit intermittently. Completion of the circuit activated a relay, which marked the activity as a vertical stroke on a smoked drum, which rotated 2 cm. per hour.

Only crayfish able to turn the switch without apparent difficulty were used in the experiment. Continuous records of locomotor activity were obtained for 7 periods of 24

hours for each animal. Results from the first four days were not used in the final analysis. The experiment was done in an aquarium 3 ft. 6 inches by 3 ft. filled with 10 inches of water. Pieces of earthenware pipe 9 inches by 5 inches were placed in each corner of the aquarium as shelter. Each 24 hour record was divided into divisions of 2 centimeters, each equivalent to one hour. Locomotor activity was measured for each hour by measuring the width of each mark on the kymograph to the nearest tenth of a millimeter and summing them. The locomotor activity of ten animals was recorded under normal diurnal conditions of light and dark.

Results.

Table 3.19: The hourly locomotor activity of ten crayfish, each observed for three days, after a period of acclimatization to the recording apparatus of four days. Figures for hourly activity are totals for thirty days.

P.M.				A.M.			
Time	Activity	Time	Activity	Time	Activity	Time	Activity
12	11.1	6	55.8	12	25.5	6	2.2
1	9.8	7	29.2	1	21.2	7	2.7
2	12.8	8	24.6	2	14.1	8	3.8
3	23.2	9	31.0	3	14.8	9	0.0
4	14.5	10	27.3	4	14.0	10	1.2
5	33.3	11	16.1	5	3.0	11	7.0

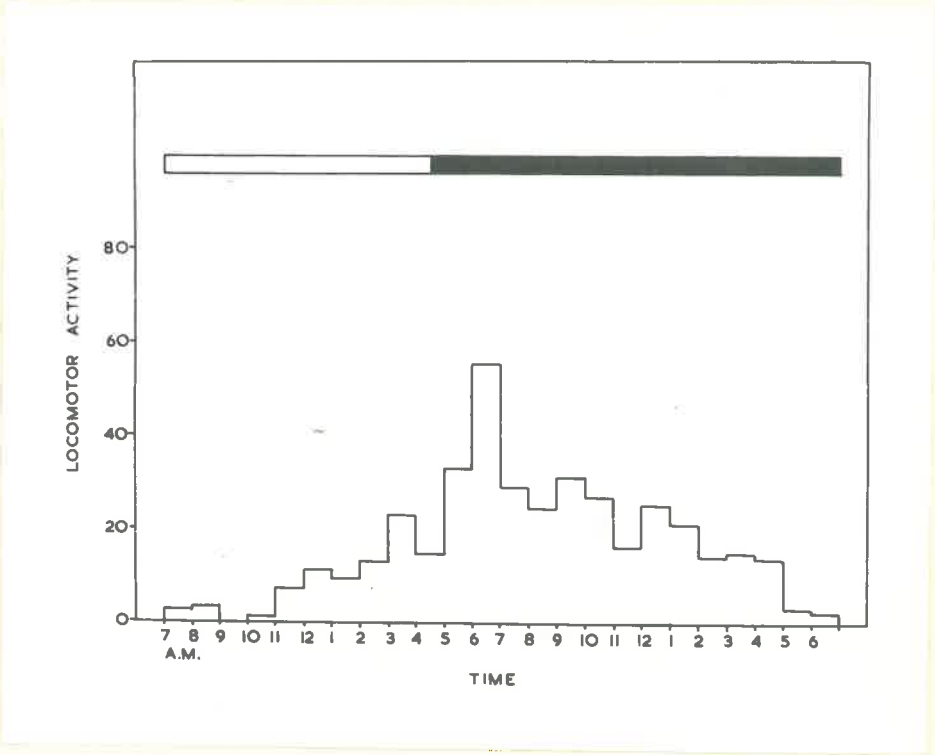


Figure 3.09: Locomotor activity for normal diurnal period of light and dark.

It can be seen from figure 3.09 that locomotor activity is rhythmic, crayfish remaining more or less dormant during the day, becoming active during late afternoon and remaining active for most of the night.

Discussion. The pattern of locomotor activity corresponds quite closely to the pattern of feeding under the same conditions. In both cases most activity occurred during the night with maximum activity at dusk. Locomotor activity was recorded during September and October, whilst

feeding activity was recorded during June and July, which accounts for the difference in the time of dusk.

Although the peak of feeding activity at dusk can be correlated closely with a similar peak of locomotor activity, locomotor activity remains at a much higher level during the remaining hours of darkness than does feeding activity. As excess food was provided during the experiments, the concentrated feeding activity during the early hours of darkness probably means that sufficient food was eaten during this period and further feeding was unnecessary. Had food been limited then the rather high level of locomotor activity during most of the period of darkness would allow active foraging during this period.

4. Growth.

4.0 Introduction. A summary of the literature concerning the growth-rate of the family Palinuridae has been given by Lindberg (1955). Most of this literature is confined to the Genus Panulirus, but he concluded that the Palinuridae as a whole moults twice a year with an annual increase in length of approximately one inch.

Young (1926) observed a small specimen of J.lalandei maintained in an aquarium for three years and two months. During this time it moulted eight times and increased in length from 4.2 cm. to 14 cm. in total length. Von Bonde and Marchand (1935) showed that specimens 9 to 10 cm. in carapace-length moulted once or twice a year in captivity. Bradstock (1950) recovered two tagged animals after one year, which had increased in length 2.1 and 1.9 cm. from 21.5 and 24.8 cm. in total length respectively.

Growth-rate of J.lalandei has been studied by three previous authors. In each case the number of animals observed were few and the significance of conclusions consequently doubtful.

Travis (1954-57) published four papers dealing with the moulting cycle of the spiny lobster Panulirus argus. The first paper in the series describes the growth and other physical changes associated with lobsters that were living in the laboratory. I have used Travis' methods to describe

the moulting cycle and estimate the growth-rate of J.lalandei.

4.1 Linear relationships.

4.11 Definitions. Three measurements of length have been used in the study of the Palinuridae. These three measurements are also used to define minimum legal lengths below which crayfish may not be caught.

(a) Total carapace-length (T.C.L.). Several measurements are used under this heading, but in this investigation it is the length measured from the posterior margin of the carapace to the point of union of the second antennae in the midline.

(b) Rostrum carapace-length (R.C.L.). This length is measured from the posterior margin of the carapace to the anterior tip of the rostrum in the midline.

(c) Total length (T.L.). This length is measured from the posterior margin of the telson to the point of union of the second antennae while the animal is extended on a flat surface.

4.12 Comparison of measurements. Total length is laborious to measure and the accuracy is limited by the ready distortion of the abdomen. The carapace, being rigid, can be measured accurately with a vernier caliper. Both measurements of carapace have been used in different phases of this investigation. Initially R.C.L. was used exclusively. It proved satisfactory for animals 4 to 8 cm. in carapace-

length as the rostrum of these small animals was rarely absent and had a constant shape. In larger animals the rostrum was found to be variable in shape and was missing more often. Ecdysis also affected the shape and presence of the rostrum.

All three measurements are used by the various State and Commonwealth authorities for measurements of minimum legal lengths, also measurements used by other authors are not constant. This lack of uniformity makes comparison of results difficult in the absence of suitable conversion factors. In order to calculate relevant conversion factors and to determine whether increase in carapace-length is a valid index of growth, the relationships of total carapace-length to rostrum carapace-length and total carapace-length to total length were calculated.

Method and materials. Animals were grouped in size-classes increasing by two millimeters in total-carapace length. Mean values for the measurements concerned were then calculated for each class and plotted against each other. Total length was measured to the nearest tenth of a centimeter and carapace-length to the nearest tenth of a millimeter with a vernier caliper. Sexes were treated separately and together using measurements from 136 males and 245 females ranging in length from 3.9 to 14.8 cm. T.C.L. Conversion factors were calculated for means at

intervals of one centimeter T.C.L. The mean value of these factors was then used as the conversion factor.

T.C.L. and R.C.L. Similar results were obtained for both sexes. the relationship approaching a straight line. The conversion factor of R.C.L. in cm. to T.C.L. in cm. was 1.042. Since T.C.L. and R.C.L. are directly related either measurement could be used for practical purposes such as measurement of minimum legal length. For reasons given previously T.C.L. is recommended for accurate measurements of growth.

T.C.L. and T.L. Results are shown in figure 4.01.

It can be seen that the relationship approaches a straight line for both sexes and increases in carapace-length are directly proportional to increases in total length. The ratio T.L. to T.C.L. also tends to be larger in females than males.

Most Australian authorities measure minimum legal lengths in inches while metric measurements of carapace-length are usually quoted in the literature. A conversion factor of total carapace-length in centimeters to total length in inches therefore seemed the most useful.

Conversion factor: (a) Male = 1.001.

(b) Female = 1.022.

For all practical purposes the total carapace-length in centimeters can be converted directly to total length in

inches since the conversion factor is approximately one.

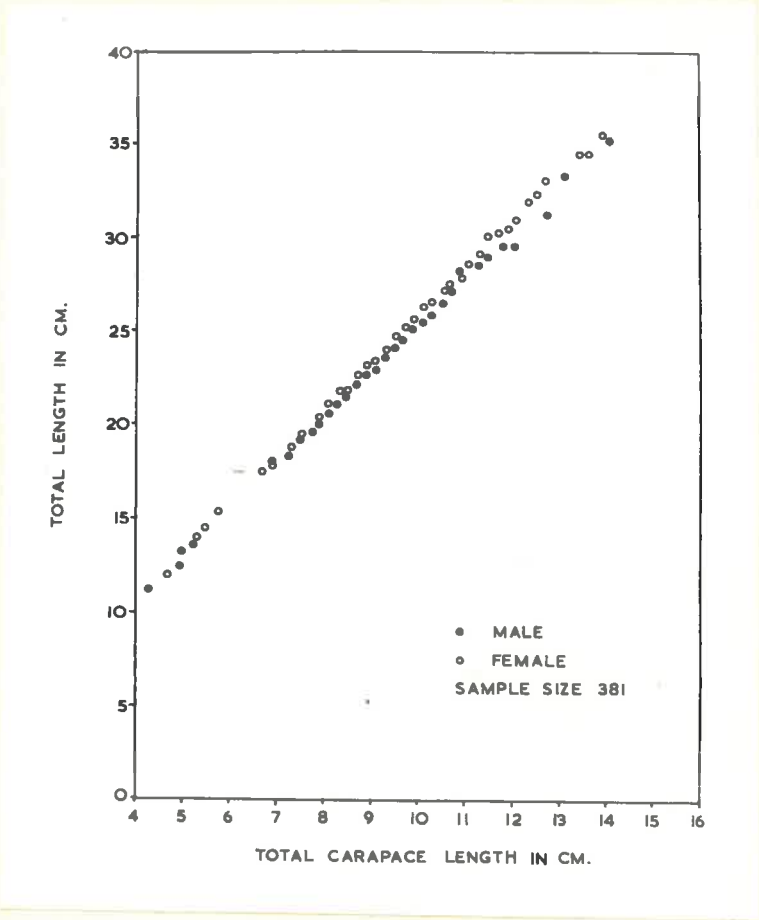


Figure 4.01: Relationship between total carapace-length and total length.

Length and weight. Results are shown in figure 4.02. It can be seen that males and females bear approximately the same relationship within the limits of the observations. Lindberg (1955) obtained similar results for male and female P.interruptus up to 11 cm. T.C.L. (approx.). Above this length males tended to be 110 to 140 grams heavier than females due to growth in density and volume rather than length.

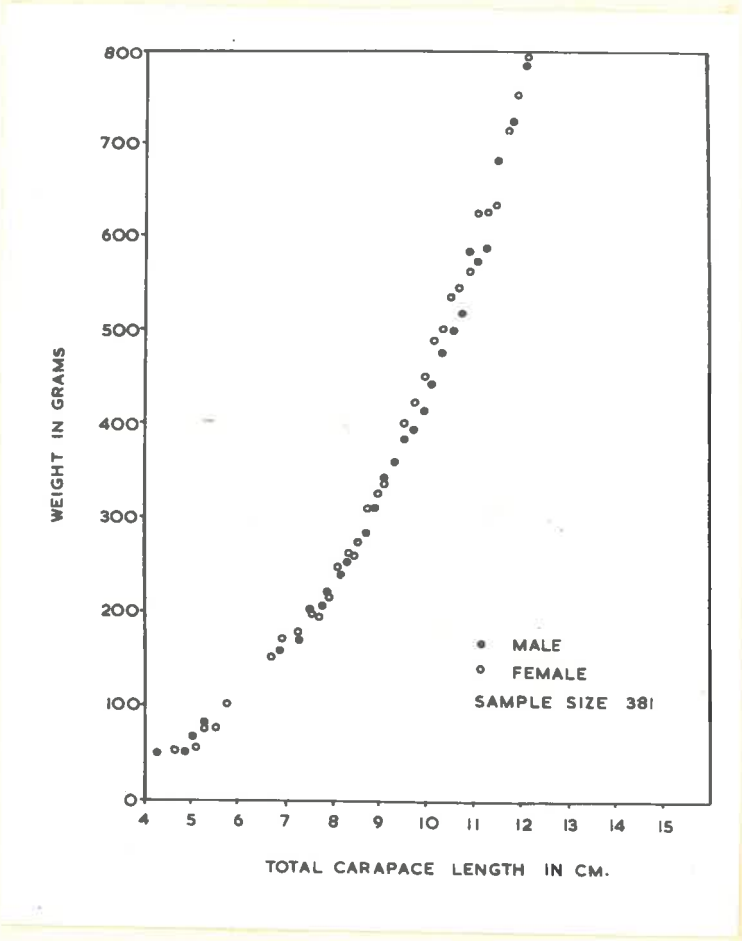


Figure 4.02: Relationship between length and weight.

Usually weight is a function of length and may be expressed by the equation $W = cL^n$, where W is the weight, L the length and c and n are constants. The logarithmic form of this equation is used in this study.

Weights and lengths of 431 female and 161 male crayfish were measured as described previously and means calculated

for classes increasing by 2 mm. T.C.L. When converted to logarithms and plotted graphically the means gave a straight line relationship. The lines of best fit calculated by the method of least squares are expressed by the following equations.

(a) Female: $\log.W = 2.7389 \log.L - 0.2609$

(b) Male: $\log.W = 2.9449 \log.L - 0.2760$

Thus the weight very nearly varies in proportion to the cube of the carapace-length.

4.2 Moulting.

4.21 The moulting cycle. Drach (1939) divided the moulting cycle of Crustacea into four stages A,B,C,D on varying morphological characters of the skeleton and tissues. This method of description has been generally accepted and is the method used here.

Stage A (postmoult). This stage immediately follows moult and lasts between 12 and 24 hours. The exoskeleton has the consistency of a thin membrane and is rather like india rubber to touch. The principal layer of the exoskeleton begins to be deposited.

Stage B (postmoult). Calcification begins accompanied by further thickening of the principal layer. This stage lasts from the second to the seventh day following moult, after which time the skeleton is quite hard, although the branchiostegites remain soft.

Animals in stages A and B do not feed and usually remain dormant in a secluded part of the aquarium. Great care must be observed in handling as appendages are readily lost by autospasy.

Stage C (intermoult). This is a period of active feeding. The membranous and principal layers are completed as is calcification. The duration of stage C is variable dependant mainly on the size of the animal. The minimum period observed was 73 days for an animal of 5 cm. T.C.L., the maximum 287 days for an animal of 8 cm. T.C.L.

Stage D (premoult). This is the period immediately preceding ecdysis, during which the old skeleton is broken down by resorption of mineral and organic materials. The new skeleton gradually forms beneath the old. Such animals are quite weak and tend to avoid others.

Detection of premoult animals is simplified by the appearance of an area of resorption or ecdysial line on the branchiostegites. Considerable softening occurs along this line, which may be detected as early as three weeks but usually about two weeks before moult. The ecdysial line acts as a hinge to allow the carapace to lift, only accidental splitting occurs along the line at ecdysis.

This description is essentially similar to that described for P.argus by Travis (1954), however differences were apparent in periods of time, appearance of ecdysial

line and rate of hardening. The shortest intermoult period observed for J.lalandei, 90 days, was almost twice the mean summer intermoult period described by Travis. Stages A and B are similar, but hardening of the skeleton is more rapid in J.lalandei. At the end of stage B, the carapace of P.argus is rigid in certain areas and the skeleton has the consistency of parchment. In J.lalandei the skeleton is uniformly hard after two or three days and the branchiostegites are only slightly soft after seven days. The appearance of an ecdysial line prior to moult is marked in P.argus since a potential line is not evident through intermoult. A potential ecdysial line, marked by a lack of pigment is present in all stages of J.lalandei. Resorption can not readily be identified by sight, except for some distortion of the branchiostegites below the line in the latter part of stage D. The ecdysial line is readily identified by softening of the skeleton along it. It is a very thin area of almost complete resorption.

4.22 Ecdysis. During the course of this investigation 195 moults occurred, all of which took place late at night or during the early hours of the morning. Although the process of ecdysis was not actually observed, a study of exuviae and animals that died during moult showed no evidence that the process differed markedly from that of P.argus.

The intersegmental membrane joining cephalo-thorax to abdomen splits dorsally. An articulating condyle attaching the branchial chamber to the branchiostegites posteriorly, loosens and the carapace is tipped forward. The ecdysial line acting as a hinge allows the carapace to rise sufficiently for the cephalo-thorax to be withdrawn, antennae first, followed by the legs. The abdominal segments are finally freed from the old skeleton allowing the animal to escape completely. Failure to complete the ecdysial process in the above pattern usually resulted in the death of the animal. Travis found that ecdysis was completed in 3 to 10 minutes. Lindberg found that P.interruptus completed moulting in about 15 minutes and it was evident from animals dying at moult that the time taken to complete moult is critical for J.lalandei.

Appendages were often caught in the old skeleton by swelling before they had been freed. In some such cases as many as nine walking legs have been autotomized in an attempt to complete ecdysis.

4.23 Change in weight at moult.

Method and materials. All weights were measured to the nearest gram on a triple beam balance. Weights were recorded daily for at least four days preceding moult and on the day following. Thereafter weights were recorded at intervals of seven days up to thirty five days

following moult. Ten animals from three classes, 5 to 5.9, 6 to 6.9 and 8 to 8.9 cm. T.C.L. were observed. Changes in weight were converted to percentage increases above the previous intermoult weight and means for the ten animals in each class calculated.

Before weighing, each animal was dried superficially by swabbing all external water with towelling and shaking the branchial chambers dry. All weights were measured between 9 a.m. and 10 a.m.

Since J.lalandei moults during the early hours of the morning, weights recorded on the day preceding moult were thus recorded 15 to 19 hours before ecdysis and those on the day following, 5 to 9 hours after ecdysis.

Results. Results are shown in figure 4.3. Similar results were obtained for animals 5 to 8.9 cm. T.C.L.

A small but detectable increase occurs two days before the moult and weight increases significantly on the day preceding ecdysis. Weights recorded on the day following moult show an average increase of 13.2, 13.6 and 5.5 per cent for the three size-classes observed. Weight then increases slowly until 35 days following moult when it becomes stable at the new intermoult level.

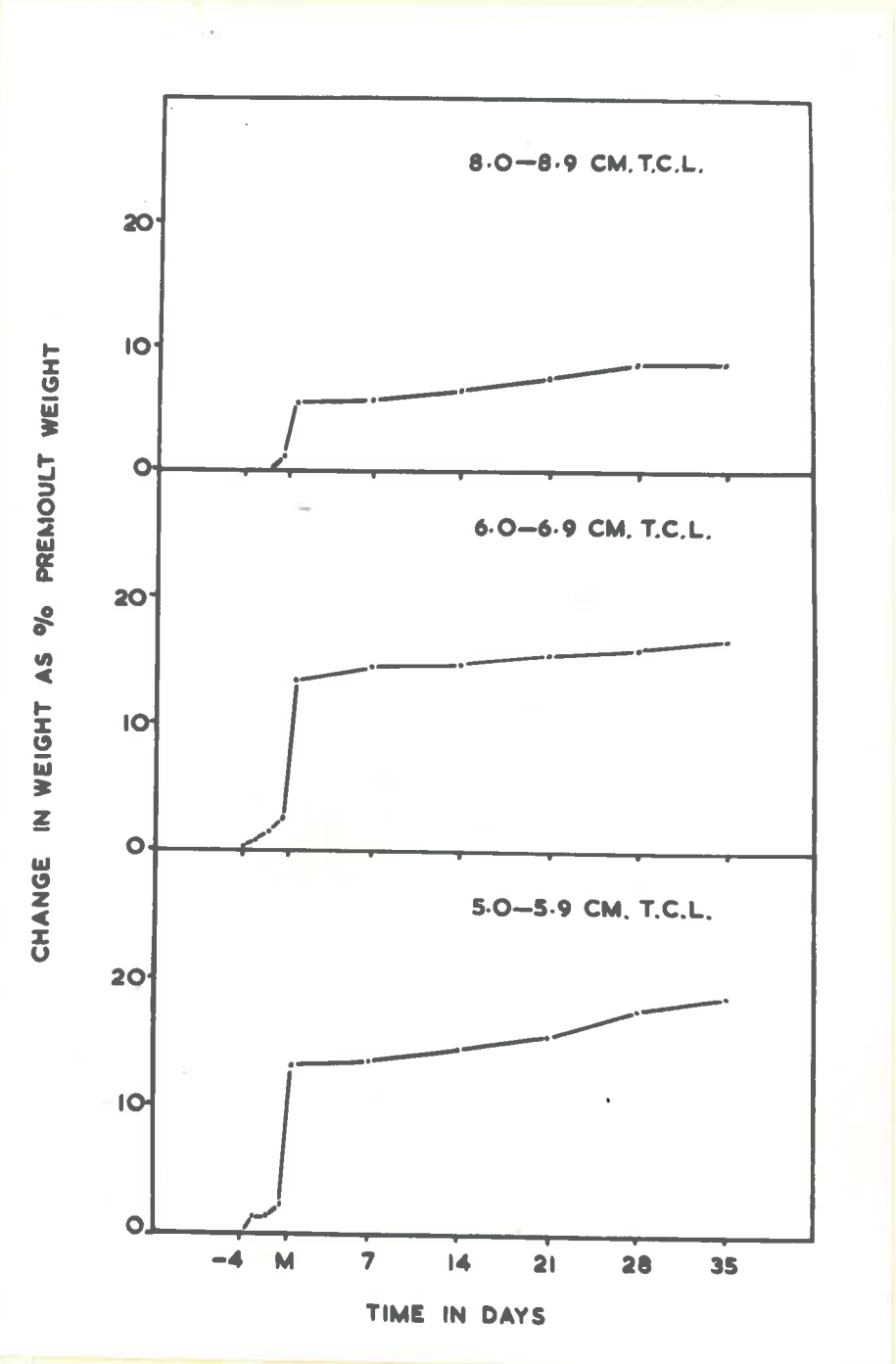


Figure 4.03: Increase in weight at moult.

Discussion. The sudden increase in weight apparent a few hours after ecdysis was not recorded by Travis for P.argus or by Guyselman (1953) for Uca pugilator. Both these authors found that weight increased a short time preceding ecdysis followed by a sharp decrease following ecdysis, which they attributed primarily to loss of exuviae. Both animals then required several days to regain the pre-moult weight, which reached a constant new level after 28 to 35 days in P.argus.

Robertson (1960) described a similar change in weight for Carcinas maenas as that described here for J.lalandei.

Robertson weighed only 8 animals, on the day before and the day after moulting; all increased in weight during this period by 18 to 68.5 per cent (mean of 40.4 per cent).

4.24 Uptake of water at moult. It has been shown that increases in weight preceding moult are due to uptake of water, Drach (1939), Guyselman (1953), Travis (1954), Robertson (1960). Results from seven sources have also been compared by Robertson (1960). The uptake of water at moult for J.lalandei is shown in table 4.01. The abbreviations are those of Guyselman and Travis and figures are average values from ten animals in each size-class.

Table 4.01: Uptake of water at moult.

R.C.L. in cm.	Weight in gm.					E as % I	W3 as % I
	I	W1	E	W2	W3		
5-5.9	93.0	95.1	8.8	106.3	19.0	9.7	21.1
6-6.9	173.5	178.2	18.8	196.4	36.9	11.0	21.9
8-8.9	364.4	368.7	33.3	385.4	51.1	9.1	14.0

I = The wet weight of intermoult animals.

W1 = The wet weight of animals at 9 a.m. on the day before moult.

W2 = The wet weight of animals at 9 a.m. on the day following moult.

E = The wet weight of exuviae.

W3 = W2 - (W1 - E) = The weight of water absorbed during the 24 hour period from 9 a.m. on the day before to 9 a.m. on the day following moult.

E as a percentage of I = The weight of exuviae expressed as a percentage of the previous intermoult weight.

W3 as a percentage of I = The weight of water absorbed expressed as a percentage of the previous intermoult weight.

Comparison of results with those of Travis is difficult since her observations were made on larger animals. However comparison of weights of exuviae of the two species shows

that the exuvium forms about 9.6 per cent of the intermoult weight in J.lalandei while that of P.argus forms approximately 20 per cent.

The average percentage of water absorbed by the three size-classes, 5 through 8.9 cm. T.C.L. is 18.3 compared with 18.8 estimated from Travis' figures (using I instead of W1 to calculate W3 since W1 of Travis was not available for J.lalandei.). It appears then, that similar amounts of water are absorbed during the same period of time in both species. The much lighter exuvium of J.lalandei compared with P.argus allows the weight to increase directly after moult whereas a loss in weight occurs in P.argus.

4.25 Temperature and growth.

4.251 Temperature of water and moulting.

References to the effect of temperature on the moulting cycle of Crustacea have been made by Drach (1939, 1949), Truitt (1939), and Travis (1954). These authors found that the frequency of moulting increased i.e. the period of intermoult was shorter with increasing temperature of water. Travis found that most moults occurred during periods when the temperature of the water was increasing. Growth of P.argus was therefore effectively limited to seven months of the year.

Such a striking correlation between temperature and moulting was not apparent for J.lalandei during this

investigation. Figure 4.04 shows the number of animals moulting expressed as a percentage of the total number of animals in the laboratory for each month of a period of two years plotted with the average monthly temperature of water. The frequency of moulting for February and March is omitted as the number of animals in stock for these two months was too low to allow comparison with the remaining months.

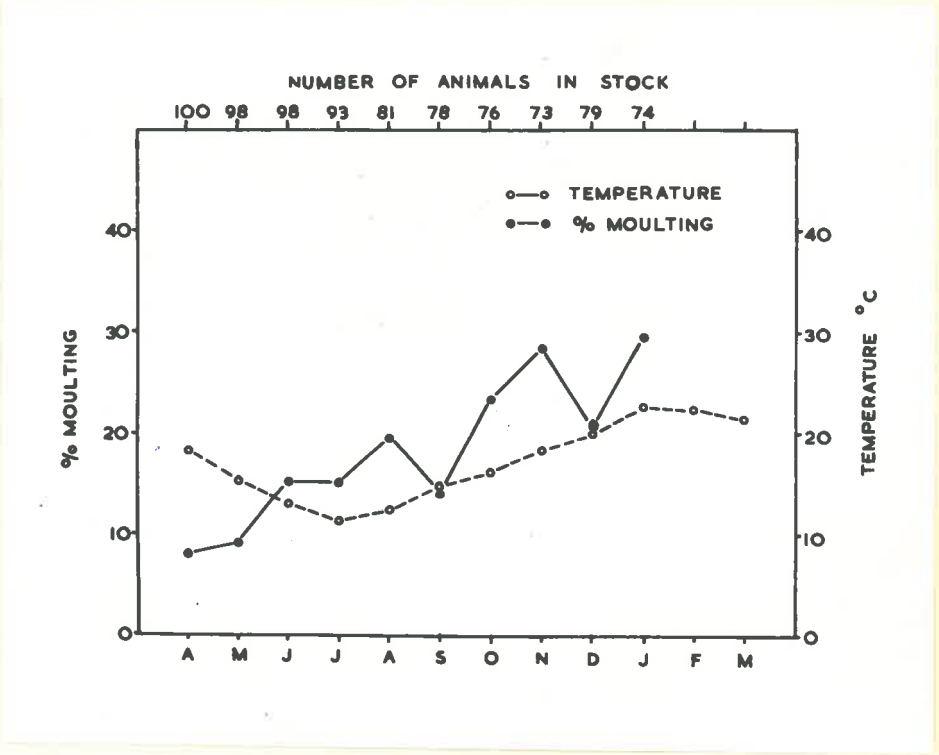


Figure 4.04: The relationship between water-temperature and moulting.

It can be seen that the frequency of moulting tends to increase with increasing temperature, although frequency of moulting does not remain at low levels nor reach a level higher than 30 per cent. In the case of P.argus, moulting virtually ceases during the five months of lowest temperatures. Increase in the temperature of the water is accompanied by a rapid increase in the frequency of moulting, which remains above 40 per cent for the four months of highest temperatures.

4.252 Temperature and the period of intermoult.

Supplementary evidence of temperature affecting the moulting cycle was provided by correlating the period of intermoult with the temperature of the water. Since the number of animals in any one size-class moulting during each month was low, a direct correlation was not possible. Data obtained during 1959 through 1961 were divided into two periods of six months, July to December, a period of rising temperature and January to June, a period of decreasing temperature.

The average period of intermoult of 33 animals 5 to 5.9 cm. T.C.L. during July to December was 137 days and 158 days during January to June. An analysis of variance showed that the two classes differed significantly (P between 1 and 5 per cent) indicating that increasing temperature increases the rate of moulting. The analysis of variance

is shown in table 4.02.

Table 4.02: Analysis of variance of data used in section 4.252.

Source of Variation	S.S	D.F.	Mean S.	Var. Ratio
Between Classes	3,709.4	1	3,709.4	6.34
Within Classes	17,882.1	31	576.8	P between 1% and 5%
Total	21,591.5	32		

4.26 Size and moulting. A number of authors, reviewed by Travis (1954) found that Crustacea moult less frequently as they become bigger. Travis, herself found that the average summer intermoult period increased progressively for a range of P.argus 2 to 8.9 cm. in carapace-length.

Summer intermoult periods could not be used for this comparison as the number of J.lalandei kept in captivity for more than one moult was small. Table 4.03 therefore includes all intermoult periods observed.

It can be seen that the intermoult period increases progressively with increase in size. The average summer intermoult periods observed by Travis for P.argus are approximately one third of those observed for the same size of J.lalandei. Because moulting is confined to seven months of the year in P.argus however, only one or two more moults per annum occurred.

Table 4.03: The average intermoult periods of various sized crayfish.

R.C.L. in cm.	Number of Animals	Average Intermoult in days	Estimated no. moults per year	Number observed
5-5.9	34	145±4.7	3	3 (16 animals)
6-6.9	20	159±6.7	3	3 (6 animals)
7-7.9	6	173±10.2	3	3 (2 animals)
8-8.9	3	234	2	2 (2 animals)

4.3 Growth of captive animals. The growth-rate of decapod crustaceans has been measured for animals in captivity and for tagged animals living naturally and it has been inferred from records of changing distribution of sizes in a natural population. Burkenroad (1951) using Penaeus duorarum as an example has discussed the validity of results obtained by these methods and their application to natural populations. A combination of all three methods probably gives the best assessment of natural growth-rate. Because I did not have suitable access to natural populations I measured the growth-rate of animals living in captivity.

4.31 Growth by weight. Weight increases were measured 35 days after moult when the crayfish had reached a stable weight. This time was relatively constant and did not vary significantly with size or time of year. Animals lacking appendages were not used for these observations. Table 4.04 shows the increase in weight after moult of 54

crayfish ranging in length from 5 to 8.9 cm. T.C.L.

Table 4.04: Growth by weight of 54 captive crayfish.

R.C.L. in cm.	Number of Animals	Increment in grams	Mean increment	Mean percentage increment	Calculated annual % increment
5-5.9	18	0 to 38	17.5±1.9	17.8	53
6-6.9	18	-7 to 42	20.8±3.1	14.0	42
7-7.9	8	-3 to 48	31.1±5.6	13.7	41
8-8.9	10	22 to 44	32.8±2.3	8.7	17

Percentage increases in weight at moult observed for J.lalandei are nearly 4 per cent higher than those observed for P.argus by Travis. The annual percentage increase in weight based on the number of moults observed per year is similar as P.argus moults more frequently than J.lalandei. The percentage increase in weight at moult decreases with increase in size. Templeman (1940) and Travis (1954) made similar observations for Homarus americanus and P.argus.

4.32 Growth by length. Increase in rostrum carapace-length at moult was observed for animals ranging in length from 4 to 9.9 cm. R.C.L. The measurements were taken not less than 28 days after the moult; after the skeleton had become quite hard. Table 4.05 shows increase in carapace-length recorded for 151 moults.

Table 4.05: Increase in length at moult for 151 moults.

R.C.L. in cm.	Number of Animals	Increment in mm.	Mean increment in mm.	Mean percentage increment
4-4.9	6	3.2-5.7	3.95±0.34	8.3
5-5.9	61	0.0-6.0	2.7±0.13	4.8
6-6.9	36	0.6-5.6	2.8±0.21	4.4
7-7.9	18	0.3-5.7	3.1±0.33	4.3
8-8.9	22	0.7-4.9	2.7±0.25	3.2
9-9.9	8	1.0-4.3	2.4±0.33	2.6

Analysis of variance calculated for absolute increments at moult showed no significant difference between the size-classes. The analysis is shown in table 4.06.

Table 4.06: Analysis of variance of data given in table 4.05.

Source of Variation	S.S.	D.F.	Mean S.	Var. Ratio
Between Classes	12.0	5	2.4	1.36
Within Classes	257.7	145	1.77	P>5%
Total	269.7	150		

The larger percentage growth of smaller animals compared with larger animals therefore appears to be due to smaller animals increasing in length by the same amount as larger animals.

Table 4.07 shows the annual increment based on increase in length at moult and number of moults per year.

Table 4.07: The annual increase in length based on number of moults per year and average increase per moult.

R.C.L. in cm.	Annual increment in mm. based on number of moults per year	Annual percentage increment
4-4.9	12+	25+
5-5.9	8	15
6-6.9	8	13
7-7.9	9	13
8-8.9	5	6
9-9.9	5	5

These results are similar to those obtained by Travis for P.argus.

4.33 Growth of animals maintained for one year.

Twenty one crayfish in three size-classes were maintained for more than one year. The growth of these animals is shown in table 4.08.

Comparison of these observed annual increments with those calculated previously is difficult due to the difference in numbers. However the trend of the two results is similar and serves as a cross check on information given in table 4.07.

Table 4.08: Growth of crayfish maintained for one year.

R.C.L. in cm.	Number of Animals	Number of Moults	Average annual increment in mm.	Average percentage annual increment
5-5.9	13	3	7.41	13.5
6-6.9	6	3	11.5	18.1
8-8.9	2	2	5.1	6.2

4.34 Loss of appendages and growth. Emmel (1905, 1906) demonstrated that regeneration of lost appendages at moult markedly affected growth of the animal as a whole. Travis observed moulting without growth in animals that had autotomized pereiopods or antennae.

A small proportion of the animals of three size-classes included in table 4.05 were lacking appendages prior to moult. Table 4.09 shows the mean increment at moult when regeneration occurred, compared with normal moults.

Table 4.09: The effect of regeneration on growth.

R.C.L. in cm.	Normal moults		Regeneration moults	
	Number of Animals	Mean increment in mm.	Number of Animals	Mean increment in mm.
5-5.9	48	2.84	13	2.16
6-6.9	32	2.95	4	2.02
8-8.9	14	2.89	8	1.90

It can be seen that the average increment at moult is larger when regeneration does not occur.

J.lalandei has considerable ability to regenerate appendages. Regeneration of five or more was observed on three occasions in animals of 5 cm. R.C.L.. In each case two moults were required for complete regeneration of all missing appendages. Appendages were regenerated to about ¾ normal size after the first moult and increase in length was below average. An animal lacking nine walking legs increased by 0.6 mm. R.C.L., an animal lacking six legs increased by 1.4 mm. R.C.L. and an animal lacking five legs increased by 0.9 mm. R.C.L.

4.35 Moulting without growth. Marshall (1948), Dawson and Idyll (1951) and Travis (1954) observed moulting without growth or negative growth in P.argus. All cases observed by Travis had been maintained under unfavourable conditions. Subsequent moults under more favourable conditions resulted in good growth. Lindberg (1955) reported that 36.5 per cent of captive P.interruptus that moulted failed to increase in size and that growth of animals moulting after less than a week in captivity was also greater than those kept for longer periods.

During this investigation moulting without increase in length occurred on three occasions. Two animals moulted atypically and died less than 28 days following moult.

The other animal moulted without increase in length after two months in captivity, but moulted on four subsequent occasions with good increases in length. Each moult was the first in captivity so that the history of the animals was not known.

Increase in length at moult was not always indicative of increase in weight. From the total of 66 observations of change in weight at moult, including those animals lacking appendages not included in table 4.04, 56 increased in weight, 9 decreased and one remained the same weight after moulting. Four of the nine that decreased in weight moulted atypically and died within ten days of moulting. The other five appeared to moult normally, but did not regain their previous weight. All increased in length.

4.4 Validity of data. The validity of growth-rate determined on captive animals has often been criticized, Burkenroad (1951), on the grounds that natural conditions can not be duplicated in the laboratory. Application of the above results to natural populations is therefore not possible. Although direct integration into a management-programme is unwise, growth-rate of captive animals forms a basis for further field-study and can be used as an index of minimum growth. Such knowledge is also invaluable if factors influencing growth such as hormone-balance are to be studied.

The method of determining growth outlined by Burkenroad requires observations to be made on animals during the first few days in captivity. He states that the validity of observations becomes more doubtful as the period of captivity progresses. If such is the case, it could be expected that growth at the first moult in captivity would be greater than growth at subsequent moults.

During this study 21 animals moulted three or more times. Of these, 16 showed the same or increased growth at subsequent moults. Although the number of animals used in these observations is small, they indicate that the period of captivity possibly does not materially influence growth-rate of J.lalandei maintained in captivity.

4.5 Discussion. In order to compare the growth-rate of J.lalandei as determined from this study with growth of the Palinuridae as a whole, a summary of the present state of knowledge is given below.

(1) P.japonicus.

(a) Kinoshita (1933) found that animals between 66 and 120 mm. in total length increased in length by 6 to 7 per cent at moult.

(b) Nakamura (1940) found that animals between 22 and 40 mm. in carapace-length increased in length by 9.4 to 16.7 per cent at moult. He also found that an increase from 6 to 33 mm in carapace-length required ten

moults. A further four moults were needed to reach 50 mm. and a further three to reach 65 mm. in carapace-length. Each of these periods probably represents growth for one year.

(2) P.interruptus.

(a) MacGinitie and MacGinitie (1949) reported an increase in volume of 15 to 16 per cent at moult.

(b) Lindberg (1955) found that captive animals between 16.2 and 54.4 cm. in total length moulting after one week to more than one year, increased in total length by 6 mm. ($\frac{1}{4}$ inch) per moult. An average increase in total length of 1.2 cm. was reported for six animals between 18.8 and 32.4 cm. that moulted within one week of capture.

Recovery of tagged animals between 18 and 23 cm. in total length indicated an increase of 1.5 to 2 cm. per moult, from which a yearly increase of 3 to 4 cm. ($1\frac{1}{4}$ to $1\frac{1}{2}$ inches) was calculated.

(3) P.argus.

(a) Smith (1948, 1951) reported an annual growth of one inch after an average of $2\frac{1}{2}$ moults per year.

(b) Dawson and Idyll (1951) reported an annual growth of $1\frac{1}{2}$ inches.

(c) Travis (1954) found that captive animals 40 to 89 mm. in carapace-length showed an average increase of 3 mm. per moult. Annual increase of 9 to 12 mm. in

carapace-length was observed after 3 to 5 moults, which was similar to her estimate of approximately 9 to 15 mm., calculated from the number of moults per year and average increase per moult. Increases in weight at moult ranged from almost 6 to 15 per cent for animals 50 to 89 mm. in carapace-length, from which an annual increase in weight of 17 to 75 per cent was calculated.

(4) J.lalandei.

(a) Young (1926) maintained a captive animal for three years and two months. During this time it increased from 4.2 to 14 cm. in total length after 8 moults, resulting in an average annual growth of 3 cm. in total length.

(b) Von Bonde and Marchand (1935) observed that animals of about 3½ inches in carapace-length moulted once or twice a year.

(c) Bradstock (1950) recovered two tagged animals, 21 and 25 cm. in total length after one year, which had increased in total length by 2.1 and 1.9 cm. respectively. He estimated that both animals had moulted twice, from which he deduced an increase of one centimeter in total length per moult.

(d) Present study: Captive animals 4 to 8.9 cm. R.C.L. showed an average increase in carapace-length of nearly 3 mm. at moult. Animals 5 to 7.9 cm. R.C.L. moulted 3 times per year, those between 8 and 8.9 cm., twice a year.

Thus animals 4 to 7.9 cm. R.C.L. increased by about one centimeter in carapace-length (one inch in total length) per year, animals 8 to 8.9 cm. R.C.L. by about 6 mm. R.C.L. (0.6 inches in total length). Crayfish between 5 and 8.9 cm. R.C.L. increased in weight at moult by 17.5 to 32.8 grams with a calculated annual increment of 17 to 53 per cent.

From the above summary it is possible to compare estimates of growth per annum for Panulirus and J.lalandei. Evaluation of all estimates of growth for Panulirus indicates an annual increase in total length of between 1 and 1½ inches for animals up to 9 inches. Although absolute increases at moult appear to be similar for animals within this range, annual increases in length of small animals is greater than large animals as the number of moults per annum decreases with size.

A more detailed estimate of growth-rate of J.lalandei is possible from evaluation of the above results. Like Panulirus, absolute annual increments are greater in small animals than in large. The approximate annual increment in total length is 1.2 inches for animals 2 to 5 inches, one inch for animals 5 to 8 inches, ½ to ¾ inches for animals 8 to 9 inches and ¼ to ½ inches for animals 9 to 11 inches in total length, which is similar in trend to that calculated for Panulirus.

At this rate of growth, the estimated age of a crayfish reaching the present minimum legal length in South Australia of 10 inches is 10+ years. Lindberg estimated that the age of P.interruptus at 10½ inches is 7 to 8 years, which is comparable to an estimate from Travis' figures for P.argus.

Travis observed average monthly water-temperatures of 17 to 29° C. compared with a range of 11.5 to 23° C. recorded during this study. More moults per annum were recorded for P.argus and moulting was closely correlated with temperature. Such a striking dependence of moulting on temperature was not apparent for J.lalandei. The difference in growth-rate between the two species can therefore be attributed, at least in part, to the difference in water-temperature between the two localities.

4.6 Tagging. Three types of tag have been tried for tagging spiny lobsters, but none has been thoroughly investigated. Each one has been only partly successful.

(1) External tags. Tags wired to the exoskeleton can not be used for the study of growth-rate as they are lost with the exuvium when the animal moults. Use of this type of tag is limited to short term studies of migration or for the direct observation of behaviour.

(2) Punch-marks. Identifying marks punched in the tail fan have been used by several investigators. Sheard

(1949) reported satisfactory results identifying several marked specimens of P.longipes after three moults. Wilder (1953) identified punch-marks in H.americanus after two moults and Lindberg (1955) identified a small number of tagged specimens of P.interruptus after at least one moult. Thomas (1958) used punch-marks in an extensive marking programme of H.vulgaris and Olsen (personal communication) has identified punch-marks in J.lalandei after an estimated three moults. Although this form of tagging is rapid and simple to operate in the field, individuals can not be identified. Growth is therefore calculated by statistical analysis of data obtained by recovering many tagged animals.

(3) Internal tags. Two types, a barbed strip of plastic, Smith (1948), Sheard (1949), Bradstock (1950), Lindberg (1955) and various types of metal hooks, Von Bonde (1928) and Bradstock (1950) have been used with some success. Both types are inserted into the abdominal muscle through an intersegmental membrane, the posterior end protruding. Sheard found plastic strips unsuitable in J.lalandei and P.longipes, such tags either causing many deaths or being lost at moult. Bradstock found both types of tag were retained after moult in a few animals, but reported the formation of a sheath of chitin around the tag, which may have caused loss at the next moult. Lindberg claimed limited success with plastic strips, but many were lost a short

time after insertion and after the first moult following insertion.

Since none of the above tags has proved very satisfactory an improved design of internal plastic tag, supplied by A.M.Olsen, C.S.I.R.O. Division of Fisheries and Oceanography was tested in the laboratory. These tags were obtained from U.S.A., where they have been used in the study of crabs.

The tags were small darts. The barbed end, 3 cm. long was extruded from hard but flexible plastic, which was fused to a 4 cm. length of plastic spaghetti. An identifying number was stamped on the spaghetti.

Tags were inserted into the abdominal muscle through a small slit in the dorsal intersegmental membrane connecting the second and third abdominal segments. Damage to alimentary canal and median blood vessels was reduced by inserting the tags to one side of the mid-line. Due to the flexible nature of the tags, an inserting needle was necessary. Tags and instruments were kept in 70 per cent ethyl alcohol before insertion. A small slit was made in the intersegmental membrane with a fine scalpel and the tag and holder, made from a heavy gauge hypodermic needle were pushed directly into the abdominal muscle. The barb retained the tag in the muscle, while its holder was withdrawn. About $2\frac{1}{2}$ cm. of the tag protruded from the abdomen, which was adequate for

identification.

In order to be worthwhile in a marking programme the following qualities must be fulfilled:

(1) Deaths caused by tagging should be minimal.

(2) Retention of tags through moult is essential.

(3) Tags must be durable. Identifying numbers must be permanent and tags should not be broken or lost through wear and tear.

(4) Lesions caused by tagging should be minimal.

Trial.

Ten crayfish approximately 9 cm. T.C.L. were tagged.

(1) Mortality. No deaths were attributable directly to insertion of tags. Some bleeding occurred but soon stopped. Four animals were allowed to live more than four months and one was finally killed after six months.

(2) Durability. During the fortnight immediately following tagging, small pieces of tag were removed from protruding tags by other crayfish. Some discolouration of tags at the intersegmental membrane was apparent after one week, but had not progressed after six months. Identifying numbers were still in good condition after six months and no general deterioration of the tags had occurred after this period. No tags were broken through wear and tear.

(3) Retention at moult. Six animals moulted during the trial after periods ranging from 24 to 150 days. The

tag was retained in each case and had no observeable effect on growth or development of the exoskeleton. Ecdysis did not draw tags beneath the integument or withdraw them. External lesions were small, but indentation and erosion of setae had occurred on the posterior margin of the second abdominal tergite.

(4) Internal lesions. The effect of tagging on abdominal tissue was determined by killing tagged animals periodically and observing any lesions caused by tagging. Lesions were described on gross morphological characters and 10μ sections were stained with Mallory's triple connective tissue stain and Delafield's haematoxylin (Harris modification) and eosin.

10 Days. A little necrosis was apparent at the intersegmental membrane and around the barb. The intersegmental membrane had thickened, forming a small collar around the tag. The band of muscle penetrated by the tag was white and hard, surrounded by normal muscle. Histologically the damaged muscle resembled normal muscle except for some infiltration of connective tissue.

13 Days. No necrotic tissue was apparent. the band of muscle penetrated by the tag was dense, mustard yellow, very hard and brittle. Sections were cut with difficulty and showed massive infiltration of connective tissue. There was no sign of a sheath surrounding the tag,

which was firmly embedded in the damaged muscle.

45 Days. This animal had moulted once, 34 days following insertion of the tag. The second abdominal tergite was eroded and setae had been removed where the tag had rubbed. The intersegmental membrane was sound, but had thickened to form a collar around the tag. The tag was embedded in a large mass of tissue, 2 by 1½ by 3 cm., which was detached from the surrounding normal muscle. The lesion formed a sac enclosing the barbed end of the tag. Externally the sac was brown and smooth, the tag moving easily within it.

When the sac was cut transversally, it was found to consist of an outer sheath enclosing a white amorphous mass resembling cotton-wool, which readily washed away. The histological structure of the sac was a thin outer covering of connective tissue filled with degenerating muscle.

137 Days. (two animals).

(a) This animal had moulted 45 days following insertion of the tag. A lesion just beneath the integument, 2 by 1½ by 1 cm. was present. The barb was firmly embedded in good muscle and the lesion formed a grey, black collar around the shaft of the tag. Distally the lesion was eroded.

(b) This animal had moulted 24 days following insertion of the tag. The lesion beneath the integument had also reduced to a grey, black collar, 0.5 by 0.5 by 1 cm. The

barb was firmly embedded in good muscle.

163 Days. This animal had moulted 99 days following insertion of the tag. The only apparent lesion was a thin film of blackened tissue at the point of entry. The barb was firmly embedded in good muscle, which showed no damage.

171 Days. This animal had moulted 116 days following insertion of the tag. No lesion was apparent. The tag was embedded in normal muscle and was in good condition.

Conclusions. Although from practical necessity this test was limited to a small sample of animals, results were definite enough to justify the use of this tag in field-experiments with the following expected results.

(1) Deaths following insertion should be few.

(2) Few breakages and little wear could be expected after periods of at least a year.

(3) These tags do cause substantial lesions initially, but these should not prove a great problem as damaged tissue appears to be resorbed and new muscle regenerated around the barb.

Discussion. This type of internal marker appears to be an improvement on designs used previously. The tags used by Sheard (1949) were easily lost and caused many deaths. Both these factors appear to be eliminated in the tag described here. The tags used by Bradstock (1950) were not tested in the laboratory and his results were obtained

from a limited number of returns from the field. He observed that a barbed strip of plastic did not appear harmful and was retained after one moult in a single animal. Similar claims were made for the wire-hook type of tag. No sheath of chitin was detected in lesions observed in this trial as observed by Bradstock.

Lindberg (1955) tagged 130 specimens of P.interruptus with barbed strips of plastic. Five per cent of the tags were lost within 48 hours. Of the remaining 95 per cent, 73 per cent moulted, 68 per cent of these retaining their tag. He also inferred from indirect evidence obtained from experiments in the field that many tags had been lost after two months. Tagged animals developed prominent lesions around the tag as did those recovered from the field to a lesser extent. Dawson and Idyll (1951) observed similar effects in P.argus and implied that lesions were caused in part by the material from which the tag was made.

5. Reproduction.

5.0 Introduction. The reproductive anatomy of several species of the family Palinuridae has been described. Ortmann (1896) described that of Palinurus vulgaris and Matthews (1951) described the male reproductive organs of Panulirus pencillatus in detail. Lindberg (1955) described the reproductive cycle, estimated size at sexual maturity and numbers of eggs produced by females and also described some aspects of reproductive behaviour of Panulirus interruptus. Von Bonde (1936) described the reproduction and embryology of J.lalandei. Hickman (1946) estimated numbers of eggs produced by females and size at sexual maturity of J.lalandei as did Bradstock (1950).

It would be unwise to apply Lindberg's results directly to J.lalandei and the observations made by Von Bonde, Hickman and Bradstock were made at widely separated localities and were not extensive enough to be used as bases for the management of the fishery in South Australia. The primary aim of this investigation was therefore. to obtain an estimate of size at sexual maturity and to describe the reproductive cycle, which could be used directly in the management of the South Australian crayfishery.

5.1 Materials and methods. Monthly samples of live crayfish below the minimum legal length of 10 inches were supplied for 12 months by the South Australian

Department of Fisheries and Game. Closed seasons, bad weather and slipping of fishing boats during winter prevented samples being obtained during July and August and small samples only were obtained during April, October and December. Total carapace and total lengths of each animal were recorded and the gonads examined according to their external morphology.

Preliminary examination of representative sections of the entire gonads of several specimens of both sexes showed the gonads to be homogeneous in structure and development of germ cells. Subsequently only a small portion of gonad, usually a piece 1 cm. long immediately anterior to the gonoduct was excised and fixed in Gilson's fluid. One gonoduct was also removed and fixed in Gilson's fluid for subsequent histological examination.

After dehydration in ethyl alcohol and clearing in xylene, the pieces of gonad and duct were embedded in paraffin wax, M.P. 54-56° C. and transverse sections 10 μ in thickness cut as a routine. Two slides were prepared of each specimen, one being stained with Delafield's haematoxylin (Harris modification) and eosin (1 per cent in ethyl alcohol), the other with Mallory's triple connective tissue stain. Haematoxylin and eosin was used to follow structural changes in the gonads, Mallory's stain to aid in identification of tissues and to follow the maturation

of ova.

Testes and immature ovaries were sectioned relatively easily. Ovaries containing yolk-material and vasa deferentia of mature males were extremely hard and brittle, requiring the paraffin blocks to be coated with dilute celloidin preceding each section. The observations which follow are based upon the examination of 365 female and 225 male crayfish.

5.2 The female.

5.21 General description of the reproductive organs.

The ovaries are paired rod-like organs situated on either side and dorsal to the alimentary tract. In immature and resting mature animals the ovaries normally extend from the level of the eyes to the insertion of the abdomen and may extend into the first abdominal segment as maturation progresses. A transverse bridge, partly covered by the heart connects each ovary to the genital apertures located at the base of the third walking legs.

5.22 Classification of ovarian stages. The gross morphology of immature ovaries does not vary significantly throughout the year, but mature ovaries undergo a cyclical change. The macroscopic appearance changes sufficiently throughout this cycle to allow the process to be divided into a series of recognizable stages. Hjort (1910) described seven morphological stages in the gonad of the

herring and his classification, with modifications has been accepted universally by later fishery biologists. King (1948) described five developmental stages in the ovary of Penaeus setiferus based on relative size and changes in colour derived primarily for quick identification of maturation of gonads in the field.

Seven macroscopic stages are apparent in the ovaries of J.lalandei. The microscopic structure of these stages will be described in a later section. Figure 5.01 shows the relative size and shape of the ovarian stages in situ.

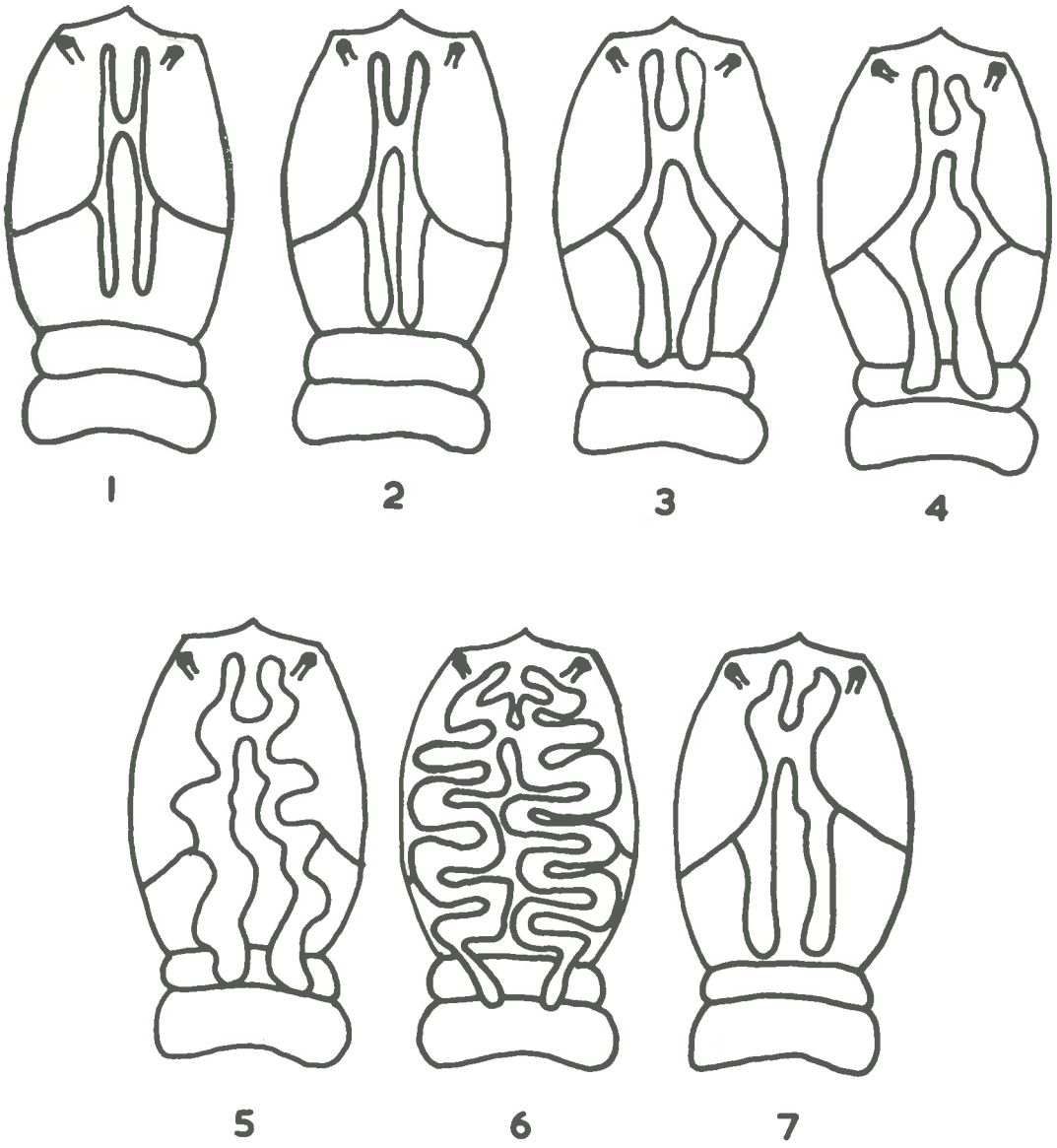


Figure 5.01: The relative size and shape of the ovarian stages in situ.

Stage 1. (immature virgins). The ovaries are straight, turgid, rod-like structures and do not extend into the abdomen. Little variation in colour is found during this stage, the organs being creamy-white and somewhat translucent. Individual ova can not be recognized.

Further stages 2 to 7 apply to maturing virgins and mature animals, which can not be distinguished on the morphology of the ovary alone.

Stage 2. The ovaries have begun to swell and may extend to the posterior margin of the thoracic cavity. The colour is a rich yellow and individual ova may be distinguished.

Stage 3. The ovaries have begun to change shape and are often arched about points of attachment. Swelling has progressed and the posterior horns usually extend into the first abdominal segment. The colour is yellow-orange and individual ova can be distinguished.

Stage 4. The ovaries are slightly buckled and have lost some of their turgidity. Swelling has increased and the organs have extended well into the first abdominal segment. The colour is bright orange and individual ova can be distinguished through an apparently thinner ovarian wall.

Stage 5. The ovaries are usually more convoluted than in stage 4. Change in colour is marked. The appearance

is no longer homogeneous, the basic colour being orange-brown with some of the ova showing through the ovarian wall as yellow-orange specks.

Stage 6. This stage immediately precedes spawning. An enormous increase in size has occurred. The ovaries now occupy all available space in the thoracic cavity. They are very swollen and increase in length has caused marked convolution. The colour is a rich brick-red. Individual ova are easily distinguished and the ovaries often occupy all available space in the first abdominal segment. Some ova appear in the proximal end of the oviduct. The ovarian wall is very fragile and is easily punctured.

Stage 7. (spent). This stage is found in crayfish carrying eggs. The ovaries have decreased in size considerably and have lost their convolutions. In cross section they have flattened dorso-ventrally and have become very flaccid. The colour is dirty grey and a few residual, yolky ova usually occur in small clumps near the extremities and oviducts. These residual eggs gradually disintegrate and finally can only be recognized as diffuse yellow patches.

Plate 5.01 compares the anatomy of the ovarian stages.

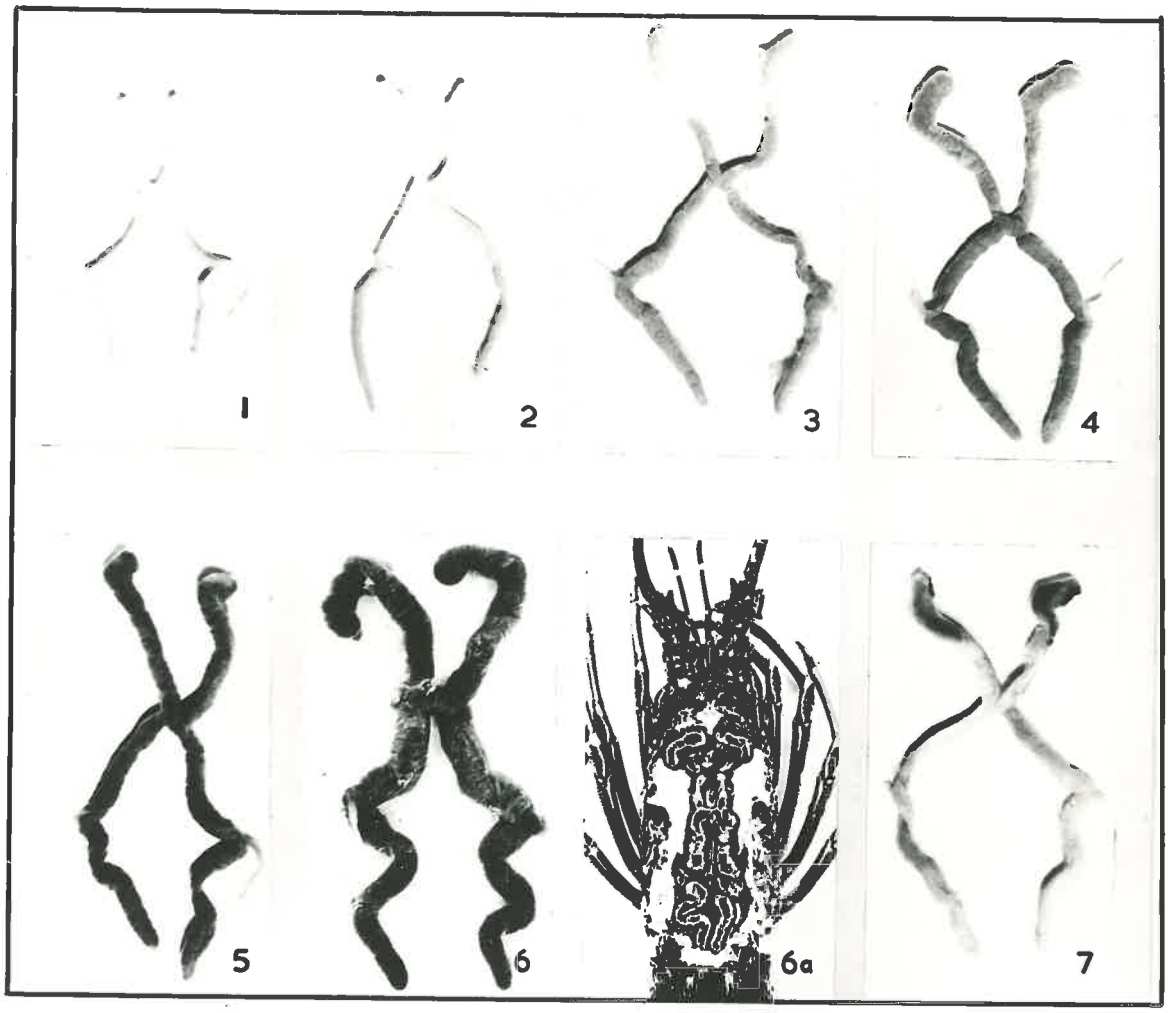


Plate 5.01: The relative size and colour of the ovarian stages.

5.23 Histology of the ovary. The general structure of the ovary is best seen in sub-mature animals. The outer wall consists of three layers: (1) An outer thin layer of pavement epithelium. (2) A central thick coat of connective tissue. (3) An inner layer of germinal epithelium. The germinal epithelium does not appear to be continuous, but is pushed away from the ovarian wall to form a small strand, the "germinal strand", running the length of each ovary and situated near the centre of the organ. No muscle could be detected in the ovarian wall.

The immature ovary is solid, containing no lumen. In fact a central lumen was only detected in freshly spent ovaries. From the central germinal strand, oogonia, primary oocytes, secondary oocytes and developing ova in that order radiate to the periphery. Septa of connective tissue extend longitudinally through each ovary and small blood sinuses, usually close to the ovarian wall are obvious in most sections. Numerous follicle cells fill the interstitial spaces between oocytes and ova.

In sections stained with haematoxylin and eosin, non-mature ova are basiphilic and stain blue. These cells have large well defined nuclei with obvious nucleoli. Ova containing yolk stain preferentially with eosin and are acidophilic. The nucleus of these cells becomes more obscure as deposition of yolk progresses. Non-mature ova stain

light purple with Mallory's triple connective tissue stain. Ova containing yolk stain blue through yellow-orange to brown-orange depending on the amount of yolk present.

5.24 Histology of ovarian stages.

Stage 1. (Plate 5.02).

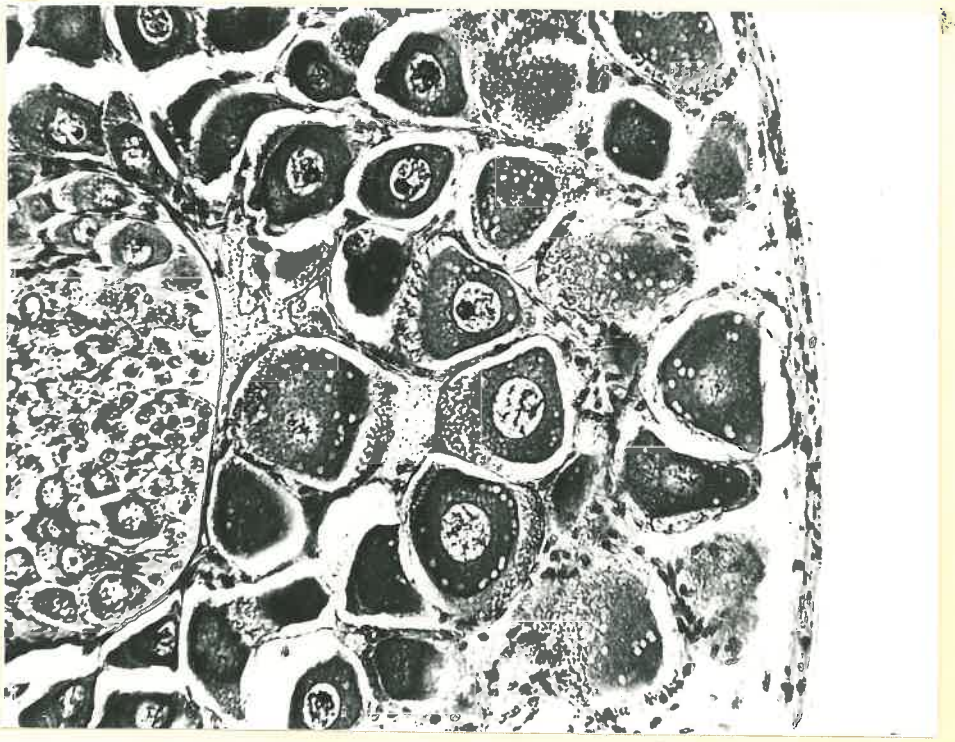


Plate 5.02: Cross-section of first stage ovary. X 135.

The ovarian wall is thin and taut, about 0.01 mm. thick. The mean maximum diameter of ova is about 0.1 mm. and all are basiphilic. Cell-nuclei are large and discreet and the larger oocytes have a few vacuoles around their circumference. No deposition of yolk is apparent and the

cytoplasm of developing ova is fine and granular. Most ova are completely surrounded by follicle cells, which tend to clump at interstices of adjoining ova.

Stage 2. (Plate 5.03).

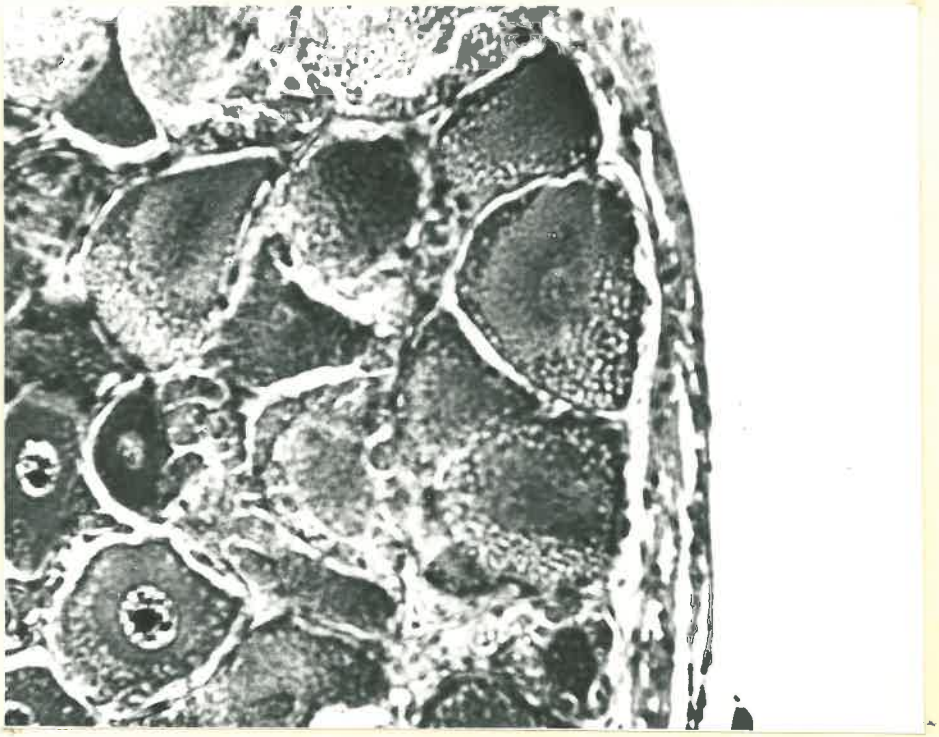


Plate 5.03: Cross-section of second stage ovary. X 135.

The ovarian wall is about 0.02 mm. thick in stages 2 to 6 and is taut and non-convoluted. The mean maximum diameter of ova is about 0.15 mm. and basiphilic cells are restricted to the germinal strand and a central radiating mass of oocytes. The nuclei of developing ova are still

easily seen and vacuolation near the circumference of the cell has increased. The cytoplasm of developing ova is still fine and granular, but deposition of yolk is between 10 and 20 per cent. Developing ova stain blue with Mallory's stain and most are surrounded by a single layer of follicle cells. The nuclei of these cells are elongated, but those grouped at interstitial spaces are round.

Stage 3. (Plate 5.04).

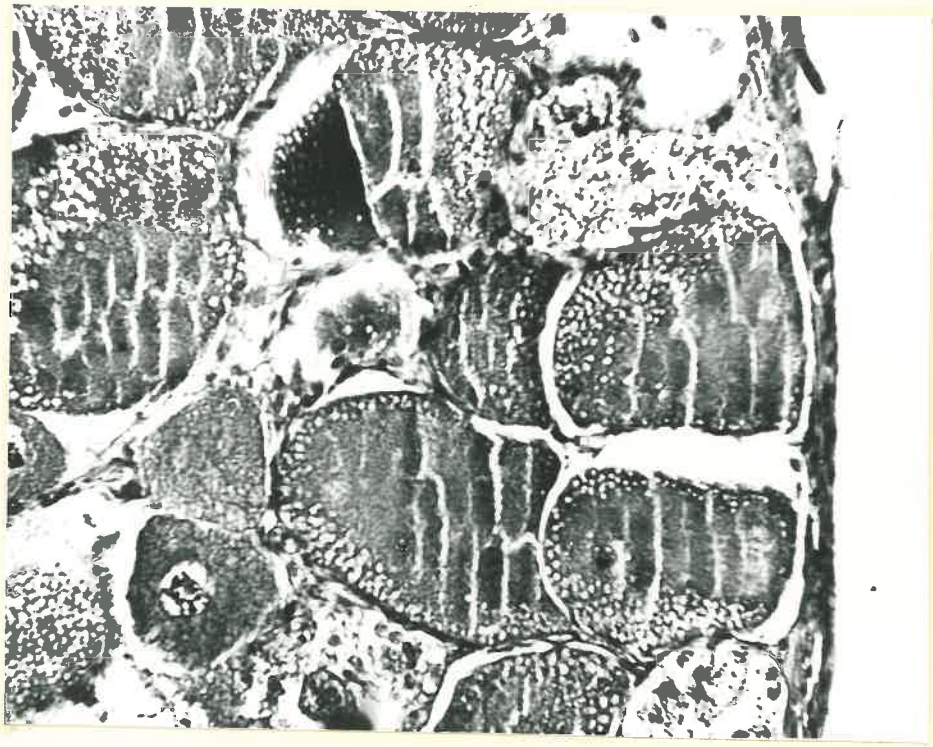


Plate 5.04: Cross-section of third stage ovary. X 135.

The maximum diameter of ova has increased to 0.22 mm.

and basiphilic cells are restricted to the germinal strand and some radiating patches of four to five oocytes. Deposition of yolk has begun to mask many nuclei. The cytoplasm of developing ova is still fairly fine grained and stains blue with Mallory's stain except for spots of heavier deposition of yolk, 20 to 40 per cent, which stains orange. Many large vacuoles are apparent in the blue stained parts of the ova. All ova containing yolk are surrounded by a single layer of follicle cells, the cytoplasm of which has become much attenuated and the nuclei flattened.

Stage 4. (Plate 5.05).

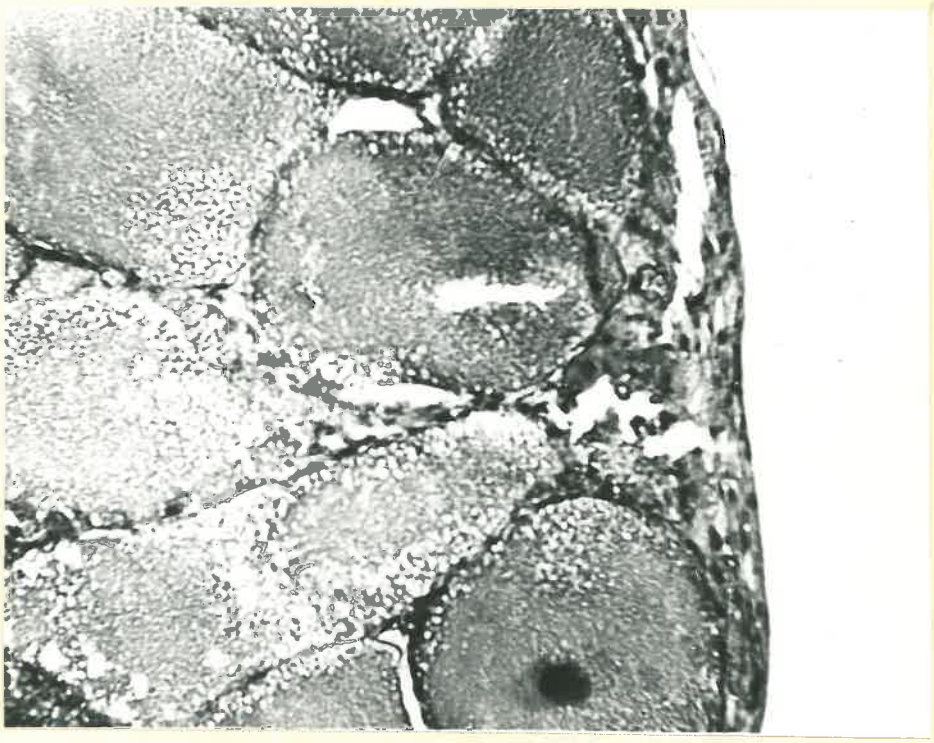


Plate 5.05: Cross-section of fourth stage ovary. X 135.

The maximum diameter of ova has increased to 0.27 mm. Basiphilic cells are restricted to the germinal strand and a few patches of oocytes. Many more nuclei are hidden and those that can be seen have lost their discreetness. Deposition of yolk has increased to about 40 to 60 per cent and the cytoplasm of developing ova has become large grained. Most ova stain orange with Mallory's stain, with only a small proportion of blue globules mixed with the orange. Few vacuoles are apparent and the germinal strand becomes difficult to see. All ova containing yolk are surrounded by a single layer of follicle cells, the nuclei of which are much flattened.

Stage 5. (Plate 5.06).

The maximum diameter of ova has increased to about 0.39 mm. Basiphilic cells are confined to the germinal strand and a few patches of one to two oocytes. Very few nuclei are obvious and those that can be seen are very diffuse in nature. Deposition of yolk has increased to about 70 to 80 per cent deposited in large globules, which stain a darker orange-brown with Mallory's stain. The germinal strand is difficult to see and follicle cells surrounding the developing ova are so flattened that it is very difficult to distinguish individual nuclei.

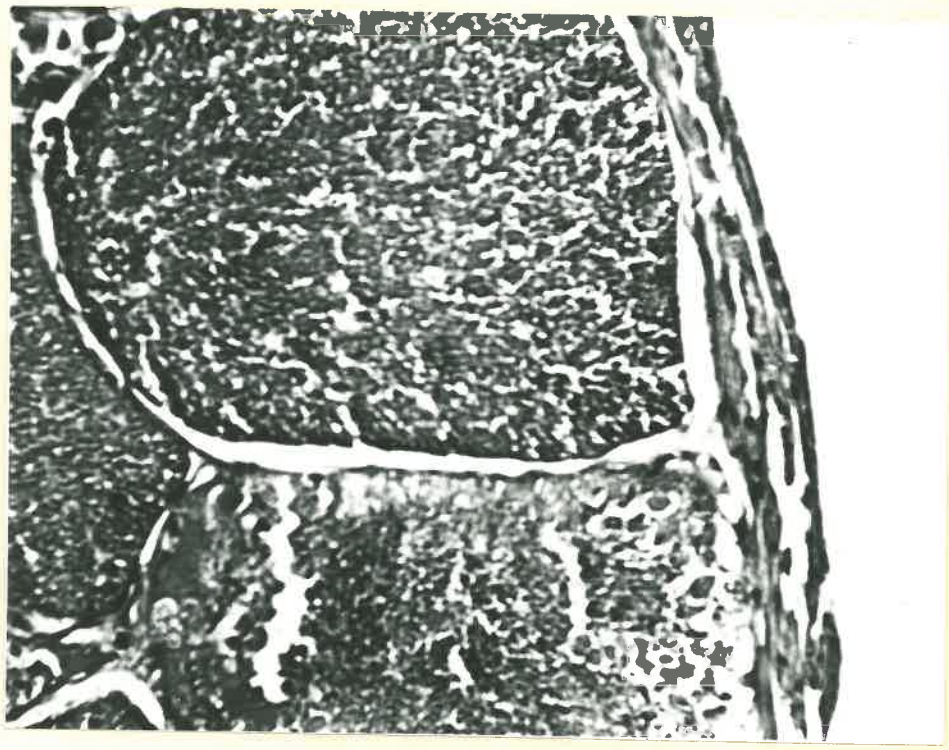


Plate 5.06: Cross-section of fifth stage ovary. X 135.

Stage 6.

The maximum diameter of ova has increased to about 0.49 mm. Basiphilic cells are not at all obvious, only a few cells per section being apparent. Almost all nuclei have disappeared. Deposition of yolk is 100 per cent, which stains a dark orange with Mallory's stain. Globules of yolk have become much more tightly packed. It is almost impossible to find the germinal strand, and follicle cells are extremely

difficult to differentiate. Sections suitable for photographing could not be cut due to the deposition of yolk.

Stage 7. (Plate 5.07).

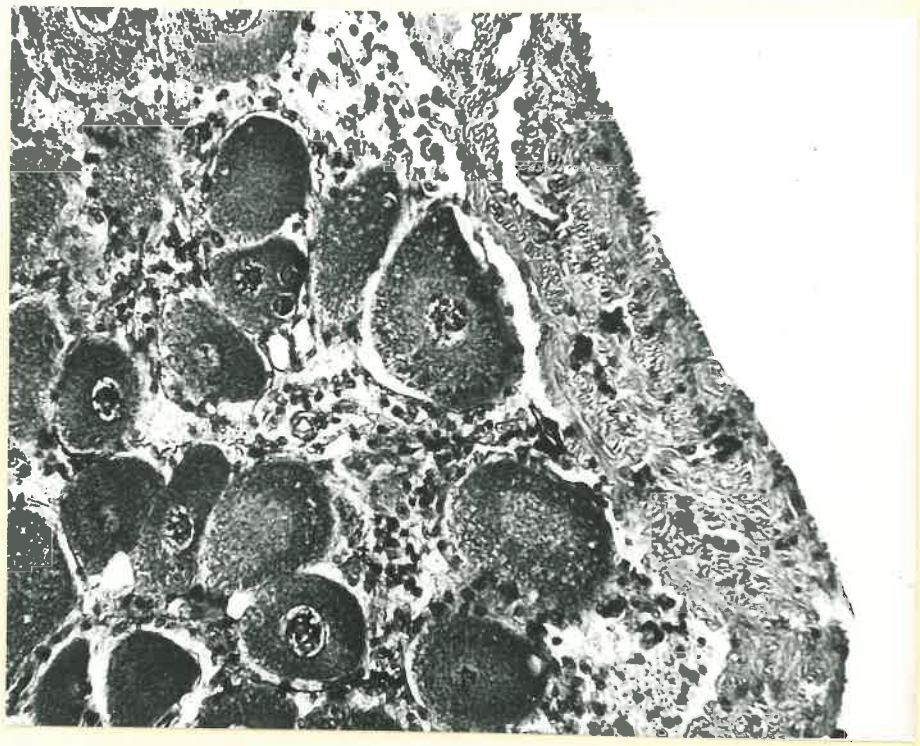


Plate 5.07: Cross-section of seventh stage ovary. X 135.

Tension on the ovarian wall has been released with consequent contraction and convolution, increasing the thickness to about 0.1 mm. The maximum diameter of ova is reduced to about 0.12 mm. The shape of the residual eggs is much distorted and they are basiphilic. Unless the animal has just spawned, no discreet, residual, yolky ova are apparent,

but some diffuse yolky material undergoing resorption is often obvious. A few vacuoles occur in the rather fine grained cytoplasm of the residual ova and the germinal strand is again obvious. The number of residual follicle cells is enormous, which occur as a tightly packed mass interstitially.

5.25 Histology of the oviduct. The oviduct is a rather flattened tube made up of three layers of tissue. (1) An outer layer of epithelium. (2) A central layer of connective tissue. (3) An inner layer of high columnar epithelium.

The lumen of the oviduct is villified and in some cases the high columnar epithelium lining the lumen may form semi-closed channels between adjoining villi, the significance of which will be discussed under "method of fertilization". Initially it appeared that the number of villi was a function of size and a possible index of maturity. The number of villi from the oviducts of 51 animals ranging in length from 7.4 to 13 cm. T.C.L. were subsequently counted. No sudden increase in number was apparent with increased size, the mean number of villi per oviduct increasing only from 5.0 for animals 7 cm. T.C.L. to 6.4 for animals above 11 cm. T.C.L.

Plate 5.08 shows a transverse section through the oviduct.

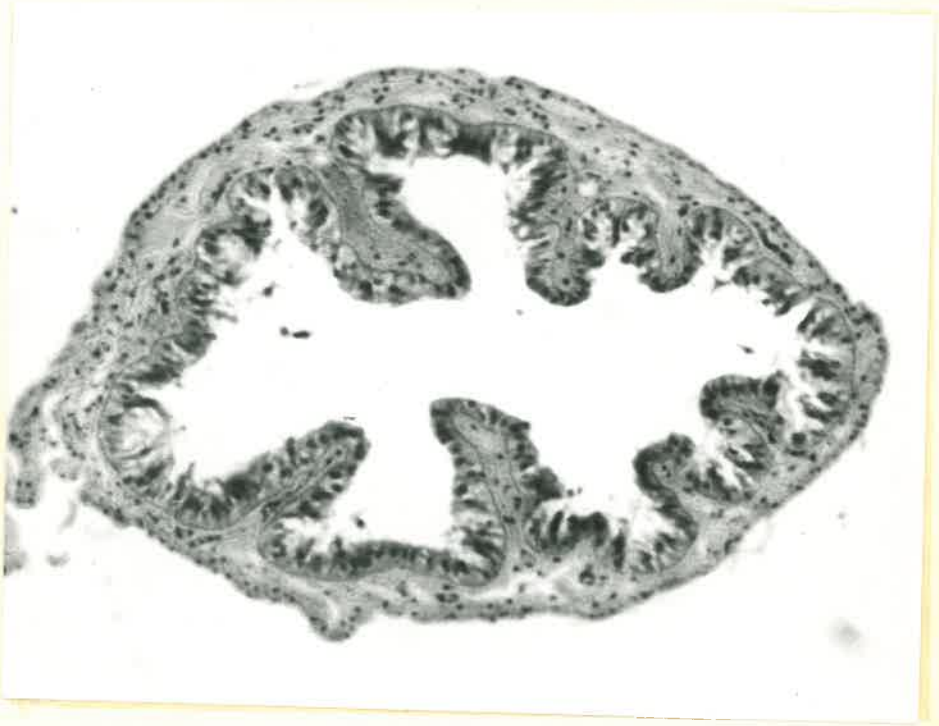


Plate 5.08: Cross-section of the oviduct. X 125.

5.26 The annual ovarian cycle. The annual cycle of ovarian maturity has not been described previously. Several authors however, have recorded the period of spawning through hatching. In general these periods have been closed to fishing to protect the females whilst carrying eggs.

Von Bonde and Marchand (1935), surveying the known grounds of South Africa at that time stated that the time of spawning depended on the location. They gave periods during

which females carrying eggs could be caught, ranging from May through February with a peak-period between October and November.

Hickman (1946) caught females carrying eggs as early as April in Tasmania and stated that extrusion of eggs continued during May and June. Hatching occurred during July, August and September and was completed by October.

Bradstock (1950) found that almost all females caught off New Zealand during May were carrying eggs. Spawning probably began during April, but no samples were obtained during this month due to a closed season. The percentage of females carrying eggs was high during May through September, but most had hatched by October.

Grua (1960) states that spawning at St. Paul and New Amsterdam probably begins in May when water temperatures have decreased to about 14° C. Most eggs have hatched by October or November.

Olsen (1960) states that eggs are carried between May and October in Tasmania and New Zealand and between June and November in South Australia.

The small number of mature females observed during the classification of stages in the ovarian cycle allowed only a preliminary description of the annual ovarian cycle.

Table 5.01 shows the monthly progression of ovarian stages observed during a period of twelve months.

Table 5.01: The monthly progression of ovarian stages.

Gonad stage	Jan.	Feb.	Mar. Apr. May	Jun. Jul. Aug.	Sep.	Oct. Nov. Dec.
2	●	O	O		O	O
3	O	●	O		O	O
4	O	●	O	No sample	O	
5		O	●		O	
6			O		O	
7					●	●

Solid circles represent the ovarian stage observed in the majority of mature females. Open circles represent other stages of maturity observed. Samples for March, April and May were small and have been grouped, as have the samples for October, November and December. It can be seen that the range of ovarian stages for any month can be large, which suggests that the maturation of ovaries is not contemporaneous among all crayfish.

Unfortunately no data were collected between June through August due mainly to a closed season for females, which lasts from June through October. It is apparent from figure 5.01 that most eggs are probably extruded and hatched during this period and that the present closed season protects females carrying eggs. However, the preliminary nature of this investigation must be stressed and future work could give slightly different results.

Evidence obtained from fishermen indicates that the period of spawning in South Australia is extended. Occasionally females carrying eggs are caught on some grounds as early or as late as February and certainly can still be caught in reasonable numbers during late December. By May, females carrying eggs are reasonably common indicating that spawning extends over several months.

An extended period of spawning indicates that males are capable of mating at any time of the year, which will be discussed in a later section. Another consequence of an extended period of spawning is that Phyllosoma larvae will be present in the plankton for most of the year. They will therefore be subject to seasonal changes in direction of surface-currents, enhancing the dispersal of larvae from a given place considerably.

5.27 Size at sexual maturity. In almost every study of a commercial species for the formulation of a management programme, one of the first questions asked is: What is the size at sexual maturity? Two views are held regarding the value of restrictions, which act solely for the protection of reproductive potential. The older theory, that animals should be protected until they have reproduced at least once has rather fallen into disfavour. Many biologists now believe that reproductive potential is not endangered by heavy fishing if the number of eggs produced

is enormous. Whatever the case, until such time as an accurate assessment of stocks can be made and such topics as growth-rate, birth-rate, death-rate and recruitment can be evaluated, protection of sexually immature animals provides a logical interim protection of the fishery.

Collection of data for such an estimation is laborious and impractical if large numbers of animals have to be dissected and their gonads examined. A reliable external criterion of maturity is therefore an advantage.

Of the 365 females examined in detail during the study of ovarian stages, 133 had mature ovaries; 120 of these (90.2 per cent) also had ovigerous setae on the pleopods. Out of the total of 365 females, 128 had ovigerous setae on the pleopods, and 118 of these (92.1 per cent) also had mature ovaries. All the animals examined were below the current minimum legal length of 10 inches in total length. Most were between 8½ and 9 inches, which is in the range of transition from immaturity to maturity. A better correlation than 90 per cent could be expected for larger animals due to the initial development of ovigerous setae at first maturity, which will be described later.

The presence or absence of ovigerous setae was then used to determine the state of sexual maturity of 855 female crayfish. Data for animals below minimum legal length were obtained from animals maintained in the laboratory. Animals

above minimum legal length were studied at crayfish processing plants. Data were arranged in classes of half centimeter T.C.L. and the percentage of sexually mature crayfish in each class calculated.

Table 5.02 shows results obtained from crayfish marketed from Port MacDonnell, Beachport, Robe, Kingston, Kangaroo Island and Port Lincoln. Table 5.03 shows results from a small sample taken from Port MacDonnell and Table 5.04 shows results from all ports excluding Port MacDonnell.

Table 5.02: Sexual maturity of females taken from Port MacDonnell, Beachport, Robe, Kingston, Kangaroo Island and Port Lincoln.

T.C.L. in cm.	Number of Animals	Number Mature	Number Immature	Percentage Mature
Below 8.0	136	0	136	0
8.0-8.49	61	2	59	3.3
8.5-8.99	70	10	60	14.2
9.0-9.49	139	39	100	35.6
9.5-9.99	111	53	58	47.6
10.0-10.49	77	45	32	58.3
10.5-10.99	73	55	18	75.4
11.0-11.49	74	63	11	85.1
11.5-11.99	57	45	12	79.0
Above 12.0	57	56	1	98.0

Table 5.03: Sexual maturity of females taken from Port MacDonnell.

T.C.L. in cm.	Number of Animals	Number Mature	Number Immature	Percentage Mature
Below 8.0	11	0	11	0
8.0-8.49	11	2	9	18.2
8.5-8.99	17	5	12	29.4
9.0-9.49	32	23	9	71.9
9.5-9.99	4	3	1	75.0

Table 5.04: Sexual maturity of females taken from all ports excluding Port MacDonnell.

T.C.L. in cm.	Number of Animals	Number Mature	Number Immature	Percentage Mature
Below 8.0	119	0	119	0
8.0-8.49	50	0	50	0
8.5-8.99	49	5	44	10.2
9.0-9.49	95	7	88	7.4
9.5-9.99	107	50	57	46.7
10.0-10.49	73	42	31	57.5
10.5-10.99	73	55	18	75.4
11.0-11.49	74	63	11	85.1
11.5-11.99	57	45	12	79.0
Above 12.0	57	56	1	98.0

It can be seen that the larger size-classes within the range 8 to 12 cm. T.C.L. contained more mature females,

but the proportion did not approach 100 per cent for any size-class except the largest.

For many years fishermen at Port MacDonnell have opposed any projected increase in minimum legal length, claiming that the population of crayfish found in their area did not grow as large as elsewhere. Table 5.03 shows the results obtained from a relatively small sample of 75 females caught near Port MacDonnell. These results indicate that female crayfish from this area mature at a smaller size than those taken elsewhere in the State. Over 70 per cent are mature between 9 and 9.49 cm. T.C.L., compared with less than 10 per cent (Table 5.04), at the same size for animals taken from five other South Australian fishing grounds.

Conclusions. The above results indicate that about 40 per cent of 10 inch female crayfish allowed to be caught under the present regulations are potentially immature. If South Australian regulations were altered to those used in Victoria and Tasmania i.e. the minimum legal length be increased to 11 cm. T.C.L. (11 inches total length), less than 20 per cent of females of this size would be immature.

Measurements made on female crayfish from Port MacDonnell tend to support the view of fishermen, that the stock found near Port MacDonnell is smaller than that occurring on other fishing grounds. Anecdotal evidence of

a dwarf stock at Victor Harbour has also been available for many years. It therefore appears that further work is necessary to delineate the South Australian stocks.

The large size-range, during which females within a population become sexually mature, indicates that sexual maturity is more likely a function of age than size, which agrees with Lindberg (1955).

Discussion. An index of sexual maturity used by other authors is the presence of viable eggs. This criterion can not be disputed but is difficult to use in practice. Data are difficult to obtain as the period during which eggs are carried is short and the capture of females carrying eggs is prohibited, eliminating marketing centres as sources of information.

Von Bonde (1936), in South Africa observed a female J.lalandei in berry, which measured 4.5 cm. in carapace-length. Challenger (1943) claims to have observed females in berry of 1.5 inches in Tasmania. Hickman (1946) also in Tasmania recorded two females, 7.2 and 7.4 cm. R.C.L. carrying eggs. Bradstock (1950), in New Zealand recorded female crayfish of 7 cm. carapace-length bearing eggs and states that all are mature at 9.7 cm. Bradstock also attempted to detect sexual maturity by finding the length at which the growth-rate of the abdomen changed significantly. This criterion was defined by Templeman (1935, 1944) for

H.americanus, who found that the width of the female abdomen increased significantly at sexual maturity. Bradstock's interpretation of his data in the absence of statistical testing is hardly justified and his claim that some animals become sexually mature at 7.2 cm. in carapace-length as determined by this method must be questioned. Lindberg (1955) found that P.interruptus became sexually mature between 19 and 23 cm. in total length and Grua (1960) states that J.lalandei becomes sexually mature between 16 and 19 cm. in total length.

All of the above authors quote cases of sexual maturity in female crayfish at a much smaller size than were observed during this study. Most of them however, have done little more than find the smallest size at which a small proportion of female crayfish become mature. This knowledge by itself is of little use in the formulation of management regulations.

5.28 Development of ovigerous setae. Eggs, when spawned are carried under the abdomen attached to the endopodites of the pleopods by means of a fringe of setae. The pleopods of immature animals do not have these ovigerous setae, but they must be developed before the first spawning or the egg-mass would be lost.

Any change in form of the exoskeleton can only occur after a moult, thus the appearance of ovigerous setae is only apparent after an animal has moulted. Since the presence

of ovigerous setae is necessary for the animal to be potentially mature, the moult at which ovigerous setae appear can be designated the maturity-moult. Either one or two moults are necessary for a complete fringe of setae to be formed. A complete fringe can develop on pleopods that had no setae prior to moult or a few setae may be formed at the moult preceding the maturity-moult. Both types of development have been observed in captive animals. The ovaries of these animals were well developed at the maturity-moult and spawning was potentially possible had fertilization occurred.

The use of ovigerous setae as an index of maturity will therefore miss maturing virgins if they are examined before their maturity-moult. This possibly explains why a better figure than 90.2 per cent was not obtained in the initial correlation between presence of ovigerous setae and maturity of ovaries. The presence of ovigerous setae in some animals with immature ovaries indicates that some female crayfish are potentially mature at least one moult before their ovaries begin to mature.

Plate 5.09 shows the complete series of female pleopods.

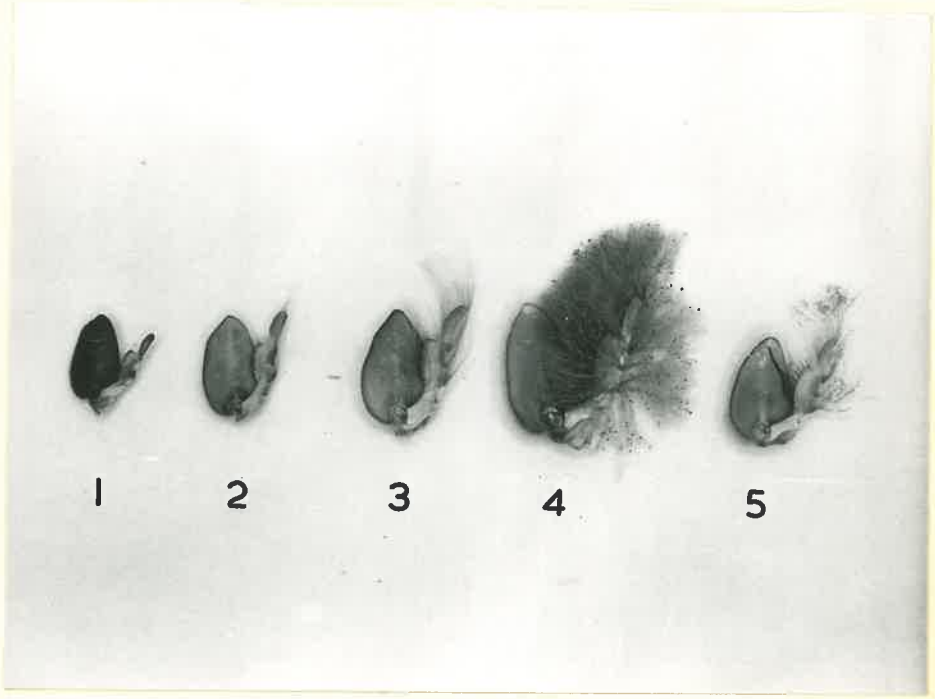


Plate 5.09: Stages in development of ovigerous setae. X $\frac{1}{2}$.

Pleopod 1 is immature and has no setae, pleopod 2 has a few setae, pleopod 3 has a complete fringe of setae and pleopods 4 and 5 were taken from animals whose eggs had hatched. In pleopod 4 the eggs have recently hatched while the eggs attached to pleopod 5 have been hatched for some time and the ovigerous setae have been cleaned of almost all the empty egg-capsules.

Once formed, ovigerous setae are permanent structures

which are retained through moult. A large mass of empty egg-capsules remains attached to the ovigerous setae on completion of hatching, which is removed by constant cleaning by the fifth walking legs. The chela of the fifth walking legs are used as combs, which gradually dislodge the old egg-capsules. Moulting is not necessary to clean ovigerous setae, although some are lost and broken during cleaning and can only be replaced at the next moult. Consequently, after the ovigerous setae have been cleaned of empty egg-capsules, the fringe is much shorter and more ragged than that developed at the moult before spawning.

Sutcliffe (1953) reported that the ovigerous setae of P.argus are often reduced to short bristles at the moult following hatching of the eggs. This shedding of ovigerous setae was not restricted to any particular size-classes and in some cases long setae were retained. Nakamura (1940) reported a similar shedding of ovigerous setae in P.japonicus as did George (personal communication) for P.longipes. No evidence that this occurred in J.lalandei was found during this investigation.

5.29 Number of eggs carried by females in berry.

Three estimates of egg-numbers have been made for J.lalandei, Von Bonde (1936), Hickman (1946) and Bradstock (1950). Von Bonde counted the number of eggs from one pleopod and weighed them. This value was then used to calculate the

total number of eggs in the egg-mass by proportion. Hickman counted the number of eggs in six, two gram samples. The mean of these estimates was then used to calculate the egg-numbers from a range of berried females. Bradstock also used this method, obtaining a mean of 7,630 ± 275 per two gram sample compared with 8,520 ± 93 obtained by Hickman. Lindberg (1955) calculated egg-numbers for P. interruptus using a mean of 8,382 eggs per one gram sample.

In this investigation, 41 berried females ranging from 9.3 to 13.9 cm. T.C.L. were provided by the South Australian Department of Fisheries and Game. One hundred eggs were taken at random from each egg-mass and their diameter measured with a micrometer eye-piece and compound microscope. Eggs were oriented slightly to prevent inclusion of egg-stalks in any measurements. The average diameter of the eggs from each crayfish was calculated and used to determine the volume of one egg, assuming it to be a sphere. The egg-mass stripped from the pleopods and preserved in 70 per cent ethyl alcohol was then placed in a cylinder of fine wire-gauze. The eggs were allowed to drain for ten minutes and the cylinder tapped on dry blotting paper until no further droplets of alcohol were expelled. The cylinder containing eggs was then placed in a 200 ml. measuring cylinder of 70 per cent ethyl alcohol, taking care to remove all bubbles of air. The displacement-volume minus the volume

of the wire-cylinder was then recorded as the total volume of eggs. The number of eggs per egg-mass was then calculated by dividing the total volume by the volume of one egg. Each estimate was corrected to the nearest thousand.

The use of alcohol as displacement fluid reduced errors due to interstitial fluid as it evaporated from interstitial spaces and had the added advantage of being the preserving fluid.

The general law of fecundity propounded by Herrick (1895) was then applied to the data. Herrick, discussing H.americanus stated that the number of eggs produced by female lobsters at each reproductive period varies in geometrical series while the lengths of the lobsters producing these eggs vary in arithmetical series. Lataste (1896) simplified this law to the formula $E = KL^3$ where K is Herrick's constant, E is the number of eggs and L the body-length.

Table 5.05 shows the estimates of egg-numbers obtained from this investigation.

Table 5.05: Number of eggs carried by various sized females.

T.C.L. in cm.	Smallest Estimate	Largest Estimate	Mean	Number in Sample
9.0-9.49	-	-	85,000	1
9.5-9.99	121,000	155,000	141,000	4
10.0-10.49	136,000	216,000	165,000	5
10.5-10.99	174,000	175,000	174,000	2
11.0-11.49	142,000	281,000	215,000	14
11.5-11.99	235,000	283,000	259,000	2
12.0-12.49	270,000	332,000	301,000	2
12.5-12.99	234,000	317,000	293,000	5
13.0-13.49	280,000	345,000	315,000	4
13.5-13.99	355,000	362,000	358,000	2

K ranged from 98 to 212 with a mean value of 149 $\pm$ 4. The number of eggs ranged from 85,000 for a female 9.3 cm. T.C.L. to 362,000 for a female 13.9 cm. T.C.L.

Discussion.

Table 5.06: Comparison of egg-numbers.

Author	Range of Length	Range of Estimates	K
Von Bonde	?	3,000-200,000	263-265
Challenger	12.5 cm. R.C.L.	850,000	-
Hickman	7.4-12.4 cm. R.C.L.	65,170-413,220	-
Bradstock	8.3-13.5 cm. R.C.L.	86,000-549,000	194±7.2
Fielder	9.3-13.9 cm. T.C.L.	85,000-362,000	149±4
Lindberg (P.interruptus)	21.5-43 cm. T.L.	50,000-837,000	82-231

It can be seen from table 5.06 that the number of eggs carried by females tends to follow Herrick's law. However the number of eggs estimated by the above authors varies considerably.

Von Bonde and Marchand (1935) estimated that the number of eggs increased with size from 3,000 to 200,000. Von Bonde (1936) however, stated that the number of eggs ranged from 3,000 to 20,000, which Bradstock (1950) thought was a misprint.

Some doubt must be cast on the estimate of Challenger (1943) as his figure for an average specimen is nearly twice the largest of the other estimates. Hickman (1946) and Bradstock (1950) using the same method, obtained comparable results. Von Bonde's minimum and maximum

estimates are much lower than later calculations and since he does not give a range of lengths with his estimates, comparison of his results is difficult. Hickman and Bradstock both obtained much higher estimates than those obtained in this investigation, differences of about 100,000 for animals of equal size being apparent. Consequently several figures throughout the range obtained volumetrically were checked gravimetrically. Of ten comparisons, eight were even lower by the gravimetric method. It therefore appears that the number of eggs increases much faster with size in Tasmania and New Zealand than in South Australia.

5.3 The male.

5.31 General description of the reproductive organs.

The testes like the ovaries are paired organs situated on either side and dorsal to the alimentary tract, joined by a transverse bridge near the heart. Testes are much smaller than ovaries and are tightly convoluted. They normally extend from the level of the eyes to the insertion of the abdomen. The vas deferens is more complex than the straight oviduct. It consists of a highly coiled proximal segment, which widens to a straight duct connecting each testis with the genital apertures located at the base of the fifth walking legs. The vas deferens is always much larger than the testis or oviduct.

5.32 Stages in maturation of the testis.

The macroscopic appearance did not change sufficiently to define stages of maturation. Reproductive organs of males below about 5 cm. T.C.L. were often difficult to find due to their transparent nature and small size. Testes of larger animals do become more opaque and discreet with age, but no change in the structure was evident with increasing size. No sudden change in gross morphology delineating sexual maturity was evident. The vas deferens however, becomes progressively swollen, the sperm-mass often protruding more than a centimeter from the genital apertures of large males during the breeding season.

5.33 Histology and development of the testis.

(1) P.pencillatus. Matthews (1951) described the development and structure of the male reproductive organs of P.pencillatus by the reconstruction of serial sections. Since the male reproductive organs of J.lalandei appear to be different in several respects, the following summary of Matthew's results are given for comparison.

Reconstruction of serial sections indicated the testis is a racemose or compound gland of freely branching ducts, which terminate in acini. A highly coiled tube traversing the testis anteriorly and posteriorly is formed at the junction of the racemose, anterior and the racemose, posterior testis. This convoluted tube, embedded in the

tissue of the testis finally emerges as the vas deferens. Cross-sections taken throughout the testis show follicles of varying degrees of maturity.

Immature follicles are completely filled with primary spermatocytes. Spermatids are formed from two divisions of primary spermatocytes, whilst some potential spermatocytes fail to develop and disintegrate. Further development of spermatids within the follicle is attributed to the action of Sertoli cells, which encompass the spermatids. Sloughing of these Sertoli cells forms a lumen from which Sertoli cells appear to radiate like spokes of a wheel.

The sperm-mass determined from sections through connecting ducts consists of four components; developing spermatids, disintegrating spermatocytes, a nutrient substance, and sloughed off Sertoli cells. The spermatophoric wall is formed by the proximal vas deferens. There is no evidence that the enlarged vas deferens forms the spermatophoric wall. The enlarged vas deferens has a glandular typhlosole-like structure, which is associated with a hyaline line. The matrix surrounding the sperm-mass is formed from this "typhlosole", Muscular contraction of the walls of the vas deferens expels the spermatophoric mass.

(2) J.lalandei. Initially testes were fixed without preliminary treatment. Reconstruction of serial

sections from such preparations gave similar results to those obtained by Matthews. However, it became obvious that such a description of a racemose gland could also be gained by sectioning a highly convoluted tube. Subsequent dissections showed that the testis, already convoluted in situ, contracted longitudinally when freed from mesenteries holding it in place. All subsequent preparations were stretched on a microscope-slide and fixed in the stretched position. Convolution was considerable as the length of a small piece of testis was usually doubled when stretched.

The wall of the testis is thin and consists of an outer layer of epithelium and an inner layer of connective tissue. No muscle could be detected. Reconstruction of serial sections showed that the testis in all but the smallest crayfish is a simple tubular structure. Of 70 testes sectioned, only 4 had not developed a lumen. These testes were taken from crayfish 3.93 to 6.91 cm. T.C.L. All testes from animals above 7 cm. T.C.L. had a well developed lumen, which usually appeared on one side of the testis.

Spermatogenesis in J.lalandei is essentially similar to that described for P.penicillatus. However, no differential development within a testis containing a lumen was detected. Sections of testes packed with primary spermatocytes were found only in testes, which had not developed a lumen.

5.34 Anatomy of the vas deferens.

(1) P.pencillatus. The proximal vas deferens embedded in the tissue of the testis has an outer wall of muscle overlying a layer of connective tissue. The lumen is lined with a uniform layer of glandular epithelium, which secretes a mucous-like substance and a granular substance, which surrounds the sperm-mass.

The enlarged vas deferens has the same outer wall of muscle and connective tissue. The glandular epithelium has folded to form a typhlosole-like structure. The epithelium of the"typhlosole"is obviously glandular, other epithelium is undifferentiated. The continuous sperm-mass is highly convoluted and is embedded in a homogeneous matrix, apparently secreted by the "typhlosole".

(2) J.lalandei. The highly convoluted proximal segment of the vas deferens is much smaller in diameter than the distal segment and is different in structure. The outer covering consists of layered muscle and connective tissue. The inner lining is high columnar epithelium. Although the layer of epithelium is continuous it is arranged unequally as two ridges of much higher cells on each side of the duct. The lumen of the duct is thus distorted into an elongated figure of eight. The epithelium is glandular.

The sperm-mass is compressed by the narrow lumen of the proximal vas deferens so that discreet groups of sperm

appear in the matrix of the enlarged vas deferens. The glandular epithelium also secretes some of the matrix of the spermatophore. A transverse section through the proximal vas deferens is shown in plate 5.10.

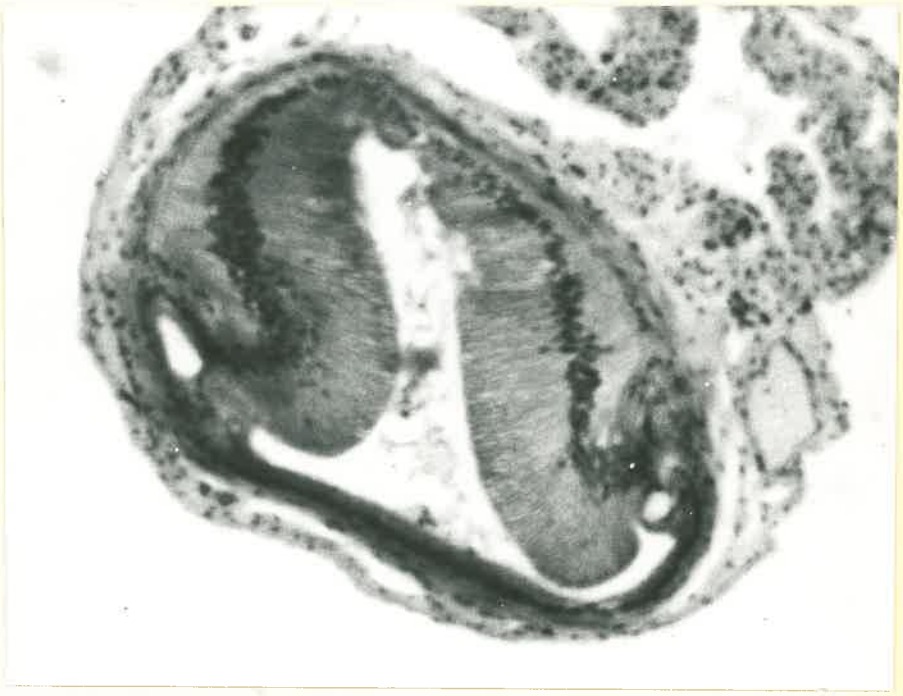


Plate 5.10: Cross-section of the proximal vas deferens. X 125.

The rather straight, enlarged portion of the vas deferens consists of an outer covering of muscle and connective tissue. The inner lining is columnar epithelium. The epithelium of the "typhlosole" is high columnar and more obviously glandular than the rest. A thin layer of a

granular substance appears at the margin of the epithelium, which forms the outer margin of the spermatophore. The sperm-mass consisting of spermatids and disintegrating spermatocytes is embedded in a matrix secreted by the glandular epithelium of the enlarged vas deferens. A transverse section through the enlarged vas deferens is shown in plate 5.11.

The major differences between the male reproductive organs of the two species is summarized in table 5.07.

Plate 5.11: Cross-section of the distal vas deferens. X 200.

Table 5.07: Differences in structure between the male reproductive organs of P.pencillatus and J.lalandei.

P.pencillatus	J.lalandei.
Testis is a racemose or compound gland.	Testis is a simple convoluted tube.
Differential follicular development of sperm cells.	Differential development not evident.
Proximal vas deferens traverses testis anteriorly and posteriorly.	Convoluted but comes directly from testis.
Sperm-mass surrounded by spermatophoric wall, secreted by proximal vas deferens.	No wall as such secreted around sperm-mass.
Proximal vas deferens evenly lined with glandular epithelium, which secretes wall of sperm-mass.	High columnar epithelium unequally arranged; glandular but does not secrete wall of sperm-mass.
Sperm-mass embedded in matrix secreted by distal vas deferens.	Matrix and granular cover of spermatophore secreted by distal vas deferens.
"Typhlosole" has deep crypt-like glands.	No deep crypts.

The most striking difference is that of actual structure. The difference between a complicated compound gland and a convoluted tube is large and probably would not be expected from two Genera of the same Family. The testis of J.lalandei could also be interpreted as a racemose gland by reconstruction of serial sections cut from unstretched testes. It is possible then, that Matthew's description is a misinterpretation of structure. The differences apparent

in the structure of the vas deferens and formation of the spermatophore are possibly related to fertilization and will be discussed in a later section.

5.35 Size at sexual maturity. Von Bonde (1936) found that males from South African stocks of J.lalandei were not mature below about 8.2 cm. in carapace-length, which is nearly twice the length stated for maturity of females.

The two smallest males observed by Hickman (1946) during his investigation of Tasmanian stocks of J.lalandei were 6.3 and 8.3 cm. R.C.L. The testes of these animals were slightly developed, the external genital apertures were distinct, but no vasa deferentia were apparent. Males were obviously mature at 9.4 cm. R.C.L. as spermatophores were observed partially extruded from the genital apertures of males of this size. However, he estimated that males attained sexual maturity on reaching a carapace-length of about 8 cm., one centimeter greater than his length of maturity for females.

Sheard (1954) found that size at sexual maturity for P.longipes varied with locality, but males tended to become mature at a larger size than females.

Lindberg (1955) could find no reliable external indication of sexual maturity for males of P.interruptus. An examination of testicular smears indicated that sexual

maturity was reached at a smaller size by males than females. Mature males, smaller than the minimum size of mature females probably did not affect greatly the reproductive activity of the population. Males appeared to be fertile throughout the year.

A reliable estimate of size at sexual maturity of males from South Australian stocks of J.lalandei can not be made from this investigation due to the small sample. No external indication of sexual maturity could be found, nor could it be determined from the macroscopic appearance of the reproductive organs. Histological examination of testes and vasa deferentia showed that a lumen containing spermatids had developed in all males larger than 7 cm. T.C.L. Spermatids were also present in the vasa deferentia of these males. These observations indicate that males are sexually mature at a smaller size than females. It is doubtful whether such small males are strong enough to mate with larger females and the amount of seminal fluid contained in the vas deferens of such males is always small. Copulation probably occurs only when the male is of equal size or larger than the female.

No annual cycle of maturation was apparent in the testis.

5.4 Mechanism of fertilization. The mechanism of fertilization has been described for several species of

Panulirus; P.interruptus, Allen (1916), Lindberg (1955); P.pencillatus, Matthews (1951); P.longipes, Sheard (1949), George (1957); P.argus, Walton Smith (1959). In each case fertilization occurs in the same manner. The male deposits a putty-like spermatophore on the sternum of the female posterior to the genital apertures some time before the eggs are released. The spermatophore, initially soft and light in colour, hardens and turns black. Eggs are said to be fertilized externally by sperm released from the spermatophore by the chela of the fifth legs of the female. The actual method of copulation has not been verified and some doubt remains concerning the stage of moult at copulation and which sex initiates mating.

Von Bonde (1936) described the act of mating for J.lalandei from observations made on captive animals. He states that the male turns a newly moulted female on her back so that their sterna are closely apposed. The spermatophores extruded by the male appear to make their way into the oviducts, where fertilization occurs at their upper ends. Eggs are laid two to three days following mating. The male is usually larger and has a harder shell than the female as it is doubtful whether males with soft shells could place a female on her back.

Initial observation of external genitalia, their relative positions, and differences in size between the sexes

indicated that internal fertilization was difficult mechanically. The observation made by Von Bonde was not extensive and his claim that fertilization was internal was based primarily on the statement that " the spermatophores are extruded and appear to make their way through the female genital apertures and so into the oviducts where fertilization takes place at their upper ends." Since no mention is made of actually finding spermatophores in the oviducts or failing to find them externally it must be taken that the above statement is an assumption.

Copulation was not observed during this investigation precluding direct description. The problem was therefore approached indirectly by comparing the external genitalia of P.longipes from which the process of fertilization is known, with those of J.lalandei. From this comparison it was hoped that an hypothesis for the method of fertilization, based on more than an assumption could be erected. Samples of P.longipes were supplied by Dr.R.W.George of the Western Australian Museum.

1. The female.

(a) The fifth walking leg. The fifth walking legs of P.longipes and J.lalandei are compared in figure 5.02.

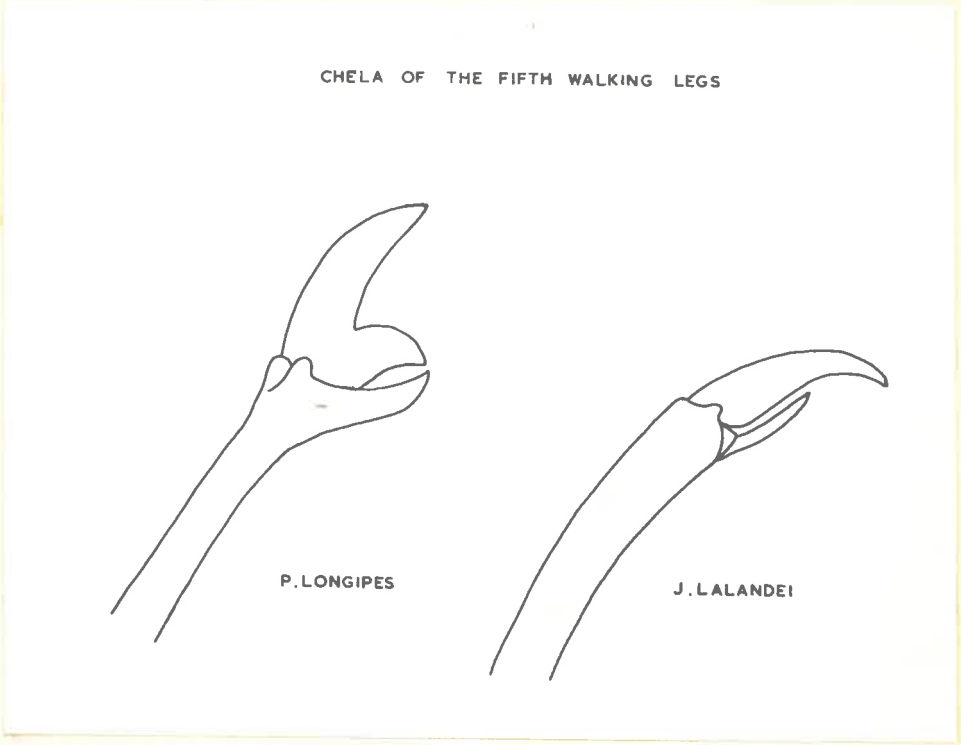


Figure 5.02: The chelate fifth walking legs of P.longipes and J.lalandei.

In P.longipes a short, stout arm projects laterally from the base of the dactylopodite, which is capable of closing against a stout extension of the propodite. The dactylopodite therefore forms a strong chela capable of pinching as well as scratching. This chela is used to break the spermatophore and then gouge it open to release sperm.

In J.lalandei the dactylopodite has no lateral arm

and is similar to those of other walking legs. A spine projects from the distal end of the propodite, which is apposed to the dactylopodite forming a chela. The spine of the propodite is much smaller than the dactylopodite and is attached by a thick membrane of chitin. The chela is therefore not very strong as the spine of the propodite does not form a solid base to the dactylopodite. Such a chela is not suited for pinching or breaking and is probably used to comb and clean the ovigerous setae of the pleopods.

(b) The last two thoracic sterna. The last two thoracic sterna of P.longipes have a smooth hairless area, presumably for the reception of spermatophores. This area is covered by tufts of short hairs in J.lalandei indicating that deposition of an external spermatophore is unlikely.

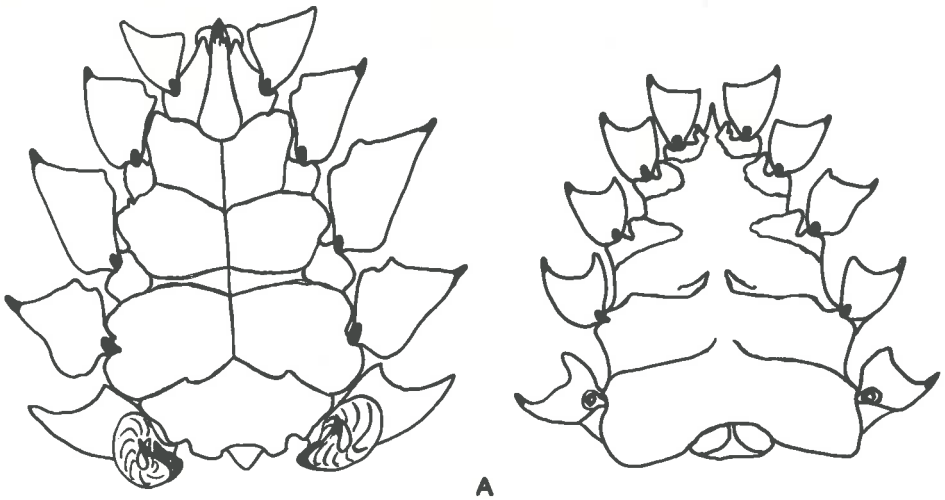
(c) The genital apertures. Both species have similar genital apertures. The rim of the aperture is raised and circular in shape. The actual opening is situated on the inner side and extends as a slit-like crescent around half the circumference. The remaining area inside the rim is filled with a chitinous membrane, which can be inverted to form a circular opening. This membrane is quite soft and easily inverted in J.lalandei, but is inverted with difficulty in P.longipes. The diameter of apertures in mature animals is 2 to 3 mm. in J.lalandei and 3 to 4 mm. in P.longipes.

2. The male.

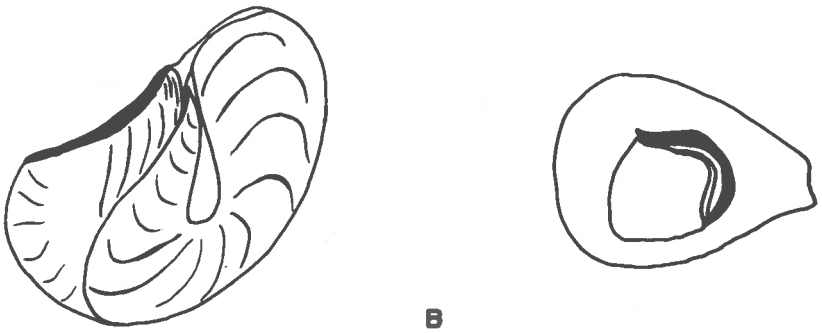
The genital apertures. (figure 5.03). The genital aperture of P.longipes has the form of an oval saucer. The actual opening to the vas deferens is slit-like and situated on the inner side of the saucer. The remaining area inside the saucer is filled with a chitinous membrane in the form of a loosely coiled tube ending in a spine. The spine is free and the tube is capable of erection. Normally the tube is coiled so that the spine effectively closes the aperture. The tube is muscular and is probably capable of autonomous movement. Its probable function is to direct the placement of the spermatophore. Movement of the fifth legs moves the apertures in an arc, accounting in part for the bilateral symmetry of the spermatophore. Apertures of mature animals may be larger than 12 mm. in diameter.

The genital aperture of J.lalandei is about four times as small as that of P.longipes, being as small as 3 mm. in diameter at first maturity. The shape is similar to the female aperture, the actual opening extending in an arc around the inner rim. The chitinous membrane filling the remaining area is folded and shaped to form a tongue-like flap, which normally closes the opening. It is unlikely that such an aperture could extrude a spermatophore similar to that of P.longipes.

P.LONGIPES J.LALANDEI



A



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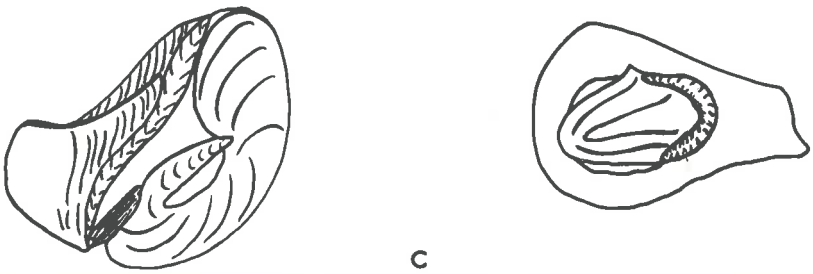

C

Figure 5.03: The male genital apertures of P.longipes and J.lalandei.

A = Genital atria in situ.
B = Genital flaps closed.
C = Genital flaps open.

It can be seen from comparison of external genitalia that the chelate fifth legs of female J.lalandei are poorly adapted to break open external spermatophores. In fact it is unlikely that external spermatophores could be attached successfully to the sterna of female J.lalandei. The soft nature of the female genital aperture in J.lalandei also indicates the possibility of introducing a spermatophore internally.

The large male genital apertures in P.longipes would allow large quantities of spermatophoric material to be extruded. Their construction also allows the spermatophore to be directed over a relatively large area reducing its thickness. A thin spermatophore would be gouged more efficiently than a thick one, with better release of sperm. It is doubtful whether the small size of the male genital aperture in J.lalandei would allow the large amount of material necessary to form an external spermatophore to be extruded.

Most aspects of the external anatomy of J.lalandei indicate poor adaptation for external fertilization. If fertilization is internal, the absence of a long intromittent organ and the small size of the apertures introduces the problem of how males can locate the female apertures for efficient transfer of spermatophores. In an attempt to answer this question a detailed examination of the male

genital aperture was made.

It has been stated that the tongue-like flap of the male genital aperture normally closes the aperture. However, this flap is capable of erection and may project more than 5 mm. in large males. Most mature males were observed in this condition during the breeding season. This observation introduced the possibility that the flap of male genital apertures could be used to locate female apertures. The validity of this suggestion appeared to lie in the mechanism of erection. The fact that most flaps were observed in the distended condition during breeding seasons indicated they were connected functionally with copulation. The structure of the male genital aperture was therefore studied from transverse sections.

Several male genital apertures were excised with some underlying muscle and a short length of vas deferens and fixed in Gilson's fluid. The acetic acid of this fixative decalcified the skeleton, which was softened further with 8 per cent phenol in 75 per cent methyl alcohol. After embedding in paraffin wax, M.P. 58° C., serial sections, 15μ thick were cut. Sections were stained with Delafield's haematoxylin (Harris modification) and eosin.

The flap had no muscle attachment, eliminating the possibility of erection through contraction of muscles. The underlying tissues contained large blood-spaces, suggesting

the flap was distended by an increase in blood-pressure. It has been suggested by Von Bonde, that mating occurs a few weeks following moulting by the male. Since increase in size at moult is caused primarily by an increase in tissue-fluid it is possible that erection of this flap is a consequence of moulting. Von Bonde also stated that the female moulted a few hours prior to mating. At this stage the skeleton is very soft and the chitinous membrane of the female aperture would be inverted easily. This would therefore be the best time for the male to locate the female apertures and maintain its position by insertion of the genital flaps.

Examination of the oviduct failed to reveal a dilatation or sac that could be used as a seminal vesicle. Without such a vesicle it was difficult to see how fertilization could occur in the oviduct. Even allowing for stretching of the oviduct it would be much smaller than the corresponding vas deferens and it is doubtful whether it could hold the same amount of spermatophoric material. It was also difficult to see how sufficient spermatophore was retained to fertilize all eggs after ovulation had begun.

It has been stated previously that the oviduct is lined with high columnar epithelium, which is folded to form villi. In many cases adjacent villi formed sac-like channels. Apart from secreting a lubricating fluid or contributing

to the egg-shell, it is difficult to see the significance of villi in the oviduct. One other possible function of the villi would be to retain sperm, which could fertilize the eggs as they passed down the oviduct. This could occur only if some of the matrix of the spermatophore was removed and sperm concentrated between the villi of the oviduct. A final comparison was made between the structure of the sperm-mass and the vas deferens of J.lalandei and P.pencillatus. The purpose of this comparison was to determine whether the spermatophore of J.lalandei was more likely to be deposited externally or internally. The vas deferens of each species has been described in an earlier section. The glands of the proximal vas deferens of P.pencillatus secrete a crystalline material, which surrounds the sperm-mass. This walled sperm-mass continues into the large distal portion of the vas deferens. Here it becomes convoluted and embedded in a matrix secreted by a large glandular "typhlosole". Sections through the distal vas deferens show sperm concentrated into a strand contained within the granular spermatophoric wall, the whole embedded in a non-cellular matrix.

The proximal vas deferens of J.lalandei does not secrete a granular wall around the sperm-mass, but appears to initiate secretion of a fluid matrix. A discreet strand of sperm is therefore not formed. The resultant spermatophore appearing in the distal vas deferens consists of clumps

of sperm embedded in the fluid matrix. A very thin crystalline wall appears to surround the matrix.

Matthews described the spermatophoric mass of P.pencillatus as being putty-like on extrusion. At a similar stage the spermatophoric mass of J.lalandei is a sticky, jelly-like mass, which remains discreet in sea-water. It is reasonably fluid and could possibly be introduced into the oviduct. Absence of a crystalline wall around the sperm-mass would allow release of sperm on disintegration of the matrix. Such disintegration of the matrix in the oviduct would allow sperm to be stored between the villi of the oviduct until needed.

It appears on morphological grounds that Von Bonde's assumption was correct and that fertilization in J.lalandei is internal. Observations of captive animals also indicated that moulting of the female is a prerequisite to mating. Four mature females moulted between August and October. Although males were present, mating was never observed. In each cases however, the female died within two weeks of moulting without appreciable hardening of the skeleton. Post-mortem examination showed that the ovaries were ripe. No sperm was detected in the oviduct or in the ovary. No external spermatophore had been deposited. It must therefore be assumed that mating had not occurred. The fact that the four animals died without spawning may indicate that mating

is a necessary stimulus for spawning and failure to spawn may prove fatal. Lindberg (1955) states that, " It is not known whether eggs will be extruded in the absence of a sperm case, or without mating activity, but it is perhaps significant that only fertilized eggs attach to the swimmerets. The presence, in females not bearing sperm cases, of ripe ovaries late in the breeding season may indicate, in fact, that egg extrusion does not occur in the absence of mating ".

Discussion. In the absence of critical observation of mating and extrusion of eggs, three factors appear necessary for successful spawning: (1) Moulting precedes mating. (2) Spermatophores are introduced into the oviducts where fertilization occurs. (3) Mating is probably a prerequisite of spawning.

It is unlikely that both genital apertures of the male and female would often coincide during mating. It is also unlikely that eggs are extruded from one genital aperture only. If fertilization does occur in the oviduct, sperm must be present in both oviducts if half of the eggs are not to be fertilized. Further work is required to determine whether a male is able to control extrusion of spermatophores or whether some sperm is lost by release from both genital apertures when one does not coincide with a female aperture.

Another point requiring further investigation is the mechanism of spawning. Since no muscle was detected in the wall of the ovary, eggs could not be extruded by contraction of the ovarian wall. King (1948) could find no muscle in the ovarian wall of Penaeus setiferus and suggested that contraction of the cephalothoracic and abdominal muscles surrounding the ovary could extrude eggs from a mature ovary.

5.5 Abnormal development of the reproductive system.

Von Bonde, W. (1918) described a male which had an extra genital aperture, which was joined by a branch from the vas deferens of that side. Hickman (1945) observed a pseudo-hermaphrodite, which had no genital apertures. The pleopods were mixed in character and the gonad contained ova and sperm. The duct was absent on one side and ended in a blind sac on the other. He also described a female with only one genital aperture in which one oviduct was functional and the other ended blindly. An extra genital aperture, which was closed and had no duct was also observed in a female. Von Bonde, C. (1937) also described a pseudo-hermaphrodite.

Three abnormal reproductive systems were noted during this investigation. Two males, both from the same sample taken off the Althorpe Islands, had only one genital aperture. The first of 8.5 cm. T.C.L. had not developed a

functional genital aperture on the left side, which was closed by a membrane. The testis was normal, both macroscopically and microscopically. The right vas deferens was normal, but no trace of the left could be found. The second of 10.1 cm. T.C.L. had not developed a genital aperture on the right side. The testes were normal and both vasa deferentia were present. The left duct was normal, but that of the right side was detached ending in a blind sac.

A female of 7.3 cm. T.C.L. with only the left genital aperture present was also observed. The ovary was normal and both ducts were present, but the right duct ended blindly in a bulbous sac attached to the muscle where the genital aperture should have been.

6. Management of the fishery.

6.0 Introduction. It is well known that unrestricted fishing can deplete stocks to the extent of making further exploitation uneconomic. Most of the biomass of a virgin population consists of large animals, whose presence slows the growth of all individuals in the population. The initial exploitation of such a stock removes mainly these large animals. The average size of fish caught therefore decreases as fishing progresses. Removal of the large fish allows the population as a whole to grow faster and the total yield may remain constant or even increase as a consequence. It can be seen therefore, that exploitation of a fish-population can benefit the population as a whole by increasing the overall rate of growth. However, the average size of the catch soon becomes so small to be uneconomic if exploitation is not checked. The net result of unrestricted fishing is that the population which initially consisted mainly of fish too old to grow at maximum rate, soon consists of fish so young that it is unprofitable to catch them.

Theoretically the increase in weight per year could be cropped by a certain intensity of fishing. Also the crop should be greater if the stock is limited to small fish, assuming that sufficient adults survive to provide a breeding stock. In practice, intensive fishing becomes

progressively less profitable, presumably because more effort is required to catch a given weight of small fish than large ones, and small fish are unsatisfactory as food.

It can be seen that a population can be underfished or overfished, neither of which is desirable. If the rate at which stocks grow varies with intensity of fishing, it may be possible to find an optimum that suits both the fish and fishermen. The aim of the fishery-biologist is therefore to determine the most satisfactory intensity of fishing for each population and then conserve stocks by suitable restrictions.

Wilder (1958) defined conservation of stocks as " wise use ", which aimed at obtaining the maximum sustained yield. Early conservation was based primarily on protecting breeding potential by prohibiting the capture of fish before they had spawned at least once.

Herrick (1895) observed that the fishery of H.americanus was declining and concluded that the death-rate of young lobsters in nature must have been greater than that required each year for the survival of only two eggs per female. Allen (1895), in discussing H.vulgaris observed that, since fishing did not affect survival of larvae, the number of eggs produced indicated the minimum number necessary for two individuals to survive to sexual maturity. This view, implying that stocks are regulated by the absolute number

of eggs is not held by most modern conservationists.

Smith and Marshall (1945) considered that reproductive potential could not be reduced below the level of economic exploitation, if the individual production of eggs was enormous. They therefore considered that restrictions which protected reproductive potential alone, were not necessary. Ling (1958) also criticised restrictions based solely on protecting sexually immature fish. He stated that only a small fraction of a new generation need survive to maintain most of the common commercial species as the number of eggs produced by each female at each spawning is enormous. Management of a fishery should be governed by the principle that the mortality due to intensity of fishing should be balanced by natural recruitments above those necessary to offset natural mortality. A fishery is most productive only when maximum growth in terms of weight coincides with maximum mortality-rate.

Wilder (1958) stated that regulation of a fishery must be based on biological, economic and sociological factors. His objectives in the management of the lobster-fishery were to discover and apply the minimum size, which would give the greatest yield and to increase the net value of the catch by reducing the intensity of fishing.

Walton Smith (1948, 1958, 1959) also suggested that regulations at the biological, economic and sociological

levels were essential for adequate management of a fishery.

6.1 Regulations and their effect on a fishery.

The following are some of the common restrictions used to regulate a fishery and their known or possible effects.

1. Size limit. Protection of stocks by limiting the size at which animals may be caught legally is probably the most common regulation. Theoretically a minimum legal length protects sexually immature animals and is calculated so that animals are not taken until the proportion of flesh-weight to total weight is highest. A maximum legal length should protect the largest animals with greatest breeding potential.

Wilder (1958) states that the chance of increasing yield by conserving sexually immature lobsters is small. Support for minimum size limits was given by the rapid growth of lobsters near the size-limit and the observation that most deaths could be ascribed to intensive fishing. He also quotes improved commercial catches whenever size-limits have been observed. From these observations he concluded that size-limits are an efficient means of increasing the yield from a fishery. Roughley (1951) quotes the case of the crab-industry of California, which declined rapidly about 1915. Investigation showed that the minimum legal length of 6 inches allowed males to be caught before they had matured. The minimum size was raised to 7 inches,

markedly increasing production.

Conflicting evidence is provided by Thomson (1950, 1956), who found that raising the minimum legal length of the sea and yellow-eye mullet, instituted after extensive investigation had little effect on the respective fisheries.

2. Protection of females carrying eggs.

This regulation is designed to ensure a reasonable release of larvae. Wilder (1958) could find no factual basis for protecting females bearing eggs. He found however, that such a regulation was popular with fishermen, only a small proportion of the catch was affected and lobsters could be caught legally when the eggs had hatched. Although the value of such a law was doubtful Wilder did not consider it harmful to the fishery.

Walton Smith (1948) found that protection of females carrying eggs act primarily through restricting the total catch. Contrary to the observation of Wilder that protection of females carrying eggs affects only a small proportion of the catch, 29 per cent of the total catch made by Hickman (1946) over a period of 5 years were females carrying eggs. Bradstock (1950) also found that more than 50 per cent of females caught during May through September were carrying eggs.

3. Closed seasons. Seasons during which fishing is prohibited usually coincide with breeding seasons or

other periods of vulnerability. Closed seasons should reduce intensity of fishing and allow replenishment of stocks through recruitment.

Von Bonde and Marchand (1935) recommended the use of alternative regulations. They claimed that closed seasons, although reducing intensity of fishing, rarely functioned as protective restrictions.

Sheard (1949) and George (1957) both claimed accumulation of stocks of P.longipes on fishing grounds after closed seasons.

Walton Smith (1958) suggested that closed seasons functioned by reducing intensity of fishing rather than by protecting breeding potential.

Wilder (1958) found that intensity of fishing during short seasons was often higher than during year round fishing. He concluded that closed seasons failed in improving sustained yield, but were often necessary for economic reasons.

4. Closed areas. Sanctuaries allow maximum recruitment of adult stocks. Lindberg (1955) found little evidence that closed areas maintained productivity in adjacent areas and recommended that closed areas be opened for fishing.

Sheard (1949) recommended the closure of large tracts of inaccessible coast, which acted as natural sanctuaries. Walton Smith (1958) suggested that the planktonic larval

life and migration prevented localized closed areas having much effect on stocks of spiny lobsters.

5. Regulation of equipment. Regulation of equipment such as specifying design of traps and prohibiting the use of very efficient or wasteful gear reduces intensity of fishing.

6. Regulation of total catch. This regulation is difficult to enforce and can be achieved by the use of closed seasons.

6.2 History of protective legislation for crayfish in South Australia.

This history was compiled from records obtained from the Department of Fisheries and Game of South Australia.

The earliest record indicating that crayfish were not adequately protected is contained in a circular issued by the Chief Inspector of Fisheries, 1899. An experienced fisherman had stated that the close season of September through December should be changed to June through September. The Chief Inspector consequently required his staff to make enquiries on this subject and report as soon as possible. Most replies agreed with this proposal.

In a letter to the Fisheries Committee, Hobart, dated 1925, the Chief Inspector of Fisheries outlined the current regulations. Crayfish under 8 inches could not be taken. Females carrying spawn could not be taken and no females could be taken during August, September and October. The

diameter of traps could not exceed 3 ft. 6 inches.

The close season of August through October was proclaimed in 1910, but may have been in force since the letter of 1899 above. Restrictions on diameter of traps and minimum legal size were imposed under the Fisheries Act of 1917, but could have been amendments of previous regulations under the Fisheries Act of 1904.

All Proclamations and regulations were revoked in 1937 and a revised set declared. The following is a summary of these regulations. Female crayfish could not be taken between July 31 and November 1. Traps could not be larger than 4 ft. 6 inches in diameter and their entrance had to be at the top. Crayfish shorter than 8 inches could not be taken and crayfish carrying eggs could not be retained. No major reorganization of regulations has occurred since 1937, but some regulations have been amended.

Close season for females was changed from July 31-November 1 to July 1-September 30 in 1946 and to July 1-October 31 in 1947. In 1954 a close season between July 1 and October 21 for all crayfish was imposed between proclaimed boundaries. This close season was changed in 1957 to July 1-October 31 for proclaimed areas and October 1-October 31 for all other areas. In 1960 the close season for all crayfish within proclaimed boundaries was changed to June 1-October 31, and the close season for females

outside proclaimed areas from June 1 to October 31.

In 1957 the minimum legal length of 8 inches, which had stood since 1918 at least was altered to 9 inches. This size was raised to 10 inches in 1960.

Regulations in force at present (1962) are as follows:

1. Proclamations under the Fisheries Act, 1937.

It is illegal to sell crayfish below a prescribed length, or females with eggs. It is also illegal to detach eggs or to have these females in one's possession.

2. Regulations and Proclamations.

(a) Traps must be smaller than 4 ft. 6 inches in diameter and have the mouth at the top.

(b) The minimum legal length is 10 inches except that 36 crayfish of any size may be caught at Coffins Bay per day and crayfish above 8 inches can be caught at any time from the Cape Jervis area.

(c) Close season:

(1) Females: June 1 to October 31, all waters.

(2) Any crayfish: June 1 to October 31, scheduled waters. October 1 to October 31, other waters.

(3) Males: No close season in Cape Jervis area, other areas see above.

6.3 <u>The commercial importance of the crayfishery.</u>

Figure 6.01 shows the annual production of <u>J.lalandei</u>

for South Australia and its value from 1936 to 1961.

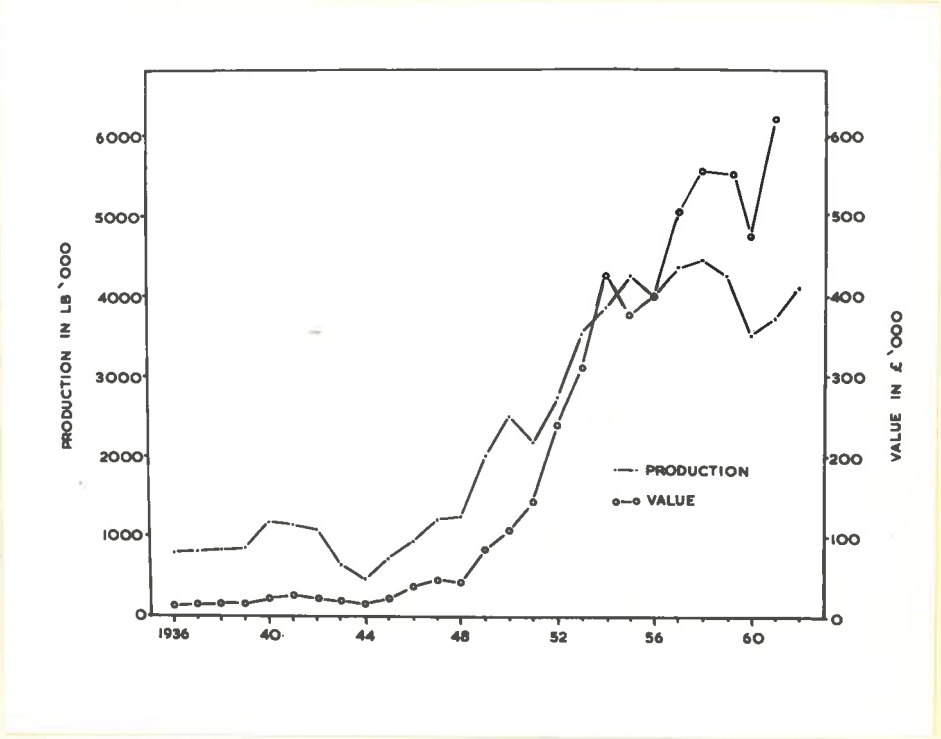

Figure 6.01: Annual production of J.lalandei from South Australia from 1936 to 1961.

Prior to World War 11, the crayfishery in South Australia was rather static and of little importance economically. Since 1945 the commercial importance of the fishery has risen steadily. The value of the catch taken during 1960-61 was £620,000 compared with £15,500 in 1936. No records of the number of men supported by the industry are available, but it has been estimated that 185 vessels

employing 380 fishermen worked full-time or part-time during 1959-60. No estimate can be made of the number employed in processing plants.

Since 1949 an important export trade has developed with the U.S.A. Figure 6.02 shows the amount of crayfish exported from South Australia to the U.S.A. annually, and its value in dollars from 1949 to 1961.

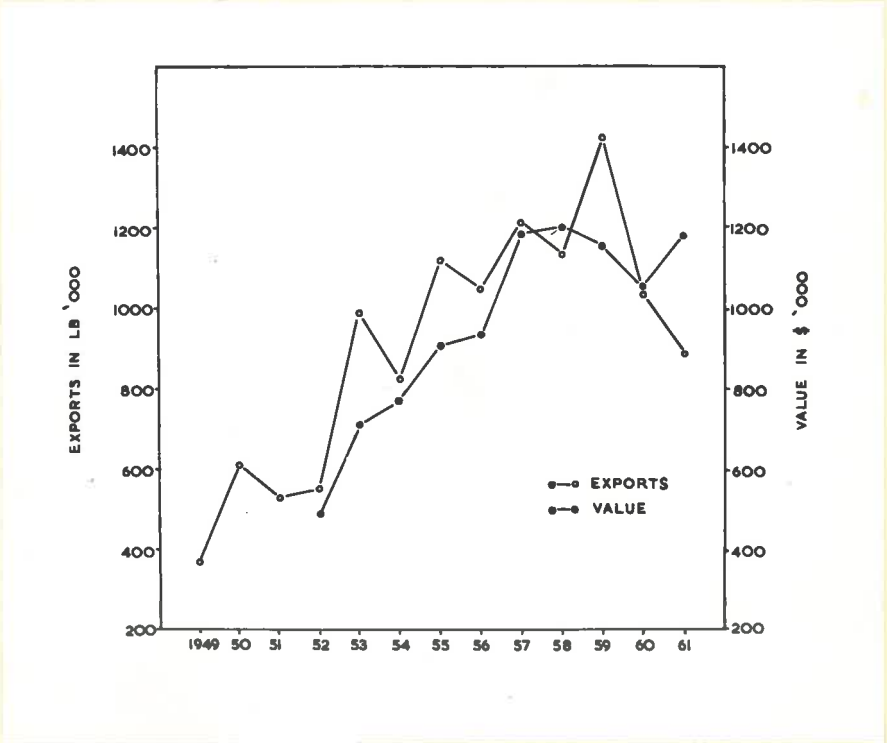

Figure 6.02: Annual exports of J.lalandei from South Australia from 1949 to 1961.

It can be seen that export of crayfish has developed into a substantial trade, earning over one million dollars

during 1960-61. The amount of crayfish exported from South Australia represents between 1/8 and 1/5 of the amount exported from Australia. Exports of crayfish (J.lalandei and P.longipes) from all States were worth over 8½ million dollars during 1960-61. It is interesting to note that only about 30 per cent of the crayfish landed in South Australia are marketed locally. The bulk of the catch is either exported overseas or marketed in another State.

It can be seen therefore, that crayfishing as an industry is of considerable importance to South Australia and every effort should be made to manage the fishery efficiently.

6.4 Factors promoting overfishing of J.lalandei.

(1) Sedentary habit. Tagging of species of the Palinuridae by Von Bonde and Marchand (1935), Sheard (1949), Bradstock (1950), Dawson and Idyll (1951), Sutcliffe (1951) and Lindberg (1955) has shown that movement is usually confined to local random searching for food. Migration connected with moulting and reproduction has been towards shallower or more broken reefs within a particular area.

(2) Limitation of fishing grounds. The need of shelter provided by underwater caves and crevices associated with a rocky bottom restricts fishing grounds to onshore and offshore reefs. As a consequence, stocks of crayfish

are concentrated in relatively small areas.

(3) Slow rate of growth. Growth within the Palinuridae has been described in a previous section. Most authors have estimated the age at sexual maturity between 5 and 10 years.

(4) Efficiency of the fishery. Sheard (1949) estimated that beehive traps were effective within a quarter of an acre. More than 60 traps can be operated by one boat so that large areas can be trapped effectively at a given time. Extensive use of echo-sounders allows potential grounds to be located quickly and efficiently and precise setting of the traps. Mechanization of ancillary equipment such as winches etc. and a ready supply of bait from fish processing factories add to the speed and efficiency of the fishery.

It can be seen that unrestricted exploitation of a slow moving, rather sedentary population crowded into limited fishing grounds could soon deplete localized stocks.

6.5 Evidence of overfishing. The legal minimum length for J.lalandei remained at 8 inches for at least the period 1918-1957. In 1957 it was increased to 9 inches and three years later, in 1960 to 10 inches. One of these increases at least, appears to be the result of a petition by the fishermen themselves. It is interesting to note that the first increase was instigated during a year of

record production. The catch increased slightly the following year, after which it decreased until 1960. It is impossible to determine whether the smaller catches after 1958 were due to raising the minimum legal length in 1957 as no data are available concerning the structure of catches. The increase of 1960 was partly due to an attempt to standardize regulations between States, but it is too early to determine the effect of this increase although the total catch for 1961 and 1962 has increased.

Without accurate figures of at least the number of fishermen employed in the industry over a period of years, calculation of any catch/effort ratio is extremely difficult. It can be assumed however, that the number of crayfishermen was at least stable between 1955 and 1962 and probably increased over this period. It must also be assumed that the efficiency of fishing and handling increased and that fishermen used increasing numbers of traps and probably travelled to more distant grounds. The annual catch during this period has stabilized and may be decreasing. It appears then, that the catch/effort ratio is decreasing, indicative of decreasing stocks.

Olsen (1960) reviewed the total catch of southern crayfish and concluded the fishery was stable in Tasmania, was declining in South Australia and had declined in Victoria. Olsen quoted the following figures based on

estimates only, for Port MacDonnell in South Australia.

1946--4 boats--20 traps/boat--35 lb./trap/day.

1950--10 boats--40 traps/boat--17 lb./trap/day.

1958--40 boats--60 traps/boat--6 lb./trap/day.

These figures indicate a declining fishery. The average catch per trap per annum calculated for Tasmanian waters was 3,000 lb. in pre-war years, 1,000 lb. in 1945-46 and 600 lb. in 1960. The corresponding figure for South Australia is approximately $\frac{1}{4}$ to $\frac{1}{3}$ of the Tasmanian figure.

Anecdotal evidence obtained from discussion with a number of fishermen also indicates that stocks are being depleted. The concensus of opinion is that the industry has survived only through improved marketing and a rising price for crayfish.

It must be stressed that the above discussion is based mainly on assumptions and estimations due to the absence of reliable statistics. However, indications are that the fishery should be regulated more stringently.

6.6 An analysis of present regulations.

(1) Regulation based on growth-rate and size at sexual maturity.

These two measurements are difficult to separate from the point of view of management. The slower an animal grows, the greater the chance of being eliminated from the population by natural causes or by trapping before it has reproduced. Exploitation of sexually immature animals

coupled with slow growth may therefore decrease significantly the rate of recruitment. This would be effected by the continual removal of potential breeding stocks, thus reducing the potential release of larvae. Slow growth allows exploitation to occur over an extended period, further decreasing the potential breeding stock.

It has been shown previously that growth of J.lalandei in captivity is slow and that sexual maturity of females did not approach 100 per cent until the total carapace-length exceeded 12 cm. However, over 75 per cent were mature above 10.5 cm. T.C.L. compared with less than 50 per cent at 10 cm. T.C.L. The age of crayfish at 10 cm. T.C.L., the present minimum legal length was estimated at 10+ years. An increase in the minimum legal length to 10.5 cm. T.C.L., about one year's growth would allow an added 25 per cent of females to spawn before they could be captured. Animals at this new minimum legal length would also be 15 per cent heavier than at the present length.

The minimum legal length enforced in Victoria and Tasmania is 4¼ inches R.C.L., which corresponds to about 11.3 inches in total length. This measurement approaches the length when almost 100 per cent of females in South Australian waters are sexually mature. An increase in the South Australian minimum legal length to correspond with Victoria and Tasmania would protect all immature females.

Although increasing the minimum legal length appears to be desirable, it is not recommended without further investigation. Evidence is available that size at sexual maturity may not be constant for all areas of the State. Raising the minimum legal length may be unwarrented in some areas and may seriously affect the catches from these areas. The minimum legal length of crayfish from Victor Harbour is relaxed to 8 inches already and it has been suggested previously that females from the Port MacDonnell area mature at a smaller size than elsewhere. If such is the case, then further investigation is necessary and different minimum legal lengths may have to be proclaimed for different areas.

Close seasons enforced at present throughout Australia tend to protect females more than males. It appears that such a case is justified for two reasons. (1) Males become sexually mature at a smaller size than females and (2) There is some evidence that males are polygamous (Olsen 1960).

The prime reason of a close season for females is to protect them during the breeding season. It appears that the present close season effectively accomplishes this. In fact the effective close season is often much longer than that proclaimed due to rough weather.

Although the value of protecting females carrying eggs

has been queried, it is the opinion of this author that every effort should be made to protect reproductive potential of this species.

6.7 Recommended changes in regulations.

(1) An increase of at least ½ inch in the minimum legal length should be considered, provided that examination of females from all areas gives a similar estimate of size at sexual maturity as that obtained in this investigation.

(2) It is also recommended that an effort be made to standardize regulations enforced by the various State authorities where possible. Minimum legal lengths and close seasons may vary with the area, but a standard method of measuring minimum legal length would be welcomed by everyone concerned with the industry.

6.8 Recommendations for future research.

The following are some basic topics that should be studied before an adequate programme of management can be designed.

(1) Collection of reliable " catch per unit effort " statistics is essential as a decrease in this ratio is a reliable indication of decreasing stocks.

(2) The precise nature of larval life should be determined. The effect of currents on dispersal of larvae and consequent larval recruitment should also be known.

(3) The need for delineating stocks is indicated.

(4) Measurements of the structure of populations by size should be taken as routine.

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