DOCTOR OF PHILOSOPHY

Some aspects of growth and behaviour in the juvenile lobster HOMARUS GAMMARUS (LINNAEUS)

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Award date:
1981

Awarding institution:
Bangor University

Some aspects of growth and behaviour in the juvenile lobster *Homarus gammarus* (Linnaeus).

A thesis submitted to the University of Wales by
BANGOR.

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in candidature for the degree of Philosophiae Doctor.

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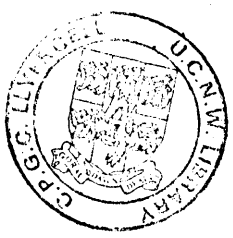
December 1981.



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Signed: .

(Candidate)

Date: 16.12.81.

This is to certify that apart from two papers appended to this thesis, the work here submitted was carried out by the candidate himself. Due acknowledgment has been made of any assistance received.

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ACKNOWLEDGEMENTS

This study was undertaken at the Fisheries Experiment Station, Conwy, by kind permission of the Ministry of Agriculture, Fisheries and Food, and at the Marine Science Laboratory of the University College of North Wales at Menai Bridge. I wish to thank the staff at both institutions for their help and encouragement.

I am particularly indebted to Dr. D.A. Jones and the late Dr. P. Walne for their advice and guidance in all matters, and to Mr. B.T. Hepper and Dr. J. Y. Kassab for counsel on the statistical analysis of results. I greatly appreciate the various secretarial, technical and computing services made available by the Ministry of Agriculture, Fisheries and Food, especially the assistance of Mr. A. Burridge of the Electronics Laboratory, Lowestoft.

The Worshipful Company of Fishmongers, Fishmongers' Hall, London, gave generous support to this study and I wish to express my gratitude for their financial investment, as well as their ready kindness and hospitality.

SUMMARY

Experiments were designed to assess the influence of a number of environmental factors on the growth and survival of laboratory reared juvenile lobsters cultured in individual containers, and to determine some of the factors affecting the locomotor and feeding activity. The effect of temperature and salinity was studied in a factorial experiment and the optimum combination for growth estimated by response surface analysis at 20.8°C and 29.8 p.p.t. Temperature and salinity levels in subsequent experiments were maintained at or around the optimum combination. Container size exerted an influence over the growth rate and significant reductions occurred when the floor area was less than $(1\text{-}2 \times \text{total length of lobster})^2$. Darkness and low intensity constant illumination were the most favourable lighting conditions but shelter provision enhanced the growth rate under a light-dark regime. Food utilisation was improved by periodic starvation, and although feeding every three days was not sufficient to sustain a high growth rate, daily feeding conferred no advantage over feeding every two days. Temperature, salinity and ration level exerted the most direct effect on the frequency of moulting, while the other factors had a greater influence on the size of the moult increment. The locomotor and feeding activity was studied under a variety of light regimes and the effect of shelter, moult stage and food availability recorded. A weak endogenous nocturnal pattern of locomotor activity was found under constant conditions but under other light regimes activity was irregular and little affected by shelter availability. Daily fed animals displayed a more pronounced nocturnal activity pattern associated with feeding activity which was generally confined to darkness with an overt rhythmic component. The daily pattern of both locomotor and feeding activity varied through the moult cycle and considerable variation in response at the individual level emphasized the flexible nature of activity in the juvenile.

CONTENTS

INTRODUCTION

The European lobster Homarus gammarus (Linnaeus) is one of the most important species of shellfish exploited around the coasts of Great Britain and has been for many years the most valuable shellfish export. The high value of the lobster is a function of consumer demand and availability, and while the cost of fresh lobsters places them in the luxury market, marketing is rarely a problem. The future availability of lobsters is not, however, assured, for despite an increased fishing effort catches have steadily declined in the traditional fisheries, although the exploitation of new stocks especially offshore populations has helped to maintain supplies.

A major reason for the decline in catches is that the size at first capture is often below the size at first maturity despite the existence in most areas of legal restrictions on the size of lobsters that may be sold. The present limits do not seem to adequately protect the breeding population, and this coupled with the high fishing mortality is likely to result in a further decline in stocks and possible recruitment failure in heavily exploited areas. For these reasons it has been recommended that the legal limits should be increased and fishing pressure reduced (I.C.E.S., 1978), but there are considerable socio-economic reasons against this, and it is unlikely that fishery management will yield any substantial benefit for a number of years.

One of the major problems in defining a management strategy is the lack of reliable data on the natural life history of the lobster and in particular the more vulnerable juvenile stages. Juveniles of less than 40mm carapace length are rarely observed in the wild (Howard and Bennett, 1979) and it is therefore impossible to estimate juvenile abundance.

This is a crucial factor in distinguishing a decline in recruitment resulting from a reduced breeding stock from that due to mortality among pre-recruits arising from, for example, pollution or increased predation.

Attempts to artificially increase the natural lobster stocks by releasing hatchery reared larvae or juveniles have been made since the late nineteenth century, particularly of the closely related American lobster, Homarus americanus(Milne-Edwards)in North America. At one time, over 20 hatcheries were in operation, together with a few in European countries, but these re-stocking programmes were not found to materially improve the fishery and most closed down (Kensler, 1970). Only two centres now remain, a government sponsored hatchery in North America at Martha's Vineyard, Massachusetts,and a co-operative venture between government and fishermen on the Brittany coast of France. The American practice involves release of fourth stage lobsters reared from wild caught females (Hughes, pers. comm.), while the French are investigating the release of older juveniles into protected areas (Lorec and Henocque, 1979).

A more proven technique of increasing the natural productivity is by providing artificial reefs. Adult lobsters are typically inhabitants of rocky and stony areas of the sea bed and studies have shown that lobsters can be attracted to otherwise unfavourable grounds by creating a suitable habitat (Scarratt, 1968; Sheehy, 1976). A number of materials have been tested, including stones, discarded car tyres and purpose built shelters, but although all are rapidly colonised and larval settlement may occur, the maintenance of a viable population depends on many other factors, including food supply.

A third alternative to the problem of matching lobster supplies to consumer demand resulted from the research carried out at the lobster hatcheries, where it was found technically feasible to culture lobsters through to marketable size under laboratory conditions. In 1972 Hughes, Sullivan and Shleser reported that H. americanus had been cultured to commercial size in two years and this stimulated an extensive research effort in North America designed to establish whether lobster farming was a commercial proposition.

At this time a shellfish cultivation unit had been in existence for a number of years at the Ministry of Agriculture, Fisheries and Food, Fisheries Experiment Station at Conwy in North Wales, under the direction of the late Dr. Peter Walne. Studies were made on the laboratory rearing and culture of several species of molluscs, including Ostrea edulis Linnaeus and Crassostrea gigas Thunberg, as well as the palaemonid and penaeid prawns. In 1974, a grant was made available by the Worshipful Company of Fishmongers, which enabled studies to be initiated on the culture of H. gammarus. One of the aims was to provide the appropriate scientific data to encourage commercial interests to investigate the economic aspects of lobster culture, and two practical texts have been prepared (Richards and Wickins, 1979; Richards, Wickins and Beard, unpub. man.). At the same time, the studies were designed to investigate the effect of certain environmental influences on crustacean moult regulation and behaviour as shown by the lobster, and it is these results that are presented in this thesis, although a proportion of the discussion is directed towards the economic implications of the results to reflect the original purpose of the investigation. In the first section the techniques used to obtain

experimental stock are described together with general methods and materials. Section 2 reports the results of experiments designed to assess the influence of a number of environmental factors on growth and survival of the juvenile lobster, and in Section 3 some aspects of juvenile activity are described. Each study is presented in the usual format for scientific papers but to prevent unnecessary repetition a complete list of references is provided at the end.

Appendix A reports some of the more practical aspects of this study, the results of nutritional studies made at the Conwy laboratory by Dr. J. Munford, and a description of a pilot plant culture system for the routine production of marketable sized lobsters. Appendix B covers eye development in the juvenile, and examines the relation between the number of ommatidia and the moult stage.

SECTION 1

JUVENILE SUPPLY AND GENERAL EXPERIMENTAL TECHNIQUES

Juveniles were reared for experimental purposes throughout the year by controlled incubation of eggs carried by wild caught females. Female lobsters were collected from a commercial pound, which was supplied mainly from the Scottish fishery, and transported to Conwy in containers filled with damp seaweed to prevent the eggs drying out. The females were stored with claws banded in a communal holding tank supplied with a constant flow of seawater, and at ambient sea temperatures (5-15°C) hatching occurred naturally between June and August.

Controlled incubation was achieved by regulating the temperature of the water in which the egg-carrying or 'berried' females were held. Complete egg development in the sea takes about 12 months but this time can be reduced to around three months at elevated temperatures. Embryonic development can be monitored from the increase in size of the pigmented eye spot, which becomes visible some 9 weeks after spawning (at 10°C), and a relationship between the water temperature and the weekly increase in the size of the eye spot has been established for Homarus americanus by Perkins (1972). The same formula was used as an initial guide to the rate of development of H. gammarus, but it has since been established that the size of the eye in newly hatched larvae is generally larger in H. gammarus, and the rate of development slightly faster at temperatures between 14 and 20°C.

Larvae could be obtained to within some six weeks of a predetermined date by entering values for the eye index (average greatest diameter of the eye spot) and incubation period into Perkins' formula to give

an estimate of the appropriate incubation temperature. In practice it was found more convenient to maintain a hatching system at a fixed temperature, and to introduce selected females into the system an appropriate length of time before the desired hatching date. It was not possible to retard development by maintaining females at temperatures below ambient.

During the development of controlled hatching techniques, incubation was carried out at 20°C in a closed recirculation system, at 17-18°C in a throughflow system, and at 13-15°C in a semi-closed recirculation system. High temperatures and closed systems were not found to be sufficiently reliable in producing the required numbers of larvae and subsequent juvenile viability was often poor. The best hatches were obtained during the normal hatching ~~system~~ season or when eggs were incubated at 13-15°C. Controlled incubation from an early development stage was also more successful. The incubation of many broods provided sufficient data to determine the rate of embryonic development at 13-15°C and adequate prediction of hatching time from the initial eye index became possible (Richards and Wickins, 1979).

When the eggs hatched, the larvae were retained in the hatching tanks (one per female) by a filter screen on the standpipe drain, and were removed each morning by handnet for transfer to the larval rearing system. The average hatch from females of 1-2 kg was 3500 larvae, some 20-30% of the estimated number of eggs originally carried (Hepper and Gough, 1978). This was mainly due to egg loss under captive conditions although females were occasionally observed to feed on the newly hatched larvae.

Larval rearing.

Larvae were reared communally through to the fourth stage in a variety of containers designed to maintain good water quality and reduce cannibalism by keeping the larvae and food dispersed in the water column. A container was ultimately designed similar to that described by Hughes, Shleser and Tchobanoglous (1974), in which larvae and food were kept dispersed by a spiral upwelling water flow. Water was introduced at 3-4 $1.min^{-1}$ from a manifold with angled outlets at the base of a round-bottomed circular fibreglass 40 litre tank, and drained via a centrally positioned standpipe surrounded with mesh to prevent escape of the larvae. Water quality was preserved by partial recirculation with a supply of 2-3 $1.min^{-1}$ fresh seawater, or by biological filtration coupled with partial replacement of the system volume three times each week. Solid waste was removed by a mechanical filter. Ambient salinity seawater was used and the temperature maintained at 20±2°C, which had been estimated in earlier experiments to be favourable for larval development (Hepper, pers. comm.).

Up to 2000 newly hatched larvae were stocked in each rearing tank and fed daily on either chopped Mytilus edulis Linnaeus flesh, frozen Artemia or frozen mysid shrimps; the most successful single food was mysid shrimps. Rations were roughly calculated to provide twice as many food particles as the number of larvae, so that the larvae were more likely to encounter food than another larva. Live grown Artemia is an attractive and stable food and is reported to be the best diet for H. americanus larvae (Hughes et al., 1974), but it was not possible to produce sufficient quantities for larval rearing at the Conwy laboratory.

Larvae were reared to the fourth stage in 11-14 days and were then

transferred to individual containers. Survival varied considerably during larval rearing but on average was between 15 and 20%. Some authorities maintain that the fourth stage is a megalopa larva (Wells, 1976), and in much of the literature on H. americanus the word juvenile is used to describe lobsters from the fifth stage. The stage four lobster is, however, clearly a postlarva, differing considerably in shape from the first three pelagic stages (described by Nichols and Lawton, 1978) and undergoes no significant morphological change during subsequent moults. Stage four lobsters are active swimmers but will readily adopt a benthic habit and make burrows in suitable substrates (Berrill and Stewart, 1973), while in the sea, lobsters are thought to settle to the sea bed during the fourth stage because fifth stage lobsters are not found in the plankton and stage fours are less frequently observed than the first three stages. In this study, the term juvenile is used to describe lobsters from the fourth stage onward, and lobster age calculated from the date of moult into stage four.

Incubation and larval rearing techniques were continuously developed during the course of this study and this was reflected by the number of hatched larvae per female and percent survival to stage four. During growth experiments juvenile viability also appeared to be related to the conditions experienced during incubation and larval rearing, and this is discussed in the appropriate sections.

Culture systems

Juveniles were maintained in individual containers to prevent fighting and cannibalism and containers of 25, 64 or 115 cm^2 floor area were used, all of which were larger than the calculated optimum area for

the size of lobster (Section 2.2). Containers were provided with small holes, mesh covered openings, or a mesh floor to allow water exchange and were held in shallow fibreglass trays with a water depth of 7-8 cms. Water circulation and aeration were maintained by either an overhead sprinkler or siphon system. The latter was found most satisfactory because the flow rate from sprinkler tubes could be reduced or stopped by salt deposition or detritus accumulation. The siphon system allowed a 2.5 cm change in depth of the water level every 8-10 minutes and was achieved by fitting a cover over the standpipe drain. This cover had a wide slot 2-3 cms below the top of the standpipe and there was a slight gap between the top of the standpipe and the top of the cover. Exact measurements were determined by trial and error and were influenced by the dimensions of standpipe and cover as well as by the rate of water inflow.

In both methods of water circulation a reservoir was provided to increase the system volume, generally to allow 2-3 litres per individual, and to enable water to be changed without disturbing the lobsters. Water was pumped from the reservoir into the trays and drained back through a mechanical filter. Water quality was preserved by replacing 50% of the system volume two to three times each week with fresh, filtered, ultra-violet light irradiated seawater. Biological filtration through a percolating gravel filter was incorporated in later experiments with the filter size based on $1m^3$ filter volume for each 50 kg of lobsters and food (Wickins, pers.comm.) and once the filter had matured water replacement was reduced to a 25% change twice weekly. Water samples were occasionally analysed to ensure that concentrations of toxic nitrogenous compounds were

kept within 'safe' levels (Wickins, 1981). Water temperature was maintained at 20±1°C by air heating following the establishment of the optimum temperature for growth (Section 2.1) and ambient salinity seawater was generally used. When necessary the salinity was adjusted to 30-32 p.p.t. by dilution with deionised tap water or the addition of a concentrated solution of artificial seawater formulated from Lyman and Fleming (1940).

During the summer months algal blooms (predominantly Phaeocystis pouchetti Lagerheim) occur in the waters around Conwy and cause extensive fouling of the seawater supply, while freshwater run off from the nearby mountains affects both salinity and the concentration of heavy metals in the seawater. Reserve seawater storage facilities were available but good quality water could not always be guaranteed and an adverse effect on lobster growth and survival from poor water quality was often suspected. It was not however within the scope of this study to investigate this problem.

When sufficient juveniles were available, suitable individuals were selected for experimental purposes. Some selection was made at transfer from the larval rearing system and rejection criteria included small size, pale colouration, deformed limbs or absence of chelae. Following isolation, moult data was recorded and individuals could be further selected on the basis of moult increment and inter-moult period.

Juveniles required for activity studies were cultured up to twelve months old in a closed recirculation system in appropriately sized containers. Water quality was maintained by replacing 50% of the system volume every two weeks.

Diets

Frozen *Artemia* used for rearing larvae was obtained from commercial suppliers, while mysids could be collected locally and stored deep frozen. The main diet for juveniles was the mantle tissue of *Mytilus edulis*, and mussels were collected locally and stored in running seawater. The biochemical composition and hence the nutritional value of mussels varies throughout the year (Dare and Edwards, 1975) and a dietary supplement of frozen *Crangon crangon* (Linnaeus)or *Artemia* was usually provided once a week. All foods were fed fresh each day between 0830 and 1000h, and any uneaten food removed the following day. The biochemical composition of the diets as a percentage of the ash-free dry weight was as follows:

	Percent ash	Lipid	Glycogen	Protein	Non-protein nitrogen
Mussel tissue (average yearly value)	9.9	13.6	3.2	66.1	1.3
Crangon	14.9	6.4	1.6	61.6	5.7
Artemia	18.4	11.3	12.1	42.8	2.9

Measurements and records

The size of lobsters was measured by recording the carapace length (CL), defined as the distance between the posterior margin of the eye socket and the posterior of the carapace measured along the median line. Wet weights were also recorded after blotting off excess water, and dry weights ascertained after freeze-drying in a Chemlab Instruments Model SB4. The CL of cast exuviae and date of moult were routinely recorded, although exuviae were rapidly consumed during the early postmoult stages. When no exuvial fragments were visible, ecdysis could sometimes be recorded from the appearance of the newly moulted individual, together with some slight morphological differences based

on those found in H. americanus (Templeman, 1948). The increase in CL with time is approximately linear (Richards and Wickins, 1979) and allowed the prediction of growth rate outside experimental periods.

Daily food consumption was monitored in some trials. Pieces of mussel tissue were weighed after blotting dry and the weight remaining the following day recorded. Losses due to the 'tearing' feeding action (Barker and Gibson, 1977) could not be estimated,but losses due to decomposition and leaching were estimated from the loss in weight of mussel tissue left in an empty container for 24 hours. The amount of food uneaten by the juveniles was corrected for the percent loss on the arbitrary assumption that losses only occurred from the uneaten food. This was considered to give a sufficient estimate for comparative purposes.

Biochemical analyses

Methods used for the analysis of ash, carbohydrate, lipid, protein, and non-protein nitrogen were as follows:

Protein and non-protein nitrogen. 5-8 mg replicates of finely ground freeze dried tissue were digested in 2 mls Kjeldahl digest mixture (60 mls distilled water, 340 mls concentrated sulphuric acid, 10 BDH selenium catalyst tablets) and the resultant digest diluted to 100 mls by the addition of distilled water. The total nitrogen content was subsequently assayed by the phenol-hypochlorite colourmetric method of Holland and Hannant (1973) using ammonium sulphate as a standard. Protein nitrogen was estimated by digesting the precipitated protein fraction after homogenisation with 5% TCA. Nitrogen values were converted to their protein equivalent by the multiplication factor of 6.25. The difference between the nitrogen estimated from the

total tissue and nitrogen from TCA extract was equivalent to the non-protein nitrogen (mainly free amino acids).

Carbohydrate. 5-10 mg replicates of the finely ground freeze dried tissue was homogenised in 5% TCA and the protein fraction precipitated overnight at 4°C. Following centrifugation, aliquots of the supernatant containing the dissolved carbohydrate fraction were assayed by the anthrone method of Strickland and Parsons (1968). The carbohydrate content was estimated from a calibration against a glucose standard.

Lipid. 4 mls of 2:1 (v/v) chloroform-methanol were added to 3-7 mg replicates of freeze dried tissue and allowed to extract for two hours at room temperature. 0.8 mls of 0.7% sodium chloride were subsequently added and the extract left overnight at 4°C. This resulted in the separation of the phases with the dissolved lipid in the chloroform phase. By the addition of chloroform this volume was made up to 4.0 mls. 1.0 ml aliquots were taken, evaporated to dryness at 80-100°C, and assayed colourmetrically after charring with concentrated sulphuric acid (Marsh and Weinstein, 1966). Calibration was against a cholesterol standard. Barnes and Blackstock (1973), investigating the use of the sulphophosphovanillin method for total lipid assay, found that the colour obtained with 800µg cholesterol was the same as that for 1000 µg of blood serum lipids. It was therefore assumed that 80 µg cholesterol = 100 µg total lipid.

Ash. Approximately 20 mg replicates of freeze dried tissue were ignited to constant weight at 460°C. The resultant weight loss was assumed to represent the ash free dry weight.

Statistical methods.

Except where otherwise stated, standard statistical procedures were used in data analysis, by methods described by Bailey (1959) and Steel and Torrie (1960). Treatment mean values are generally tabulated with the appropriate 95% confidence limits.

SECTION 2

The effect of some environmental factors on the growth and survival of Juvenile Lobsters.

2.1 TEMPERATURE AND SALINITY

Introduction

Temperature and salinity are two of the major factors affecting the distribution of marine poikilotherms. Extensive studies have been made on the physiological and behavioural responses of marine animals to different levels of these factors (Kinne, 1963; 1964), but there is less information available of the effect on growth rates.

The effect of temperature and salinity on crustacean larval development has received some attention, including studies on the crabs Panopeus (Costlow, Bookhout and Monroe, 1962) and Cardiosoma (Costlow and Bookhout, 1968), the shrimps Crangon (Regnault and Costlow, 1970) and Palaemonetes (Sandifer, 1973) and both the American and European lobsters Homarus americanus (Templeman, 1936a) and H. gammarus (Gompel and Legendre, 1927). These authors demonstrated the presence of optimum levels of temperature and salinity in both isolation and combination, the effect of suboptimum levels, and the changes in optima for different stages.

The effect of temperature and salinity on postlarval growth and survival has previously been limited to studies on the lethal limits for holding wild caught lobsters (McLeese, 1956) and effects on moult regulation in, for example Carcinus (Adelung, 1971), Cancer (Anderson and Ford, 1976), Geocarcinus (Bliss and Boyer, 1964), Cardiosoma (Costlow and Bookhout, 1968) and Crangon (Meixner, 1969).

Recent interest in the commercial culture of the economically important species has now stimulated investigations to determine the optimum

levels of temperature and salinity for overall growth. Among these investigations are those on the intensive culture of the penaeid shrimps (Zein-Eldin and Aldrich, 1965; Venkatoramaiah, Lakshmi and Gunter, 1974), Palaemon (Reeve, 1969; Forster, 1970) and H. americanus (Hughes, Sullivan and Shleser, 1972).

The importance of temperature on the growth of lobsters was first demonstrated by Hughes and Mattheisson (1962), who reported that the optimum temperature for larval development in H.americanus was 20-23°C, while Hughes et al. (1972) recorded fastest juvenile growth at 22-24°C. Previous larval rearing experiments at the Conwy laboratory showed good growth of H. gammarus at 20-24°C (Hepper, pers. comm.). The effect of salinity on postlarval growth of H. gammarus has not been reported, although salinity can effect larval size in H. americanus (Templeman, 1936a).

This study was designed to record the effect of temperature and salinity on the growth of juvenile H.gammarus reared in individual containers. A range of temperature and salinity levels were chosen and the treatments arranged to test the effects of each factor, both in isolation and in combination, and to estimate the optimum combination for growth.

Materials and methods

The study was arranged to a factorial design, with four levels of temperature - 16,20,24 and 28°C - combined with five levels of salinity - 20,24,28,32 and 36 p.p.t. After a period of acclimation, juvenile growth was monitored for six weeks, with up to eight animals per treatment. Two replicates were carried out.

The temperature in each treatment was maintained to within 1°C by water baths fitted with thermostatically controlled immersion heaters or refrigerated cooling coils as appropriate. The salinity of the laboratory seawater supply was adjusted to the treatment levels by the addition of either deionised tap water or concentrated artificial seawater (68.66 p.p.t.). The artificial seawater was made up according to the formula of Lyman and Fleming (1940), which has been found superior to other formulations in studies at this laboratory (Helm, pers.comm.). Artificial seawater made from proprietary salts has been found suitable for the rearing of juvenile H. americanus (Gallagher and Brown, 1976) and holding adult lobsters (Needler, 1953; Wilder and McLeese, 1957) but a subsidiary trial was made to ensure that this was also the case in juvenile H. gammarus. In this trial two groups of 14 juveniles were cultured for six weeks at a salinity of 30 p.p.t. prepared in two different ways and at a temperature of 22±1°C. One treatment was natural seawater diluted when necessary to 30 p.p.t., and the other contained 17% artificial seawater salts, which was equivalent to the maximum amount used in the factorial experiment. To achieve this composition, ambient salinity seawater was first diluted to 25 p.p.t. and then adjusted to 30 p.p.t. by the addition of concentrated artificial seawater. All salinity determinations were made with a refractometer. All juveniles were held individually in plastic 64 cm^2 containers. Each treatment of the factorial experiment consisted of eight containers placed in 47 x 25 x 29 cm deep plastic tanks inside one of four water baths. Each bath

held five tanks and maintained the temperature at the appropriate level. The volume of water in each tank was 20.5 l at one of the five salinity levels. A plastic frame inside each tank held the eight containers just above the water surface. Water circulation and aeration in each tank was maintained by an overhead sprinkler tube. Separate pumps drew water from the bottom of each tank and delivered 0.3 $l.min^{-1}$ to each container. The water left the containers through small holes in the side wall and a plastic cover over each tank helped to reduce evaporation.

The artificial seawater trial was conducted in two larger plastic tanks, each capable of holding 14 containers in a water volume of 36 l. Water circulation and aeration was as described above and the temperature maintained by air heating of the laboratory. The water quality in all trials was preserved by changing the treatment water once each week.

Experimental stock were obtained from the progeny of caught wild ovigerous females and the larvae reared to the fourth stage by mass culture techniques. When sufficient stage four lobsters were available selection of suitable individuals was carried out (Section 1).

Juveniles were transferred to individual containers in the experimental systems and held at a temperature of 20±1°C and salinity of 32±2 p.p.t. Halfway through the fourth stage, initial samples were sacrificed and the remainder randomly assigned to the experimental treatments. Acclimation of animals in the factorial experiment was carried out over a period of six days by increments of approximately $1^{o}C.day^{-1}$ and 2 $p.p.t.day^{-1}$. This was considered to be an adequate regime based on the findings of McLeese (1956). Some mortality occurred during the acclimation period and it was not always possible to replace these losses. In some treatments therefore, the number of animals was less than eight.

Juveniles were fed daily throughout on fresh mussel flesh and uneaten food removed the following day. Moult dates and carapace length (CL) of cast

exuviae were routinely recorded and at the end of each trial the final CL was measured before dry weight and biochemical analysis, by the methods described in Section 1.

Analysis of results. Analyses of variance were made by the Ministry of Agriculture, Fisheries and Food, Appropriation Accounts and Data Processing Division, programme ACMR. The determination of the optimum levels for temperature and salinity was carried out by Response Surface analysis according to the methods outlined by Box (1956) and Box and Youle (1955) of which a summary is provided here. Standard statistical procedures were used elsewhere.

The basis of the Response Surface method is the derivation of a mathematical function to describe the effect of various levels of temperature and salinity on the growth of juvenile lobsters, with the assumption that the response varies in a predictable manner with different combinations of the two factors. The relationship between the response and the factor levels is most easily visualised geometrically. The relation between the response y and a single factor x_1 may be represented by a curve, so the relation between y and two factors x_1 and x_2 is represented by a surface, the Response Surface. This is, in effect, a three-dimensional graph and can be more conveniently illustrated by a contour diagram showing areas of equal response at combinations of x_1 and x_2.

The calculation of the Response Surface involves fitting a polynomial equation to the experimentally determined responses at each factor combination and a quadratic form, including terms up to the second degree, was used:

$$y = b_0 + b_1x_1 + b_2x_2 + b_{11}x_1^2 + b_{22}x_2^2 + b_{12}x_1x_2 \quad \ldots\ldots\ldots\ldots \quad (1)$$

where y = response (mean dry weight of survivors)
x_1 = temperature level
x_2 = salinity level
b_0 = constant
b_1 = linear effect of temperature
b_2 = linear effect of salinity
b_{11} = quadratic effect of temperature
b_{22} = quadratic effect of salinity
b_{12} = interaction effect of temperature and salinity

Multiple linear regression is used to calculate the constants or regression coefficients of the equation and the experimental points are fitted to the polynomial by the method of Least Squares. The effect on each factor is then estimated from the observed response at all levels of that factor and combination of factors. From the quadratic equation the response at other factor levels can be estimated, although extrapolation outside the experimental range may give misleading results. The maximum theoretical yield is found by differentiating the equation first to x_1 and then x_2 and equating the result to zero. This provides the values of x_1 and x_2 that are the loci of the centre and the maximum yield can be estimated by substitution in the original equation.

Yield contours are built up by calculating the loci of all points that satisfy the equation for a given level of response, the contours representing percentages of the maximum theoretical yield. Direct substitution of a value for the percentage response, together with either x_1 or x_2 will give a quadratic equation in x_2 or x_1 and this can be solved to find the appropriate value of x_2 or x_1.

Outline calculations. The levels of temperature and salinity were coded to ease computation and a table of independent variables compiled for each combination of temperature and salinity (Table 1).

The values of the independent variables have the following properties:

$$\frac{\Sigma x_1}{n} = \frac{\Sigma x_2}{n} = \frac{\Sigma x_1 x_2}{n} = 0$$

$$\frac{\Sigma x_1^2}{n} = 5 \quad \text{and} \quad \frac{\Sigma x_2^2}{n} = 2$$

Therefore the mean response $y = b_0 + 5b_{11} + 2b_{22}$ (2)

and subtracting this from equation 1 yields the equation used to estimate the regression coefficients.

$$y = y_0 x_0 + b_1 x_1 + b_2 x_2 + b_{11}(x_1^2 - 5) + b_{22}(x_2^2 - 2) + b_{12} x_1 x_2 \ldots\ldots\ldots\ldots$$

(x_0 is introduced as a dummy variable equal to unity)

The effect of each factor is estimated in the following way. The sum of products for any two columns in Table 1 is zero, so the estimates are calculated by taking sums of the products of the observations (y's) with the elements of the appropriate independent variable and dividing by the sums of squares of the elements of the independent variables.

$$y_0 = \Sigma y x_0 / \Sigma x_0^2$$
$$b_1 = \Sigma y x_1 / \Sigma x_1^2$$
$$b_2 = \Sigma y x_2 / \Sigma x_2^2$$
$$b_{11} = \Sigma y (x_1^2 - 5) / \Sigma (x_1^2 - 5)^2$$
$$b_{22} = \Sigma y (x_2^2 - 2) / \Sigma (x_2^2 - 2)^2$$
$$b_{12} = \Sigma y (x_1 x_2) / \Sigma (x_1 x_2)^2$$

The value of b_0 is found by substitution of the estimates in equation 2 and the solutions to the coefficients substituted into equation 1 to calculate the maximum theoretical yield and the yield contours.

Table 1. Values of independent variables in regression equation.

Treatment		x_0	x_1	x_2	x_1^2-5	x_2^2-2	x_1x_2	Yield
°C	p.p.t.							
16	20	1	-3	-2	4	2	6	y_1
	24	1	-3	-1	4	-1	3	y_2
	28	1	-3	0	4	-2	0	y_3
	32	1	-3	1	4	-1	-3	y_4
	36	1	-3	2	4	2	6	y_5
20	20	1	-1	-2	-4	2	2	y_6
	24	1	-1	-1	-4	-1	1	y_7
	28	1	-1	0	-4	-2	0	y_8
	32	1	-1	1	-4	-1	-1	y_9
	36	1	-1	2	-4	2	-2	y_{10}
24	20	1	1	-2	-4	2	-2	y_{11}
	24	1	1	-1	-4	-1	-1	y_{12}
	28	1	1	0	-4	-2	0	y_{13}
	32	1	1	1	-4	-1	1	y_{14}
	36	1	1	2	-4	2	2	y_{15}
28	20	1	3	-2	4	2	-6	y_{16}
	24	1	3	-1	4	-1	-3	y_{17}
	28	1	3	0	4	-2	0	y_{18}
	32	1	3	1	4	-1	3	y_{19}
	36	1	3	2	4	2	6	y_{20}
	Σx^2	20	100	40	320	56	200	

Coded values for temperature and salinity levels.

Temperature	x_1	Salinity	x_2
16	-3	20	-2
20	-1	24	-1
24	+1	28	0
28	+3	32	+1
		36	+2

Results

In both factorial trials the fastest growth rate was found at a temperature of 20°C and salinity of 28 p.p.t.; a complete record of the dry weight, carapace length and survival data is presented in Table 2.

With the exception of the 28°C treatments, where almost total mortality occurred, the greatest mean weight at all salinity levels was found at 20°C and the lowest at 16°C. At temperatures of 16,20 and 24°C the highest mean weights were found at salinities of 28 or 32 p.p.t., as were the only survivors of the 28°C treatment. Juvenile response to the two factors was similar in both trials, with the exception that in the first trial at the 36 p.p.t. salinity level the mean weight at 24°C was greater than at 20°C.

An analysis of variance was made on each trial result (Table 3) and utilised each individual juvenile dry weight as a replicate. The programme required equal numbers per treatment and, where necessary, randomly chosen values were excluded. This analysis showed significant effects of both temperature and salinity on the growth rate but no significant interaction. The residual mean square in both cases was high due to the large amount of individual variation within treatments, especially so in the first trial.

Husbandry techniques, particularly those of larval rearing, had been improved by the second trial and resulted in better postlarval survival and subsequent juvenile viability. This is evident from the more uniform growth in each treatment and generally better survival. Nevertheless, treatment values between the two trials only differed in magnitude and after grouping the data from both trials further analysis was therefore made by the Response Surface technique.

The growth rate in the factorial trials was not influenced by the use of artificial seawater salts for salinity adjustment because there was no difference between mean dry weight, mean carapace length or survival in

juveniles reared in natural or artificial seawater (Table 2).

Determination of optimum conditions. The maximum recorded yield at a temperature of 20°C, in combination with a salinity of 28 p.p.t., was not necessarily the optimum combination. Response surface analysis allows the effect of other combinations to be estimated, as well as the maximum theoretical yield and the optimum combination of temperature and salinity. The yield responses, as grouped mean dry weights of surviving juveniles, were entered in Table 1 and the constants estimated as already described.

Constant estimated	Σx^2	Σyx	Estimate ±standard error	Component sums of squares
y_0	20	820.4	41.0 ± 3.4	33650.4
b_1	100	-561.4	-5.61 ± 0.8	3151.6
b_2	40	136.4	3.4 ± 1.3	464.9
b_{11}	320	-1134.4	-3.5 ± 0.5	4021.2
b_{22}	56	-229.9	-4.1 ± 1.1	943.9
b_{12}	200	-66.7	-0.3 ± 0.6	22.2
				42254.2

Residual sums of squares 652.3
Total sums of squares 42906.5

Now $b_0 = y_0 - 5b_{11} - 2b_{22}$ (equation 2)

Therefore $b_0 = 66.9 \pm 3.4$

The calculated regression equation was therefore:

$$y = 66.9 - 5.6x_1 + 3.4x_2 - 3.5x_1^2 - 4.1x_2^2 - 0.3x_1x_2 \quad \ldots\ldots\ldots \quad (3)$$

Although the residual sums of squares was high, it was not considered useful to include higher order terms in the polynomial. After the fitting of the mean was allowed for, a large proportion of the total sums of squares was

ascribable to the regression equation and the magnitude of the estimates relative to their standard errors confirmed that an adequate fit was provided. At the same time, comparison of the observed responses with the responses estimated from equation 3 showed a high correlation of 0.97.

The position of maximum theoretical yield of 70.0 mg was at the locus where $x_1 = -0.8$ and $x_2 = 0.4$. These values, decoded, represented a temperature of $20.8^{\circ}C$ and salinity of 29.8 p.p.t.

In Figure 1 the response is represented by contours of equal percentage of the maximum yield. Temperature had a greater effect on growth than salinity and this was expected from the relative sizes of the coefficients in the regression equation. Within the experimental range, temperatures above the optimum had a more adverse effect on yield than lower temperatures, e.g. at the optimum salinity of 30 p.p.t. and temperature of $24^{\circ}C$ ($3^{\circ}C$ above the optimum) the estimated yield was 83%, while at $3^{\circ}C$ below the optimum yield at the same salinity would be 90% (these yield differences increase at temperatures further from the optimum).

The yield was hardly affected by salinity over a broad range and at the optimum temperature 95% yield was estimated between 26 and 33 p.p.t. Equal changes in salinity level above or below the optimum value had similar effects.

Although interaction effects were not significant, higher yields were estimated over a wider salinity range at temperatures below the optimum, than at temperatures above the optimum, and indicated a greater salinity tolerance at lower temperatures. At a lower salinity of 26 p.p.t. and temperature $3^{\circ}C$ above the optimum, the yield was 79%, while at a temperature $3^{\circ}C$ below the optimum the yield was 87%.

For practical purposes the central contour of Figure 1 is the most important. In this area 95% of the maximum theoretical growth may be obtained with a salinity range of 33.4 - 26.1 p.p.t. and temperature range of 18.5 - $22.3^{\circ}C$.

At the optimum level of each factor the tolerance to any level of the other factor is greatest. Greatest salinity tolerance occurs at the optimum temperature of 21°C but at 22.3°C 95% yield is only achieved at the optimum salinity of 30 p.p.t.

The effect of temperature and salinity on moulting. Dry weight data gives an accurate estimate of the rate of tissue growth but does not illustrate the pattern of growth, which is a combination of length of intermoult period and size of moult increment. Moult data can however be unreliable, especially when records are limited, e.g. two animals may have the same dry weight but different carapace length if one had just moulted. Nevertheless, the available records help to explain the differences in growth rate.

Final CL data corresponded fairly closely with the dry weight data (Table 2) and confirmed that differences in dry weight were the result of differences in animal size, although treatment differences were not so well marked. There was insufficient data to calculate mean intermoult periods for each treatment but during the trials unnoticed ecdyses could often be registered from comparison of CL measurements and an estimate of the moult frequency was based on the average number of moults from both trials in each treatment (Table 4). Moulting was most frequent at 20°C and at salinities between 24 and 32 p.p.t. and illustrates that the differences in growth were partly due to differences in the length of the intermoult period.

The mean carapace length of successive stages of juveniles from both trials provided an estimate of the moult increment (Table 5), for larger stage sizes can only arise through bigger size increments at moult. The mean CL at stages 5,6 and 7 was greatest at the lowest temperature and values decreased at higher temperatures. There was little influence of salinity on stage size, except at the extreme levels of 20 and 36 p.p.t.

The moult data was not suitable for more detailed analysis but differences in

the growth rate bore a closer relation to moult frequency than moult increment. There was an apparent antagonistic effect between moult increment and intermoult period, for while the moult frequency is highest at the optimum level of both temperature and salinity, the moult increment is increased at temperatures below the optimum.

Survival in both trials was poor at 28°C but inspection of the data revealed that juveniles held at 20 and 36 p.p.t. survived for a shorter period and weighed less at death than juveniles at other salinities. At other temperatures the percent survival was not apparently affected by either temperature or salinity (Table 2). The generally poorer survival in the first trial was probably due to lower juvenile viability, although consistently smaller stage CL in the first trial may be indicative of genetic differences. Hedgecock, Nelson and Shleser (1976) found significant variation in H. americanus, both within and between full sibling families grown under identical conditions and Reeve (1969) also demonstrated absolute growth differences between separate brood prawn populations, although the optimum factor levels did not differ.

Biochemical analysis. The analyses of survivors body tissue illustrated that temperature and salinity may affect the body composition (Tables 6 and 7) and analyses of variance of treatment values were carried out, excluding the 28°C treatments, to determine the main effects (Tables 8 and 9).

Over all treatments, carbohydrate levels were very low and comprised only 1 - 4% of the ash-free dry weight, lipid was found in slightly larger amounts of 5 - 10% but the dominant component was nitrogen, mainly as protein. Salinity exerted a significant affect on the ash weight in both trials, with a greater proportion of ash at the highest salinities. In the second trial a temperature affect was found with maximum ash weight at 20°C. Salinity affected the proportion of lipid in the second trial, with a maximum at 28 p.p.t. but this did not occur in the first trial. There were no obvious

effects of either factor on carbohydrate levels but a significant effect of temperature was found on protein level in the first trial. Non-protein nitrogen, consisting mainly of free amino acids, was affected by salinity in the first trial with lower levels at 32 and 36 p.p.t. but this was not apparent in the second trial.

A comparison between the body composition of juveniles and the growth rate at the different treatments revealed that poorer growth rates were generally associated with lower levels of lipid, protein and ash.

Table 2. Mean dry weight and carapace length of surviving lobsters and percent survival after six weeks growth at various combinations of temperature and salinity and in the artificial seawater trial.

Treatment °C	p.p.t	Dry weight (mg) I	Dry weight (mg) II.	Carapace length (mm) I	Carapace length (mm) II	Percent survival I	Percent survival II
16	20	19.0±19.2	36.6± 4.5	5.53±2.09	6.43±0.16	60	87.5
	24	32.7±25.3	43.1± 6.35	6.06±1.07	6.74±0.64	80	100
	28	37.0	55.3± 5.5	6.52	7.30±0.66	16.7	100
	32	46.0±16.1	49.5± 6.0	7.26±0.88	6.94±0.50	100	100
	36	43.3±37.5	48.8± 8.1	5.98±0.64	6.69±0.30	80	87.5
20	20	44.9±19.3	45.4± 6.9	6.86±0.96	7.44±0.45	100	100
	24	56.1±21.4	65.5±15.6	7.39±0.55	7.89±0.60	91.4	100
	28	64.5±23.4	77.4± 8.2	7.28±0.98	8.18±0.21	100	87.5
	32	53.8±31.2	73.5± 6.9	7.11±1.08	7.89±0.20	83.3	87.5
	36	47.1±20.4	61.2±15.8	6.61±0.12	7.62±0.59	83.3	87.5
24	20	30.6±24.2	44.9± 7.2	6.24±1.80	7.17±0.52	71.4	87.5
	24	44.3± 6.8	47.6±11.08	7.06±1.39	7.12±0.43	60	100
	28	54.4±34.1	60.5± 7.7	7.07±2.45	7.46±0.25	57.1	87.5
	32	50.3±20.8	62.2±11.4	6.87±0.86	7.40±0.39	85.7	100
	36	59.8±20.9	54.5±15.0	7.00±0.82	6.98±0.67	66.7	87.5
28	20	-	-	-	-	0	0
	24	-	-	-	-	0	0
	28	-	29.8	-	6.33	0	12.5
	32	18.2± 6.6	-	5.33	-	28.6	0
	36	-	-	-	-	0	0
Initial sample		8.6± 3.3	14.1± 1.7	4.54±0.06	4.76±0.08		
Natural seawater			55.6±10.3		7.50±0.31		92.3
Artificial seawater			54.5± 6.8		7.46±0.31		92.3
Initial sample			11.8± 2.0		4.66±0.13		

Table 3. Analysis of variance of juvenile dry weights after six weeks growth at various combinations of temperature and salinity. Tabulated values ± standard error of mean.

Trial I

Mean Temperature level	Dry weight (mg)	Mean Salinity level	Dry weight (mg)
16	23.6± 5.3	20	16.9± 4.8
20	46.7± 5.3	24	22.5± 4.8
24	37.1± 5.3	28	27.0± 4.8
28	1.5± 5.3	32	40.2± 4.8
		36	29.6± 4.8

Source of variation	Sums of squares	d.f.	Mean square	F ratio	
Temperature	28852.2	3	9617.4	20.86	$p < 0.01$
Salinity	6038.3	4	1509.6	3.28	$p < 0.05$
Interaction	9214.6	12	767.9	1.67	N.S.
Residual	36878.5	80	460.9		
Total	80983.6	99			

Trial II

Mean Temperature level	Dry weight (mg)	Mean Salinity level	Dry weight (mg)
16	43.6± 2.9	20	28.4± 3.2
20	58.5± 2.9	24	39.8± 3.2
24	50.3± 2.9	28	45.0± 3.2
28	0.9± 2.9	32	44.0± 3.2
		36	34.4± 3.2

Source of variation	Sums of squares	d.f.	Mean square	F ratio	
Temperature	69409.1	3	23136.4	8.08	$p < 0.01$
Salinity	5378.6	4	1344.7	4.69	$p < 0.05$
Interaction	2249.0	12	187.4	0.65	N.S.
Residual	34361.6	120	286.4		
Total	111398.2	139			

Figure 1. Estimation of the percentage maximum weight of juvenile lobsters based on the fitted response surface to observed weights when grown under 20 combinations of temperature and salinity.

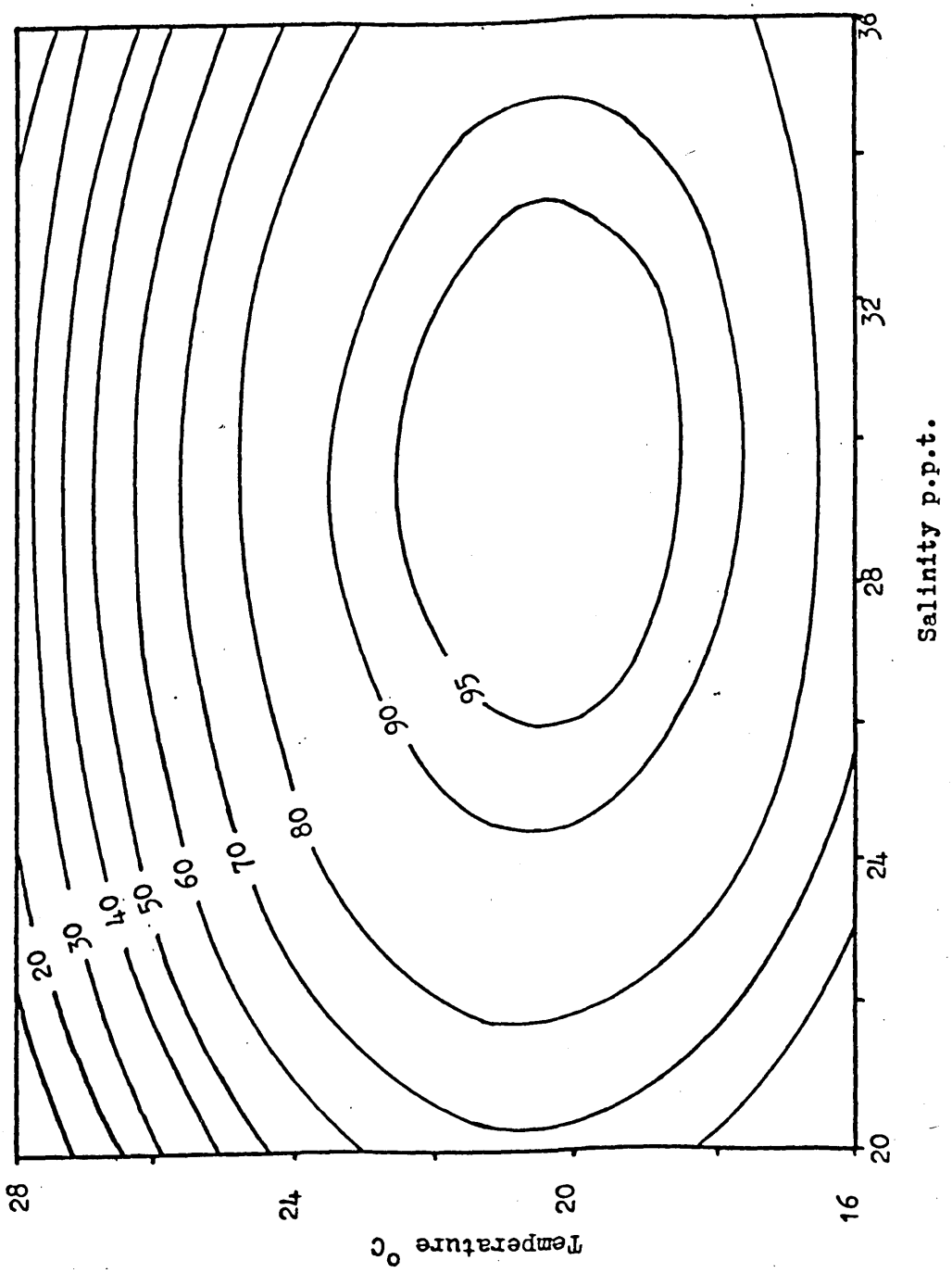


Table 4. The moult frequency at different combinations of temperature and salinity, tabulated as the average number of moults by each juvenile for both trials during the six week experimental period.

Salinity (p.p.t.)	Temperature (°C) 16	20	24	28	Mean salinity
20	1.60	2.00	1.62	0	1.31
24	1.91	2.54	2.27	0	1.68
28	1.78	2.15	1.91	2.00	1.96
32	1.54	2.00	1.92	1.00	1.62
36	1.45	1.92	1.82	0	1.30
Mean temperature	1.66	2.12	1.91	0.60	

Table 5. Carapace length (mm) of successive stages of juveniles grown at various combinations of temperature and salinity for six weeks, tabulated as the mean for both trials.

Mean temperature values	Stage 4	5	6	7
16	4.61±0.16	5.52±0.14	6.50±0.15	8.11±0.42
20	4.78±0.26	5.46±0.15	6.47±0.13	7.78±0.18
24	4.67±0.19	5.39±0.19	6.38±0.17	7.48±0.23
28	4.77±0.25	5.38±0.14	6.09±0.31	-

Mean salinity values	Stage 4	5	6	7
20	4.65±0.23	5.40±0.18	6.31±0.32	7.65±0.19
24	4.75±0.12	5.47±0.16	6.57±0.53	7.57±0.69
28	4.85±0.36	5.36±0.19	6.47±0.19	7.97±0.37
32	4.67±0.19	5.52±0.20	6.35±0.26	7.75±0.36
36	4.34±0.21	5.42±0.20	6.34±0.21	7.58±0.39

Table 6. Proximate analysis of juveniles cultured under various combinations of temperature and salinity for six weeks. Values are presented as percentages of the ash free dry weight.

Trial I	Treatment °C	p.p.t.	Percent ash	Lipid	Carbohydrate	Protein	Non-protein nitrogen
	16	20	20.4	6.6	2.5	28.7	5.5
		24	26.6	9.6	1.7	34.8	5.7
		28	29.5	7.8	2.2	28.7	8.8
		32	27.9	12.7	2.3	40.4	5.1
		36	32.3	8.6	1.3	37.2	3.6
	20	20	27.4	11.7	2.5	36.6	3.0
		24	27.8	8.3	2.8	41.9	2.2
		28	30.1	9.7	2.6	43.6	3.6
		32	34.1	7.6	1.6	37.8	3.0
		36	24.9	9.8	1.9	44.5	3.3
	24	20	26.1	12.0	2.7	47.1	3.4
		24	28.1	8.2	2.2	41.5	3.5
		28	29.8	9.7	2.8	51.2	3.3
		32	30.9	9.8	2.9	48.3	2.0
		36	34.7	11.6	2.8	41.4	2.5
	28	20	-	-	-	-	-
		24	-	-	-	-	-
		28	-	-	-	-	-
		32	39.5	5.9	0.9	43.3	4.5
		36	-	-	-	-	-
Initial sample			23.4	6.6	1.4	53.8	2.6

Table 7 Proximate analysis of juveniles cultured under various combinations of temperature and salinity for six weeks. Values are presented as percentages of the ash free dry weight.

Trial II	Treatment °C	p.p.t	Percent ash	Lipid	Carbohydrate	Protein	Non-protein nitrogen
	16	20	29.0	8.9	3.2	45.5	4.4
		24	28.5	9.0	3.4	62.1	1.5
		28	32.4	10.0	3.7	55.7	2.7
		32	32.4	8.4	2.2	53.9	2.1
		36	35.5	7.7	2.0	49.7	2.7
	20	20	31.8	10.0	3.2	58.5	3.3
		24	30.6	8.7	3.3	52.8	2.5
		28	32.0	10.9	3.4	56.1	1.6
		32	32.7	7.8	2.5	49.9	2.0
		36	35.1	7.4	2.1	55.6	1.4
	24	20	26.9	7.6	4.0	56.8	2.8
		24	28.0	7.9	2.9	54.3	1.8
		28	30.4	7.5	3.2	52.7	1.8
		32	31.2	7.7	2.9	55.6	1.9
		36	31.0	9.4	3.1	49.4	3.2
	28	20	-	-	-	-	-
		24	-	-	-	-	-
		28	40.9	6.3	0.3	76.0	0.7
		32	-	-	-	-	-
		36	-	-	-	-	-
Initial sample			36.0	7.6	3.1	47.5	2.6

Table 8. Analysis of variance for proximate analysis of juveniles grown under various combinations of temperature and salinity for six weeks.

Trial I	Component	Source of variation	Mean square	Variance ratio	
	Ash	Temperature	10.9	2.3	N.S.
		Salinity	27.4	5.7	$p < 0.01$
		Residual	4.8		
	Lipid	Temperature	1.8	0.4	N.S.
		Salinity	1.3	0.3	N.S.
		Residual	4.6		
	Carbohydrate	Temperature	0.6	3.2	N.S.
		Salinity	0.2	0.8	N.S.
		Residual	0.2		
	Protein	Temperature	179.9	7.5	$p < 0.01$
		Salinity	10.3	0.4	N.S.
		Residual	23.9		
	Non-protein nitrogen	Temperature	4.0	3.5	N.S.
		Salinity	6.4	5.6	$p < 0.05$
		Residual	1.2		

Table 9. Analysis of variance for proximate analysis of juveniles grown under various combinations of temperature and salinity for six weeks.

Trial II	Component	Source of variation	Mean Square	Variance ratio	
	Ash	Temperature	10.8	13.9	$p < 0.01$
		Salinity	10.1	12.9	$p < 0.01$
		Residual	0.8		
	Lipid	Temperature	1.3	1.0	N.S.
		Salinity	1.0	0.8	N.S.
		Residual	1.3		
	Carbohydrate	Temperature	0.2	1.0	N.S.
		Salinity	0.7	3.9	$p < 0.05$
		Residual	0.2		
	Protein	Temperature	1.8	0.1	N.S.
		Salinity	9.9	0.4	N.S.
		Residual	24.3		
	Non-protein nitrogen	Temperature	0.7	0.2	N.S.
		Salinity	5.2	1.4	N.S.
		Residual	3.6		

Discussion

Temperature has probably the most direct effect of all environmental factors on the moult cycle in most, if not all, species. Ecdysis cannot occur until after the necessary tissue growth and the rate of tissue growth depends on the metabolic rate and food supply. In all species so far studied, the growth rate increases with temperature up to a level dependent on the physiological capacity of the species, and at higher temperatures growth rate declines and survival is reduced. Examples include Palaemon (Forster, 1970; Kamiguchi, 1971), Palaemonetes (Sandifer, 1973) and the penaeid shrimps (Zein-Eldin and Aldrich, 1965; Zein-Eldin and Griffith, 1966).

In H.gammarus a more marked reduction in growth rate occurs at temperatures above the optimum than at lower temperatures and the same response is found in Penaeus setiferus (Linnaeus). Maximum growth rate occurs at 32.5°C but the same reduction in size is found at both 35 and 22.5°C (Zein-Eldin and Griffith, 1969). The effect of higher temperatures on survival may be masked by losses due to cannibalism, for aggressive interactions generally increase with temperature due to higher activity levels and a greater proportion of vulnerable newly moulted individuals. The optimum temperature for growth of communally reared P. aztecus Ives is 30°C but the optimum for survival is 22°C (Zein-Eldin and Griffith, 1966), and Zein-Eldin and Aldrich (1965) demonstrated that cannibalism was the main reason for poor survival at temperatures up to the optimum for growth by experiments with individually reared P.aztecus.

The growth rate is invariably affected by the influence of temperature on the length of the intermoult period but the influence of moult

increment on the growth rate may be underestimated because of a lack of reliable moult data. In H. gammarus the moult increment is inversely proportional to the temperature and is greatest at temperatures nearer the normal environmental range. Geocarcinus exhibits reduced moult increments at temperatures 6°C above the optimum value (Bliss and Boyer, 1964), as does Callinectes at temperatures above 20°C (Leffler, 1972). The antagonistic effect of temperature on moult increment and moult frequency found in H. gammarus has also been observed in Cancer, where the greatest moult frequency is at 22°C and greatest mean carapace width at 18°C (Anderson and Ford, 1976). A similar effect occurs in Palaemonetes, for although the rate of larval development is very similar at either 25 or 30°C, the number of larval instars is lower at 25°C (Sandifer, 1973).

The moult increment in H. americanus is apparently unaffected by temperature. Hughes et al. (1972) reported that the average carapace length of moult stages were no different whether reared at 22-24°C or at ambient sea temperature (2-12°C), or compared to values predicted from sampling wild populations (from Wilder, 1953). Adelung (1971) reported that temperature only affected the intermoult period in Carcinus and that the optimum temperature was the same (30°C) for crabs with both eyestalks removed as for untreated specimens. The absolute growth rate was greater in the treated crabs but the same optimum temperature for individuals without the centres of production of MIH apparently demonstrated that moulting in Carcinus was entirely dependent on tissue growth.

Although temperature clearly exerts a fundamental influence over the rate of tissue growth and therefore intermoult period, it does

not satisfactorily account for differences in moult increment. Larger moult increments are presumably a response to more favourable conditions and this indicates that separate processes regulate moult frequency and increment. The results of most studies are consistent with the theory suggested by Adelung (1971) that moult frequency is determined by metabolic rate, where the growth rate increases with temperature until the physiological capacity of the individual is exceeded, but evidence presented in following sections of this thesis shows that the moult increment may be under nervous control.

Experiments with juveniles cultured at constant temperature with plentiful food demonstrate that reduced moult increments occur at adverse levels of some environmental variables, such as amount of living space and shelter availability, that have no obvious direct effect on the metabolic rate. Moult increment responses to temperature may therefore reflect the unfavourable nature of temperatures above 16°C, despite the faster rate of tissue growth, and it would be interesting to study the responses at temperatures more usually experienced in the natural environment. A behavioural response to temperature has been demonstrated in H. americanus. Adult lobsters held in a thermal gradient initially showed a preference for a temperature of 17°C but subsequently two optima became apparent at 14 and 26°C (Reynolds and Casterlin, 1979). The choice of 26°C seems anomalous on the basis of existing knowledge but the response to lower temperatures indicates that these are more favourable to the lobster.

The estimated optimum temperature of 21°C for growth of H. gammarus is lower than that reported for H. americanus. Juvenile growth is fastest at 22-24°C (Hughes et al., 1972) and larval development at 20-23°C (Hughes and Mattheison, 1962). A real difference in

temperature tolerance between the two species may exist for H. americanus larvae have a higher lethal temperature level, and in both species temperature tolerance increases with larval age (Gruffydd, Reiser and Machin, 1975).

The salinity level is not critical for growth of H. gammarus within a broad range of 26-33 p.p.t. Larvae can withstand salinities between 20 and 42 p.p.t. (Gompel and Legendre, 1927) and a similar tolerance of low salinity is found in H. americanus larvae (Templeman, 1936a). Salinity effects usually reflect the salinity range experienced in the natural environment, and in populations of some essentially marine species 'brackish water pauperisation' can occur (Kinne, 1964), while good growth occurs over a broad range in Palaemonetes (Sandifer, 1973) and the penaeid shrimps (Zein-Eldin and Griffith, 1969). Lobsters are usually found in areas of full salinity seawater but have been reported in areas of half normal salinity (Cole, 1940). The larvae will actively avoid salinities of 22 p.p.t. but exhibit no preference at salinities between 32 and 27 p.p.t. (Scarratt and Raine, 1967). Templeman (1936b) reported that lobsters from areas of reduced salinity tended to moult earlier but this may be due to higher temperatures in such inshore and estuarine situations.

H. americanus is normally an osmoconformer. The body fluids remain isosmotic with the external medium at salinities between 25 and 37 p.p.t. but some hyperosmoregulation occurs at low salinities (Dall, 1970). The reduced growth of H. gammarus at low salinities probably arises through a general decrease in metabolic efficiency, for tissue hydration and osmoregulation only impose a small energy demand (Gilles, 1975). Ionic regulation in Callinectes is similar

to that of H. americanus but there is no difference in the metabolic rate of animals acclimated to salinities between 20 and 36 p.p.t. (Leffler, 1975). The effect of salinity on respiration in lobsters has not been reported but marked increases in respiratory rate generally occur only in osmoregulating species such as Carcinus (Taylor, 1977), Panopeus (Dimrock and Groves, 1975) and Crangon (Hagerman, 1970a).

In some species interaction between temperature and salinity can occur. Larval survival in Panopeus at high salinities is improved at higher temperatures (Costlow et al., 1962) and the same combination is best for larval survival in Callinectes but low salinity-high temperature, or high salinity - low temperature combinations are unsuitable (Costlow, 1967). Zein-Eldin and Aldrich (1965) demonstrated that low salinities are only tolerated by Penaeus aztecus at temperatures near the optimum for growth. Salinity tolerance in H. gammarus was unaffected at temperatures below the optimum and a greater salinity effect at higher temperatures was probably due to a general decrease in metabolic efficiency, rather than a true interaction effect.

Temperature and salinity did not exert pronounced effects on the body composition and some of the variation may be a result of size differences. Lower ash weights at reduced salinities might indicate an effect of low external calcium levels on exoskeleton calcification (Passano, 1960). Calcium accounts for up to 25% of the carapace dry weight (Hayes and Armstrong, 1961) and the carapace weight is some 32% of the total weight (Hewett, 1974). Studies on Orconectes have, however, shown that the percent ash increases with carapace length (Stein and Murphy, 1976).

Lipid and carbohydrate are the main storage products in the hepatopancreas of many crustaceans (Passano, 1960) but there was no sign that levels were particularly depleted at temperatures above the

optimum. Protein levels increased with temperature in the first trial but more confidence is attached to the results of the second trial, in which this effect was not evident. Non-protein nitrogen levels, which consist mainly of free aminoacids (Fraser et al., 1952), were not apparently related to salinity, as might be expected from the role of free amino-acids in osmoregulation (Schoffeniels and Gilles, 1970).

The results of this study are important in assessing the potential of intensive lobster culture. Despite the high market value of the lobster, a major disadvantage is the slow rate of growth in the wild, generally estimated at 5-7 years to a marketable size of 80 mm CL. The growth rate obtained in this study indicates that, at an optimum combination of temperature and salinity, the culture period could be reduced to about 2.5 years, and a similar result has been found in H. americanus (Hughes et al., 1972). Lobster culture may be economically viable if high growth rates can be maintained under intensive conditions.

Summary

1. The effect of temperature and salinity on the growth of juvenile Homarus gammarus was studied by a 4 x 5 factorial experiment - temperature levels between 16 and 28°C combined with salinities of 20 to 36 p.p.t.

2. The growth rate of juveniles from 2 to 8 weeks old was greatest at a temperature of 20°C combined with a salinity of 28 p.p.t.

3. Response surface analysis was used to predict the optimum levels for growth. These were estimated to be a temperature of 20.8°C combined with a salinity of 29.8 p.p.t. 95% of the maximum theoretical yield could be achieved over a temperature range of 19-22°C and salinity range of 27-33 p.p.t., with the maximum yield at a given level of one factor achieved at the optimum level of the other.

4. The growth rate was determined mainly by the frequency of moulting, although there was evidence that the size increase at moult was also affected.

5. Results indicate that marketable sized lobsters could be cultured in about 2.5 years.

SECTION 2.2

THE EFFECT OF CONTAINER SIZE ON THE GROWTH AND SURVIVAL OF JUVENILE LOBSTERS.

Introduction

In laboratory studies, the lobster Homarus gammarus usually has to be isolated in separate containers to prevent the fighting and cannibalism that otherwise occurs when lobsters are held communally under restricted conditions. High mortalities can occur among communally held lobsters particularly at the high temperatures required for accelerated growth rates, because an increased moult frequency prevents the establishment of any social structure or dominance heirarchy. Formation of dominance heirarchies can occur when adult lobsters are held in storage pounds (Douglis, 1954) and leads to a decrease in the number of aggressive interactions (Dunham, 1972; Squires, 1970).

Although it is possible to reduce cannibalism under communal conditions by providing suitable hiding places and a large area per lobster (Sastry and Zeitlin-Hale, 1977; Van Olst, Carlberg and Ford, 1975), these systems are often unsuitable for laboratory studies. The isolation of individual animals is necessary to ensure that each individual is exposed to the same conditions, and that results are not complicated by losses due to cannibalism. Individual rearing systems are, however, both complex, costly and more labour intensive, but they do allow a greater number of animals to be held in a restricted area.

All techniques so far suggested for commercial lobster culture also involve individual rearing for a major part of the culture period.

Individual culture is necessary to reduce the physical size of the plant and the costs of maintaining optimum conditions for growth, especially that of temperature. The long culture period also means that large juveniles represent a significant investment and even low levels of mortality cannot be tolerated.

The size of container used is, therefore, of prime importance. In laboratory studies it is necessary to ensure that the growth and survival is not adversely influenced by either too large or too small containers, while providing more space than necessary to achieve the required growth rate would increase the costs of an intensive culture unit and reduce profitability.

Apart from economic considerations, living space is an important concept in animal development generally. There is evidence in other species, especially among birds, that a personal space is required by each individual and is maintained by limiting the approach of competitors (Marler and Hamilton, 1966). Restriction of this personal space by excessive crowding can result in abnormal behaviour and physiology and there are many examples among captive animals (Wynne-Edwards, 1962). This aspect has so far received little attention among marine animals except in the context of stocking density for commercially important species.

In this study juvenile lobsters were reared in a range of container sizes to determine the influence of the container area on growth and survival. It was also hoped that the results would allow an estimate of the optimum size of container to be obtained, one that allowed the maximum utilisation of the available space with minimum inhibition of growth.

The total floor area of the container was chosen as the experimental variable rather than any other dimension mainly for practical reasons. It has not been possible to determine whether other parameters, such as shortest side, are more important to H. gammarus, but research has shown that the shape of container is not critical in H. americanus (Shleser, 1974).

A prior estimate of the container size was obtained from J. T. Hughes (Massachusetts State Lobster Hatchery) who found that container areas from four to nine times the square of the total length of the lobster were adequate for H. americanus (pers.comm.). Experimental treatments in this study were, therefore, chosen around this value, together with a larger container designed to represent an 'unrestricted' area as a baseline value.

Materials and Methods

Juvenile lobsters were reared in six sizes of container. Five were circular containers with floor areas from 6.6-181.5cm^2. The diameter of these containers were some 1.5-7.5 times the total length of the fifth stage lobster (20mm TL). A larger rectangular container of 545.2cm^2 was also included in one trial with a width nine times the total length of a fifth stage lobster.

Three trials were made. In the first trial (S1) juveniles were cultured for six weeks (from 1.5-7.5 weeks of age) in containers from 6.6-181.5cm^2. In the second trial (S2) juveniles were cultured for a further 8 weeks (from 8 to 16 weeks old) in containers from 44.2-545.2cm^2. As a result of these trials a further study (S3) was carried out in which juveniles were cultured for 12 weeks (from 1-13 weeks of age) in containers from 6.6-181.5cm^2. The numbers of lobsters used in each trial are shown in the following table.

Container area cm^2	Number of lobsters per trial S1	S2	S3
6.6	15		20
20.4	15		20
44.2	15	10	20
85.0	15	10	20
181.5	15	10	20
545.2		7	

Circular containers were made from 10cm sections of opaque PVC pipe of appropriate diameter, with a base of 1mm PVC sheet. A 2.5cm diameter hole was made 1.0cm above the base of each container to allow water exchange and each hole was covered with mesh to prevent escape of animals. Proprietary perspex aquaria were used for the

rectangular containers. These were painted black on the outside and had two water exchange ports. All containers were randomly distributed in shallow wooden or fibreglass tanks where water circulation and aeration was maintained by a siphon system which caused a change in the water level of both tanks and containers of 2.5cm every 8-10 minutes.

The water temperature was maintained throughout at 20±2°C by laboratory air heating and ambient salinity seawater was used (30-34 p.p.t.). Water quality was preserved by changing 25% of the system volume twice weekly in the first two trials, while in S3 a small percolating biological filter was incorporated and water replacement reduced to once weekly. Illumination was from south facing windows supplemented by normal laboratory artificial light up to a maximum of 300 lux.

Experimental stock were obtained from larvae hatched from wild caught females and reared to the fourth stage in mass culture as described in Section 1).

For the first two trials, 145 stage four lobsters from a single female were selected at eleven days old. Of these,75 were randomly assigned to the five treatments of S1 and an initial sample of ten sacrificed. The remaining 60 were transferred to 64.2cm^2 containers placed in the same water system and maintained under the same conditions as in S1, until 8 weeks old. At this age, due to some mortality, the surviving 37 were randomly assigned to the four treatments of S2. An initial sample estimate was made from carapace length (CL) measurements of a random sample of 15.

From a subsequent brood, 110 juveniles were selected at five days old for the third trial. Of these ten were sacrificed for an initial sample and the remainder assigned to the experimental treatments.

All juveniles were fed daily on fresh mussel (Mytilus edulis) flesh and uneaten food removed the next day. A weekly supplement of Artemia was provided during S2 and S3.

The containers were observed daily between 0900 and 1100h for the presence of cast shells or exuvial fragments. Moult dates were recorded and where possible the CL of cast shells were recorded with a low power binocular microscope.

At the termination of each trial, the CL of survivors was measured before freeze-drying and dry weight analysis.

Results

The size of container had a marked effect on both growth and survival in the first trial with increased growth rate and improved survival in the larger containers. The fastest growth rate, together with 100% survival, was found in the largest container, while in the smallest container, survival was low (60%) and the mean weight of survivors only 66% of those held in the largest containers (Table 1).

Although the best growth and survival was found at 181.5cm^2, there was no statistically significant difference between either measure in the three larger containers (44.2-181.5cm^2). The combination of improved growth and survival in the largest container may, however, represent a real advantage in terms of total yield. Growth and survival in the two smallest containers was poor with lobsters held at 6.6 and 20.4cm^2 significantly smaller than those at 181.5cm^2 and survival significantly worse than at either 85.0 or 181.5cm^2. The effect of container size on the mean CL was the same as that for the dry weight data except for a greater difference between the mean CL of lobsters reared at 44.2 and 85.0cm^2 than between the mean dry weight values.

The percentage survival appeared to be directly related to the container size, but because all the deaths occurred within the space of a few days (at around 7 weeks old) it is probable that the mortalities were not directly attributable to the container size. This is discussed later.

The size of container appeared to affect the growth rate by influencing the moult increment rather than the intermoult period.

There was insufficient data to calculate the actual moult increment for individual lobster ecdyses, but a reliable estimate can be obtained from measurements of mean stage CL, since stage size is directly proportional to the size of the moult increment.

The mean CL of successive stages showed a general increase with container size (Table 2) and at stage 7 (where the most complete stage data was available) lobsters held at 181.5cm^2 were significantly larger than in all other treatments.

There was very little difference between the duration of each stage (Table 3) with less than two days difference between any treatment in the total length of time from stage 4 to stage 7. The larger moult increments were, therefore, not apparently at the expense of lengthened intermoult periods, although at stage 7 there was a slight decrease in intermoult period with container size.

In the second trial, lobsters reared in the largest containers also achieved the highest growth rate, but the dry weight of survivors was not significantly different to that of lobsters held at 85.0 or 181.5cm^2 (Table 4). Growth in the smallest containers was significantly less than in the other treatments.

As in S1 the differences in growth rate were due to differences in the size of the moult increment. Lobsters held at 545.2cm^2 were significantly larger at each stage than those held in the smallest containers, but there was less difference in stage CL between the three larger sizes of container (Table 5). There were no differences between the length of the intermoult periods in the three larger containers, but the duration of stage 8 was extended in the smallest container (Table 6).

There were no deaths during this trial, but a mortality of 62% occurred during the pre-experimental period. These deaths, at an age of seven weeks, coincided with the period of mortality in the first trial. As both groups of animals were from the same parent and were held in the same water system, it is likely that these deaths were caused by toxic substance(s) in either the water or the food supply and not as a direct result of container size. Further evidence for this is that the S2 stock maintained in containers of 64.2cm^2 suffered a higher mortality than those in S1 held at 44.2cm^2. Because of these unexplained mortalities, some doubt was placed on the reliability of the results and a further, more extensive trial, was therefore carried out.

In the third trial juveniles achieved the highest dry weight in the largest containers (181.5cm^2), but yields were only slightly less in the three smaller containers and survival was good throughout (Table 7). A significant reduction in both survival and dry weight was found in the smallest containers, 6.6cm^2. Dry weight and carapace length increased with container size with the exception of lobsters held at 20.4cm^2 that achieved a higher growth rate than those at 44.2cm^2.

Although the container size only marginally affected the final yield, the size of the moult increment was related to the size of container with the mean stage CL increasing with container size (Table 8). The differences were small, but by stage 9, juveniles held at 181.5cm^2 were significantly larger than those held in the smallest containers. The length of the intermoult period in 20.4cm^2 containers, both at individual stages and in the total time from stage 4 to stage 9, was noticeably shorter than all other treatments and accounts for the higher average CL despite reduced moult increment.

This increased frequency of moulting did not result in any improvement in dry weight. Otherwise there was very little difference between the length of the intermoult period (Table 9) apart from a slight increase in larger containers.

There was a greater difference in the effect of container size on survival between the three trials than would be expected from natural variations in juvenile viability. In the first two trials, survival was significantly reduced at a larger container size than in the third trial. The poor survival was probably due to poor quality of water or food and not as a direct result of the experimental treatments, although space restriction undoubtedly provided a further stress in the smaller containers.

The quality of water in the Conwy estuary (and probably also the nutritional value of the locally caught mussels) is known to vary seasonally, and the success of larval rearing at the Conwy laboratory has also shown seasonal variation, and it appears that the growth and survival of juveniles can be affected by seasonal factors (Richards, Beard and Wickins,unpub. data). Good growth and survival is generally achieved during the winter months (December-March), but conditions seem to deteriorate especially during late summer and autumn (July-October). The factors responsible for poor water quality have not been determined, but there is evidence of heavy metal contamination and the toxic by-products of algae blooms.

Differences in juvenile viability can also depend on the conditions experienced during egg incubation and larval development. There is a great variability (in size, frequency of abnormalities, and percent survival to stage 4) in larvae reared within the normal

hatching season of July-September, while controlled incubation to produce larvae at other times, generally results in a low percent survival, but less variability and better quality of fourth stage lobsters. At the same time variation also occurs within each hatch and the larvae that develop fastest tend to be the most viable.

These observations provide a possible explanation for the differences in response found in this study. The first two trials were carried out during the autumn and a high mortality occurred in both S1 and S2 stock. The mortality in S1 was probably compounded by the space restriction, but the average survival of these older juveniles of the batch was still better than that of the younger ones held for the second trial. It is not known whether the poor conditions were confined to the period of mortality or whether some individuals had a greater resistance to an extended period of unfavourable conditions.

The lower response of juveniles to reduced space in the third trial (the following February) could have been due to better water quality coupled with stronger experimental stock that survived well, except under the most severe space restriction and on this basis the results from S1 and S2 probably represent a more practical estimate of the effects of reduced space. The response observed in S3 may represent a minimum area requirement under otherwise favourable conditions but despite the different absolute values in response, a number of general conclusions can be made on the effect of container size.

In each trial, best survival and weight gain was achieved in the largest containers. There was no significant reduction in yield in the intermediate sizes of container, although the smallest

containers were clearly unsuitable. Furthermore, the mean stage CL showed a clear relation to container size while the length of the intermoult period was generally unaffected.

In order to illustrate the quantitative effects of container size and to compare the results of the three trials, a relationship was established between the area of the container (A) and the mean total length of the lobster (TL) at the end of each trial. The TL is not as accurate a measure of growth as dry weight, but it is a more realistic parameter to relate to container size. The mean TL was estimated from the mean CL in each trial using the equation TL(mm) = 2.82 CL(mm) + 4.03. This relationship was determined at Conwy from measurements taken of other cultured lobsters and has proved accurate for estimating the TL of lobsters up to 80mm CL.

A convenient form of the relation between TL and A was $A = (aTL)^2$ where the constant 'a' can be referred to as the 'space factor'. The appropriate values of a for each treatment together with the mean yields are shown in Table 10, and depicted graphically in Figure 1. The mean yield used in this example is the total dry weight of survivors divided by the initial number of lobsters in each treatment.

In the first trial the mean yield increased with 'a' up to a value of 4.2 with no apparent asymptote. The poor survival did, however, strongly influence the mean yield. Only where $a \leqslant 1.6$ was the growth of surviving lobsters significantly reduced in comparison to the largest containers. In the second trial there was no significant difference in the yield at values of a from 2.2-5.5, but at 1.8 growth was significantly reduced. In the third trial good growth and survival

occurred at values as low as 1.2 with a marked reduction only occurring when a ≈ 0.8.

These figures show that significant improvements in yield are unlikely to be achieved in containers where 'a' is greater than 2.0, while under certain circumstances there may be a reduced space requirement. Nevertheless, although acceptable yields were achieved in smaller containers, especially in the third trial, the effect of container size on the moult increment may be important in the long term. To illustrate this, the number of moults required to reach a CL of 80mm was estimated from the relationship between the premoult and postmoult CL data of the third trial. These estimates (Table 11) show that small differences in moult increment could result in a difference of several stages at 80mm CL. If the intermoult period remain unaffected, then a reduction in the number of moults to market size and shorter culture period would have considerable economic advantages and might justify the increased costs of larger containers.

Table 1 Mean dry weight, carapace length and percentage survival of juveniles cultured for six weeks in different sizes of container.

Container size (cm^2)	Dry wt (mg)	CL (mm)	Survival (%)
6.6	85.7 ± 14.9	8.60 ± 0.32	60
20.4	99.3 ± 16.3	8.69 ± 0.43	60
44.2	112.4 ± 24.0	9.05 ± 0.58	80
85.0	113.1 ± 11.3	9.72 ± 0.62	93.3
181.5	129.6 ± 13.2	9.97 ± 0.53	100
Initial sample	20.95 ± 5.14	4.92 ± 0.38	

Table 2 Carapace length (mm) of successive moult stages of juveniles reared in different sizes of container.

Container size (cm^2)	Stage 5	6	7	8
6.6	6.00 ± 0.29	7.18 ± 0.11	8.57 ± 0.20	9.17
20.4	6.17 ± 0.33	7.46 ± 0.27	8.75 ± 0.31	9.75
44.2	5.77 ± 0.46	7.35 ± 0.29	8.61 ± 0.36	10.42 ± 1.01
85.0	6.11 ± 0.24	7.19 ± 0.72	8.81 ± 0.76	10.76 ± 0.63
181.5	6.16 ± 0.26	7.49 ± 0.26	9.24 ± 0.26	10.82 ± 0.46

Table 3 Duration (days) of each moult stage of juveniles reared in different sizes of container.

Container size (cm^2)	Stage 5	6	7	St. 4 - 7
6.6	13.2 ± 1.5	13.9 ± 1.0	16.0	41.2 ± 2.9
20.4	14.0 ± 1.8	13.4 ± 1.3	-	39.0 ± 2.8
44.2	15.4 ± 2.2	13.9 ± 1.3	15.3 ± 1.1	40.0 ± 4.0
85.0	13.3 ± 1.3	13.2 ± 2.4	16.1 ± 0.7	39.1 ± 2.7
181.5	12.50± 1.1	13.0 ± 1.5	16.6 ± 1.0	39.4 ± 2.4

Table 4 Mean dry weight, carapace length and percentage survival of juveniles cultured for eight weeks in different sizes of container.

Container size (cm^2)	Dry wt. (mg)	CL (mm)	Survival (%)
44.2	236.9 ± 27.4	11.52 ± 0.56	100
85.0	338.0 ± 37.3	13.23 ± 0.49	100
181.5	318.0 ± 49.6	13.00 ± 0.63	100
545.2	371.1 ± 64.3	13.62 ± 0.79	100
Initial sample	-	8.32 ± 0.23	

Table 5 Carapace length (mm) of successive moult stages of juveniles reared in different sizes of container.

Container size (cm^2)	Stage 7	8	9	10
44.2	7.99 ± 0.38	9.37 ± 0.51	10.80 ± 0.65	12.33 ± 3.59
85.0	8.40 ± 0.42	9.74 ± 0.28	11.37 ± 0.41	13.39 ± 0.38
181.5	8.48 ± 0.60	9.95 ± 0.51	11.66 ± 0.50	13.15 ± 0.78
545.2	8.34 ± 0.15	9.77 ± 0.21	11.75 ± 0.30	13.89 ± 0.57

Table 6 Duration (days) of each moult stage of juveniles reared in different sizes of container.

Container size	Stage 8	9	Mean period between stage 8 and stage 10.
44.2	22.2 ± 2.4	21.0 ± 3.4	45.0 ± 6.35
85.0	20.0 ± 2.0	21.8 ± 1.8	41.0 ± 3.42
181.5	18.9 ± 3.5	21.3 ± 2.2	39.8 ± 6.77
545.2	19.6 ± 1.8	21.3 ± 1.0	40.3 ± 2.25

Table 7 Mean dry weight, carapace length and percentage survival of juveniles cultured for 12 weeks in different sizes of container.

Container size (cm^2)	Dry wt. (mg)	CL (mm)	Survival (%)
6.6	178.5 ± 49.2	10.23 ± 0.75	40
20.4	282.9 ± 22.1	12.41 ± 0.52	100
44.2	278.9 ± 16.8	12.02 ± 0.38	100
85.0	291.6 ± 19.9	12.29 ± 0.38	95
181.5	310.0 ± 26.3	12.64 ± 0.41	100
Initial sample	11.97 ± 3.4	4.59 ± 0.19	

Table 8 Carapace length (mm) of successive moult stages of juveniles reared in different sizes of container.

Container size (cm^2)	Stage 5	6	7	8	9	10
6.6	5.59±0.21	6.62±0.17	7.95±0.18	9.51±0.22	10.45±0.75	-
20.4	5.47±0.24	6.93±0.39	8.43±0.55	10.17±0.39	11.78±0.34	13.51±0.77
44.2	5.59±0.13	7.13±0.35	8.61±0.28	10.27±0.26	11.83±0.29	13.59±0.37
85.0	5.55±0.25	6.75±0.43	8.67±0.50	10.44±0.33	12.03±0.34	13.59±3.92
181.5	5.73±0.20	7.19±0.41	8.84±0.42	10.69±0.30	12.44±0.33	14.09±1.44

Table 9 Duration (days) of each moult stage of juveniles reared in different sizes of container.

Container size (cm^2)	Stage 5	6	7	8	9
6.6	11.01±1.1	12.3±0.9	16.4±1.5	20.3±2.9	-
20.4	10.6 ±0.4	12.4±0.4	15.3±0.7	19.2±0.9	20.4±0.9
44.2	10.5 ±0.4	12.9±0.4	15.8±1.0	19.2±0.7	21.0
85.0	10.9 ±0.4	12.8±0.8	15.6±0.8	19.5±0.9	21.0±4.3
181.5	10.5 ±0.4	13.1±0.8	16.1±0.8	19.8±2.0	22.5±10.7

Mean period (days) between stage 4 and stage 9.

Container size (cm^2)	
6.6	72.0 ± 6.5
20.4	67.8 ± 1.5
44.2	71.2 ± 1.8
85.0	70.9 ± 3.4
181.5	72.2 ± 2.8

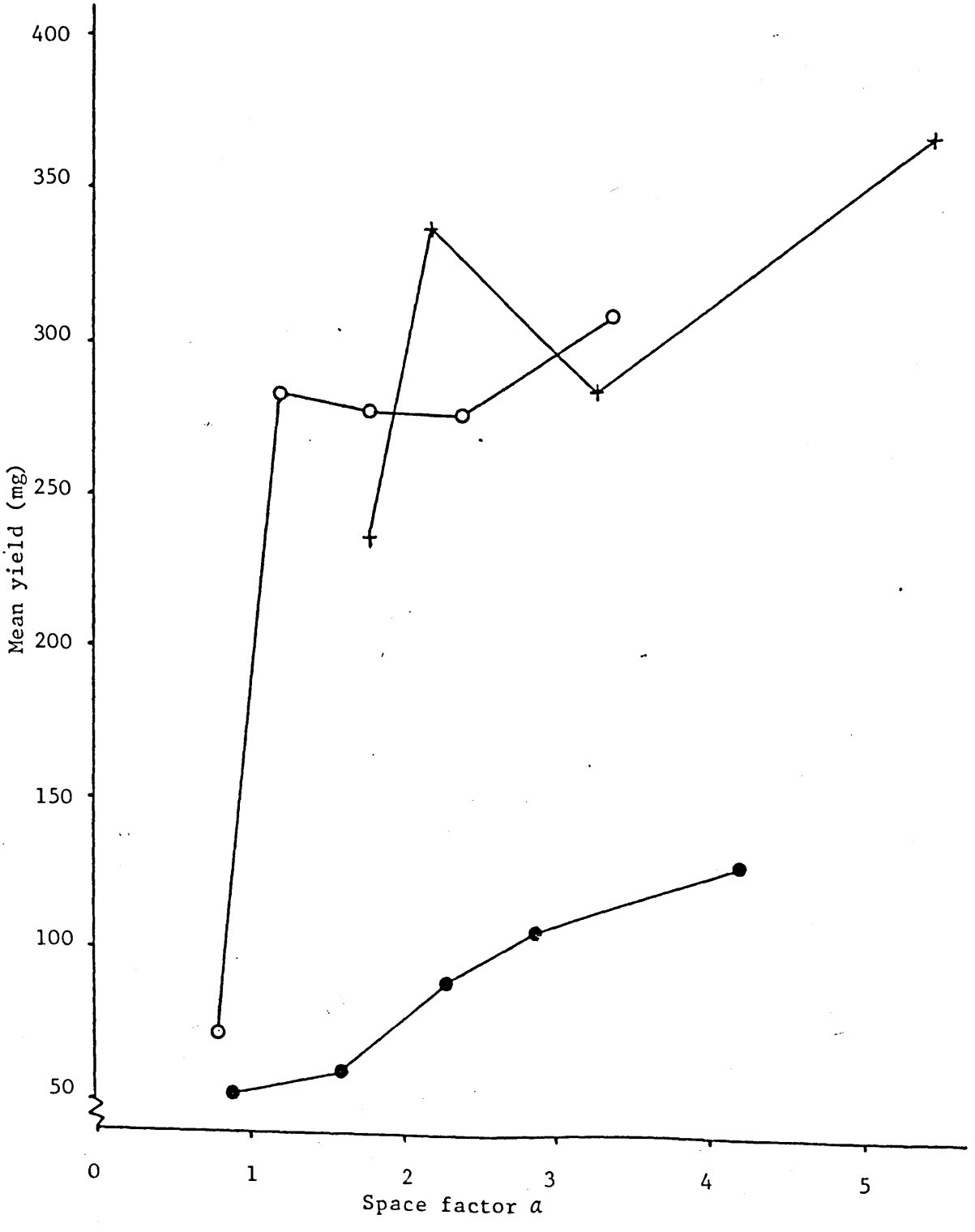
Table 10 Estimation of the space factor 'a' from the relationship between the floor area of containers and the mean total length of surviving lobsters, with the appropriate mean yields.

Container area (cm^2)		Mean total length (cm)	Space factor a	Mean yield (mg)
S1	6.6	2.8	0.9	51.4
	20.4	2.9	1.6	59.6
	44.2	3.0	2.3	89.9
	85.0	3.1	2.9	105.6
	181.5	3.2	4.2	129.6
S2	44.2	3.7	1.8	236.9
	85.0	4.1	2.2	338.0
	181.5	4.1	3.3	286.2
	545.2	4.2	5.5	371.1
S3	6.6	3.3	0.8	71.4
	20.4	3.9	1.2	282.9
	44.2	3.8	1.8	278.9
	85.0	3.9	2.4	277.0
	181.5	4.0	3.4	310.0

Table 11 Effect of container size on moult increment - estimate of moult stage at CL of 80mm from data obtained in the third trial.

Space factor of container size a	Regression equation of size increase at moult	Estimate of stage at 80mm CL
1.2	$CL_{n+1} = 1.059\ CL_n + 1.076$	35
1.8	$CL_{n+1} = 1.027\ CL_n + 1.462$	30
2.4	$CL_{n+1} = 1.077\ CL_n + 1.071$	26
3.4	$CL_{n+1} = 1.092\ CL_n + 0.963$	25

Figure 1. Mean yield of juvenile lobsters cultured in different sizes of container, the floor area represented by the value of a in the $(aTL)^2$ relationship. Closed circles S1, crosses S2, open circles S3.



Discussion

The effect of container size on the growth and survival of juvenile lobsters is most important in the design of intensive lobster culture systems which require suitable containers for rearing large numbers of individually held animals. An optimum container size is based upon a maximum growth rate at minimum cost, but the use of containers large enough to allow unrestricted growth will result in an extensive and therefore costly culture system due to the high cost of land, materials, and water heating. For this reason the choice of container size in a commercial system would be based on an economic balance between the lower capital costs of a small container system, and the higher running costs which would result from the slower growth rate. In a laboratory system, the cost is not the most important consideration but space is still a limiting resource. An optimum container might be one in which a small but predictable decrease in the growth rate could be expected without affecting survival.

The area required for unrestricted growth of H. gammarus cannot be determined from this study because the highest yield was found in the largest container tested. Nevertheless, the relationship between the space factor 'a' and the mean yield (Figure 1) showed that as the value of 'a' increased, small increases in yield were only achieved by relatively large increases in container size. The point where the rate of yield increase begins to decline indicates a suitable optimum value. The three trials gave two different estimates, which were $(1TL)^2$ and $(2TL)^2$, with the larger estimate being of more practical value. Containers of $(2TL)^2$ have been used as a basis for the design of a pilot scale culture system

at Conwy (Richards and Wickins, 1979), but a number of units of $(1.4TL)^2$ also used in the system have proved quite adequate (unpub.data).

A number of studies have been made on the space requirements of H. americanus, and for comparative purposes the various sizes of container used have been converted to the $(aTL)^2$ form. This was calculated by converting the published CL measurements to a TL value using the equation derived by Wilder (1953).

In the juvenile, growth is significantly reduced at less than $(2.14TL)^2$ while $(1.47TL)^2$ conferred no advantage (Shleser, 1974). Similar work by Van Olst et al., (1976) provided an estimate of $(4TL)^2$ for unrestricted growth, with significant reductions at less than $(2.4TL)^2$. Studies on wild caught juveniles of 50-60mm CL indicated an unrestricted area of $(3TL)^2$ and 'acceptable' space factor of 2.55 (Aiken and Waddy, 1978).

In all the above studies, the growth rate was affected before survival was appreciably reduced. Van Olst and Carlberg (1978) have since reported that survival among juveniles can be reduced before the growth rate. A mortality of 10% was recorded when the average CL (mm) was equal to 12 + (1.7 x container width cm). This is equivalent to a floor area of $(0.99\ TL)^2$ and the authors suggested that this value might be the main criteria in determining container size. In the absence of a definitive optimum value for the American lobster, $(2TL)^2$ remains the most commonly used size (Van Olst and Carlberg, 1979).

The limiting parameter of container size is generally taken to be the total floor area. Shleser (1974) found no difference in juvenile growth in either rectangular, square or circular containers

of the same area. This has been confirmed by Van Olst and Carlberg (1978) who also showed that the shortest dimension was a critical factor. The presence of corners does appear to be a beneficial design feature for lobsters invariably sit in the corners, presumably due to a sense of security (pers.obs.). Visual contact does not seem to be important, because opaque walls confer no advantage over transparent walled containers (Van Olst and Carlberg, 1978).

The lobster is the only marine animal cultured in individual containers on a routine basis, so there is a lack of comparable quantitative date for other species. The appropriate stocking density for groups of animals is usually more important, but although the amount of individual space is a determinant factor in stocking density, the effect of this cannot easily be distinguished from other limitations arising from intraspecific interactions.

Adult H. americanus has been reported to grow slower under communal conditions (McLeese, 1972; Stewart and Squires, 1968) but this was probably the result of excessive crowding rather than a direct effect of communal conditions. Aiken and Waddy (1978) found no difference between the growth of large juvenile animals held individually or in pairs, when the same area was provided for each individual, but in the fourth stage juvenile, only the dominant of the pair grows as fast as individually reared controls (Cobb, 1970). During subsequent juvenile growth, the dominant continues to grow faster than the subordinate, but by stage 11 the dominant is not as large as individually held controls (Cobb and Tamm, 1974), and the reduced growth of subordinates is due to prolonged intermoult

periods although the size increment at moult was not stated. The authors concluded that moult delay was a general response to 'communal conditions'.

The contrasting results obtained by Cobb and Tamm (1974) and Aiken and Waddy (1978) may be the result of changes in behaviour with age, for smaller juveniles do have different habits to the adult. Juvenile H. gammarus less than 40mm CL are rarely recorded in the wild either from baited traps or scientific sampling (Howard and Bennett, 1979), and extensive SCUBA studies made in the USA (Pecci et al., 1978) have also shown that juvenile lobsters spend almost the entire time with a tunnel system or shelter, and only become nocturnally active outside the limits of the refuge at a CL of more than 45mm.

Experiments on communal rearing in the USA have shown that under optimum conditions growth rates may be comparable to those achieved in individual culture. A yield of 40 lobsters.m^{-2} with a mean CL of 20mm after six months growth has been achieved from an initial stocking density of 100.m^{-2} (Van Olst and Carlberg, 1979), which is equivalent to an area per individual at 6 months old of $(2.7TL)^2$. A typical size for individually reared animals at the same age is around 23mm CL (Hedgecock, Nelson and Shleser, 1976), although less space is required $(1.13TL)^2$ because cannibalism is avoided.

Although a larger area is needed in communal conditions, the high stocking densities that can be achieved indicate that the lobster is not such a solitary and aggressive animal as is generally believed. Inhibition of growth has been observed in other solitary species held under communal conditions, such as Geocarcinus (Bliss

and Boyer, 1964) and Diogenes (Rossi, 1971), while more typically gregarious species show reduced growth when reared in isolation. These include Panulirus (Chittleborough, 1976), Carcinus (Klein-Breteler, 1975a) and Cancer (Anderson and Ford, 1976).

Studies designed to observe the natural distribution of lobsters have been inconclusive. Cobb (1969) showed that adult lobsters tended to avoid occupied shelters, but there was no definite spacing. This result, taken in conjunction with underwater observations suggested that lobster distribution was mainly dependent on the distribution of suitable hiding places, rather than on any self regulating density mechanism. Lobsters have been frequently observed sharing shelters, and as many as 35% of available refuges or artificial reefs may be shared by one or more individuals (Sheehy,1976). Shelter sharing is, however, usually between individuals of disparate size, and large lobsters only disperse randomly when shelters are more than 2.4m apart (Anon, 1974). An exception to this is shelter sharing during the pair formation associated with mating (Atema et al., 1979). From these and other similar studies, Cooper and Uzmann (1980) have concluded that lobsters in the wild are rarely aggressive except when determining dominance status.

Behavioural studies may help to explain space requirements. In Pagurus there is a relation between the onset of agonistic behaviour and the distance separating competitors. On average, agonistic acts begin when competitors are within 6.3cm, and this distance increases with the size of the individual (Hazlett, 1979). Restriction of personal space is more likely to be the reason for reduced growth in small containers, rather than any territorial demands, because

personal space is an individual requirement, whereas territorial behaviour involves the social structure of interacting individuals. It may in fact be wrong to class lobster interactions as part of a dominance heirarchy and an 'aggressive order' based on size and aggression may be a better term because a dominance heirarchy is properly the result of interactions within a group.

The extent to which lobsters adapt to unfavourable living conditions in the natural environment is not known, but reduced growth has been recorded in other crustaceans. Flint and Goldman (1977) found that the size of crayfish was related to the amount of stone cover and hiding places, and because differences in size occurred within age classes the moult increment was probably affected. Larger moult increments have also been reported for Jasus found on 'better' grounds (Newman and Pollock, 1974), while Chittleborough (1976) observed poorer growth in Panulirus from areas with a high population density.

These observations cannot be confidently attributed to space effects because food availability will also vary, but the reduction in moult increment found in H. gammarus under restricted conditions indicates a similar response may occur in the wild. Reduction in the moult increment was the main response of large juvenile H. americanus held in small containers (Aiken and Waddy, 1978), while in younger juveniles, the intermoult period was also affected, but not to the same extent as the moult increment (Van Olst and Carlberg, 1978). Hermit crabs show a similar response when restricted in the choice of shell size with a reduction in the moult increment while the intermoult period remains unchanged (Fotheringham, 1976).

Although the mechanisms underlying the responses of lobsters to restricted or crowded conditions are not understood, the effects are probably similar to those observed in many other vertebrate species, where crowded conditions can give rise to behavioural and metabolic disorders, the symptoms of stress. There are many examples of growth inhibition among captive vertebrate animals, including the classic experiments on goldfish and tadpoles held in small containers, and the effects on growth seem to be associated with the regulation of population density in the natural environment, for reproductive success also varies with the suitability of the environmental conditions (see for example Wynne-Edwards, 1962). In the lobster, as in other invertebrates, effects on the growth rate are the most overt signs of stressful conditions, providing that there are no other obvious limiting factors such as temperature, oxygen, or food supply. Lobsters held under restricted conditions do exhibit one of the general symptoms of stress, hyperglycaemia (Telford, 1968), and although the role of adrenalin has not been identified, adrenalin does excite crustacean hearts, as do aqueous extracts of brain and eyestalks (Passano,1960). Further work is necessary before it can be established whether stress reactions exert an influence over the hormones controlling the moult cycle.

Summary.

1. Juvenile lobsters were reared in a number of different sized containers to observe the effect of floor area on growth and survival up to three months old.

2. The growth rate increased with container size from the smallest ($6.6cm^2$) to the largest ($545.2cm^2$). The smallest containers significantly reduced both growth and survival, but the largest containers did not give rise to significant improvements in yield.

3. An optimum container size for juvenile culture was established based on the relationship between the floor area and the average TL of juveniles at three months old. The results from two trials indicated an optimum value of $(2TL)^2$, while $(1TL)^2$ was found adequate in a further trial. Differences in the vigour of the experimental stock and in the quality of the water or food supply were probably responsible for the difference in the two estimates.

4. The growth rate was influenced mainly by effects on the size of the moult increment, which increased with the size of container.

5. The implication of these results is discussed in relation to the economics of intensive lobster culture, and to other examples of growth inhibition under restricted conditions arising from space limitation or crowding.

SECTION 2.3

THE EFFECT OF LIGHTING CONDITIONS ON THE GROWTH AND SURVIVAL OF JUVENILE LOBSTERS

Introduction

The daily and seasonal changes in photoperiod and light intensity are conspicuous features of the natural environment of most animals. The amount of variation to which crustaceans are exposed depends on the nature of the habitat, especially depth of aquatic species, but even so the behaviour patterns of most species, particularly those of locomotor and feeding activity, are closely linked to the circadian cycle of illumination.

Physiological processes are usually affected indirectly by the influence of light quality and quantity on the levels of other environmental variables, such as temperature and food supply, but there is evidence that light can directly effect development. Photoperiodism may be important in the regulation of seasonal moulting which is common among the larger temperate and arctic species, particularly in adult individuals. Wild caught Orconectes can be induced to moult in the autumn by providing 'long day' photoperiods (Aiken, 1969), while 'short days' accelerate ovarian growth and nutrient accumulation (Armitage, Buikema and Williems, 1973). A seasonal influence over the initiation of ecdysis has also been found in H.americanus (Aiken and Waddy, 1976). Lobsters held at $10^{o}C$ under a natural light dark regime (nLD) showed faster premoult development in the summer months (May to August) than in the winter months (October to March) and the regulatory centre for this seasonal effect seemed to be in the eyestalks.

A photoperiodic mechanism would be of adaptive value to the individual in maintaining an appropriate timing relationship with the seasonal activities of moulting and reproduction, but the same effect could be achieved by responses to changes in other seasonally variable factors. In order to establish the

importance of light alone, long term studies are required to monitor the development under nLD regimes, under otherwise constant conditions.

In con trast to the seasonal changes in photoperiod, daily cycles of illumination have a more direct effect on growth and survival. This is a result of the behavioural responses which are mainly determined by the prevailing conditions, although in many species the presence of an endogenous component can be demonstrated (see for example Allen, 1972). The regular changes in illumination tend to result in rhythmic patterns of circadian behaviour such as locomotor activity, and each species has a basic pattern that helps it to successfully occupy a particular niche. At the same time the behaviour pattern effectively limits the potential for development by restricting the time spent in such activities as habitat selection and foraging for food. It is, therefore, possible that growth could be enhanced by manipulation of the lighting conditions to provide continually 'favourable' conditions. This will depend on the nature of the underlying physiological processes responsible for the expression of normal rhythmic behaviour, for light regimes different to that of the normal circadian organisation could cause metabolic dysphasia.

Among the existing literature, examples can be found of beneficial effects arising under a variety of artificial light regimes (aLD), although differences in experimental technique and stock origin probably account for as much of the variation as do basic differences in the response of each species. Long day photoperiods of 16 or more hours light enhance growth in Orconectes (Armitage et al., 1973) and adult H.americanus (Aiken and Waddy, 1976), while short days with eight or less hours of light are most favourable for Carcinus (Adelung, 1971) and Faxonella (Mobberly, 1963). Growth seems to be generally inhibited by constant illumination (LL) except in those species where photoperiod has little or no effect, e.g. Palaemon paucidens De Haan (Kamiguchi, 1971), Ocypode (Rao, 1965) and Panulirus (Chittleborough, 1975).

Constant darkness (DD) is unfavourable in Panulirus, but beneficial for the growth of Camaroides (Kurata, 1962), Penaeus duorarum Burkenroad (Bishop, 1970) and juvenile H. americanus (Cobb, 1969). Studies on Palaemon serratus Pennant emphasise the effect of stock origin on the response to light regime. Reeve (1969) found that nLD was most suitable for the larval stages, laboratory reared juveniles grew best under DD (Forster, 1970), and wild caught specimens responded most favourably to long day photoperiods (Van Wormhoudt and Ceccaldi, 1975).

Non circadian light regimes other than 6:6LD, LL and DD have been rarely investigated, although recent observations on Palaemon elegans Rathke showed that random or 8:8 LD light regimes only depressed growth (in comparison with 12:12LD) in the short term (Dalley, 1980).

The results of these studies indicates that the development of H. gammarus may also be affected by the lighting conditions, and that the growth rate might be enhanced by the choice of a suitable light regime. In the following experiments this was investigated by recording the growth and survival of juvenile lobsters reared under a selection of lighting conditions.

Observations were also made on the effect of light intensity.

Materials and methods

Two trials were carried out in which juvenile lobsters were reared for 12 weeks under the following lighting conditions:

	Light regime		Light intensity (lux)	
1.	Continuous illumination	(LL)	340	
	12:12 Light-dark	(LD)	340	(0800-2000h)
	Continual darkness	(DD)	<1	
	nLD (sunrise to sunset) at midpoint of trial		16:8	
2.	LL		5	
	LL		220	
	18:6 LD		5	(0800-0200h)
	18:6 LD		220	
	6:18 LD		5	(0800-1400h)
	6:18 LD		220	" "
	DD		<1	
	nLD at mid point of trial		12:12	

Experimental stock for each trial were obtained from the progeny of a separate wild caught ovigerous female and the larvae reared to the fourth stage by the mass culture techniques described in Section 1. At this stage lobsters were transferred to individual 25cm^2 containers held in shallow fibreglass trays with water circulated to each container by a siphon device. A temperature of 20 $\pm$ 1^{o}C was maintained throughout by air heating of the building, ambient salinity seawater was used (30 - 34 ppt), and 25% of the system volume was replaced twice each week. Juveniles were fed daily on the fresh mantle tissue of Mytilus edulis with a weekly supplement of frozen Artemia.

When juveniles attained the fifth stage suitable individuals were selected (Section 1) and transferred to individual containers of either 64cm^2 (Trial 1) or 115cm^2 (Trial 2). These containers were placed in shallow fibreglass trays

inside separate lightproof boxes with photoperiod and light intensity control. In each trial all treatments held a common water supply.

Experimental stock were kept until approximately halfway through the fifth stage under a nLD regime supplemented with normal laboratory lighting (maximum intensity 300 lux). Initial samples were then taken for analysis and the remainder randomly assigned to the experimental treatments, 20 per treatment in Trial 1 and 24 per treatment in Trial 2. For the following 12 week experimental period, illumination was provided by either 25w or 100w incandescent bulbs arranged to provide uniform illumination at the water surface, and the light intensity adjusted by rheostat controls.

Juveniles were fed each day between 1000 and 1200h an amount of food slightly in excess of the daily requirement and uneaten food removed. At the same time the size of cast shells was measured and dead animals removed. All observations were made using a torch fitted with a Kodak No.25 Wratten gelatin filter. This light was expected to produce negligible disturbance to lobsters at the transmitted wavelength of $>$590nm (Kampa, Abbot and Boden, 1963).

At the end of each experiment the carapace length (CL) of all survivors was measured and the weight recorded after freeze-drying. In addition, the wet weight of juveniles in the first trial was recorded after six and nine weeks (which corresponded to the age at stage 8 and stage 9). An estimate of the food consumption was made during Trial 1 by recording the amount of food eaten during the eighth stage from a sample of 15 lobsters in each treatment, to allow comparison between individuals of similar size and moult stage. As each juvenile moulted into stage 8, weighed portions of mussel flesh in slight excess of the daily requirement were provided each day, and this was continued until each individual moulted into stage 9. The amount consumed was calculated from the weight of food uneaten the following day, after correction for the loss in weight due to decomposition and leaching. This 'wastage' was estimated from several trials to be equivalent to a loss in weight of 25% over a 24h period.

Results

In the first trial the best growth was found under DD (Table 1), but the differences between treatment means for dry weight and CL of survivors were not statistically significant. Constant illumination was clearly the best condition in terms of total yield of survivors, giving a 20% increase over DD and twice the yield of LD. The differences in yield reflected survival rates which were poor in all treatments and significantly worse ($p<0.05$) in LD compared to that in LL. The poor survival was mainly due to a high mortality during stage 9 and was probably not directly attributable to the experimental light regimes. Of the mortalities, 89% of those in DD died during stage 9, 85% of those in LD and 62% of those in LL. A group of 20 juveniles held for other purposes in the same water system also suffered a mortality of 71% during the same period and these individuals were exposed to a nLD photoperiod. Treatments did, however, differentially affect survival for the highest mortality in LD was associated with the poorest growth rate, although the growth rate in all treatments seemed to be retarded around the period of mortality (Figure 1). Seasonal variation in water quality was thought to be responsible for these cases of high mortality (see Section 2.2).

The observed differences in the growth rate were not apparently due to variation in the duration of the intermoult periods, but rather to an effect on the average stage size, and thus on the size of the moult increment (Table 2). There were no marked treatment differences between the length of the intermoult period up to stage 8, and the total times to stage 9 were very similar. There was a greater difference in the duration of the ninth stage, but this was mainly due to a small sample size.

The average stage size increased in proportion to the dry weight of survivors, and lobsters held under DD were significantly larger at stage 9 than in the other treatments. Differences at stage 10 were less marked due to a small

sample size which arose because few individuals had moulted into the tenth stage by the end of the trial and the values for duration of stage 9 and CL of stage 10 were, therefore, unrepresentative of the population mean. The smaller individuals with shorter intermoult periods are generally the first to moult

Food consumption. The total weight of food consumed by juveniles in each treatment was used to obtain an estimate of the food conversion rate (FCR), and this was calculated from the total weight increase of the sampled individuals from stage 8 to 9. Only an indirect estimate of FCR could be made because the difference in weight between one stage and the next is not truly a measure of the amount of tissue growth during the previous intermoult period. The measures and estimates shown in Table 3 can, however, be used for between treatment comparisons.

Lobsters consumed a greater total quantity of food under DD, and put on more weight than in the other treatments. In LL the weight gain was only slightly reduced, but this was achieved at the lowest level of food intake. As the sizes of the lobsters under LL and LD were very similar, the lower food consumption under LL was due to a lower daily intake as percentage of body weight. The larger animals in DD consumed a smaller proportion of food each day in terms of % body weight.d^{-1}, than those under LD.

These factors are the reason for differences in the FCR, where a good FCR resulted from a higher weight gain in DD, and lower daily food intake in LL. The poor FCR in LD was the result of both a high daily intake and low weight increase.

Despite the limited scope of these observations, the differences in food consumption provided further evidence that the light regime exerted a real influence over the growth of juvenile lobsters. Even so, the high mortality in all treatments placed some doubt on the reliability of the results and a further trial was carried out with a more extensive array of treatments.

In the second trial, survival was over 90% in all treatments, only five lobsters died out of a total of 168, and the average growth rate was better than that in the first trial. The fastest growth rate was recorded in juveniles held under low intensity constant illumination LL(L) (photoperiod abbreviations are followed by a L (5 lux) or H (220 lux) to indicate the light intensity). DD was only slightly less favourable, but the high light intensity regimes all gave poor growth (Table 4). The treatment effects were more pronounced in this trial and the differences between treatment mean for dry weight were, in most cases, statistically distinguishable (Table 5).

The mean yield showed a general decline with increases in both length of photophase and light intensity and thus with the total quantity of light received each day. This is graphically represented in Figure 2 where a relationship between the mean dry weight and the quantity of light (lux - hours) is indicated from the fit between the calculated regression line and the observed values. The LL(L) treatment was an exception, for a better yield was achieved under this condition than under a similar quantity of light in a light-dark cycle.

Significant treatment effects were observed on both intermoult period and stage size, but the higher growth rates were more closely associated with large stage size (and, therefore, on larger moult increments) than with short intermoult periods (Table 6). By the 10th stage lobsters held under LL(L) were significantly larger ($p < 0.05$) than all the other treatments except DD, although the average carapace length was only slightly less in 6:18(L).

There was less between treatment variation in the length of the intermoult periods, with a maximum of only 2.4 days difference in the average duration of stage 9 between the best and worst treatment. Despite this, the length of the intermoult period in LL(L) was significantly less than in all the

other treatments except DD and, notably, LL(H), whilst 6:18(L) was significantly worse than the top ranked treatments. Some conditions may, therefore, favour a higher moult frequency, resulting from shorter intermoult periods, without enhancing the overall growth rate.

Table 1. Mean dry weight and carapace length of survivors, percent survival and total yield of juveniles cultured for 12 weeks under different light schedules.

Treatment	Dry weight (mg)	Carapace length (mm)	Survival (%)	Yield (mg)
LL	348.6 ± 30.5	13.07 ± 0.39	70	4880.4
LD	338.8 ± 56.9	13.13 ± 0.73	35	2371.6
DD	369.9 ± 38.9	13.57 ± 0.44	55	4068.9
Initial sample	23.9 2.0	5.06 0.12		

Table 2. Carapace length (mm) of successive moult stages of juveniles cultured under different light schedules.

Treatment	Stage 5	6	7
LL	5.96 ± 0.04	7.27 ± 0.31	8.83 ± 0.19
LD	6.05 ± 0.09	7.34 ± 2.07	8.68 ± 0.19
DD	6.09 ± 0.36	7.67 ± 0	8.91 ± 0.22

	8	9	10
LL	10.38 ± 0.17	11.84 ± 0.23	13.16 ± 0.38
LD	10.29 ± 0.22	11.76 ± 0.24	13.13 ± 0.73
DD	10.76 ± 0.26	12.43 ± 0.32	13.66 ± 0.42

Duration (days) of successive stages.

	5	6	7	8	9
LL	10.1 ± 0.6	11.3 ± 0.6	14.2 ± 0.5	16.6 ± 1.18	17.8 ± 1.26
LD	9.9 ± 0.3	11.3 ± 0.7	13.2 ± 0.4	16.7 ± 0.6	19.9 ± 1.0
DD	8.9 ± 0.3	10.5 ± 0.8	13.0 ± 0.9	16.8 ± 0.6	19.9 ± 1.3

Mean time (days) from stage 4 to stage 9.

LL	51.9 ± 1.9
LD	52.3 ± 1.8
DD	49.9 ± 1.3

Figure 1. Growth of juvenile lobsters reared under three light regimes, closed circles DD; open circles LL; crosses LD. Note growth rate decline after 8 weeks and mean age at death of 9.5 weeks.

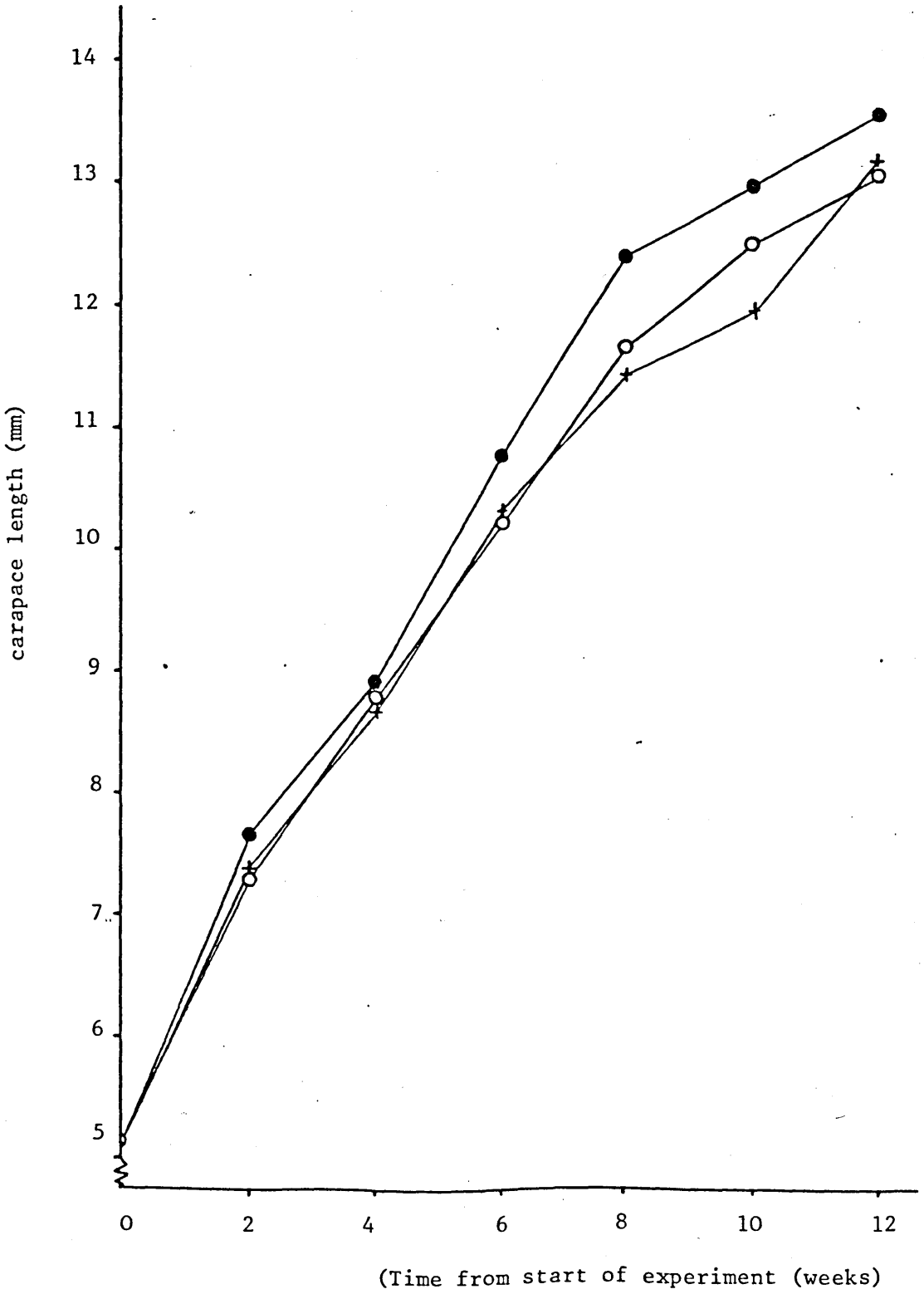


Table 3. Mean wet weight of selected juveniles at the beginning and end of food consumption study.

Treatment	Wet wt. stage 8 (g)	Wet wt. stage 9 (g)	Duration of stage 8 (days)
LL	0.59 ± 0.03	0.90 ± 0.06	16.9 ± 0.9
LD	0.62 ± 0.05	0.89 ± 0.07	16.4 ± 0.07
DD	0.67 ± 0.05	0.99 ± 0.07	16.7 ± 0.6

Food consumption and weight increase of selected juveniles cultured under different light schedules.

	Total food consumption during stage 8 (g)	%bw.day^{-1}	Wt. increase 8-9 (g)	FCR
LL	20.86	13.9	4.65	4.5:1
LD	22.97	15.1	4.05	5.7:1
DD	24.26	14.4	4.95	4.9:1

Table 4. Mean dry weight, carapace length and percent survival of juveniles cultured for 12 weeks under different combinations of photoperiod and light intensity.

Treatment	Dry weight (mg)	Carapace length (mm)	Survival (%)
LL (H)	408.5 ± 51.7	14.44 ± 0.55	92
LL (L)	519.7 ± 22.6	15.69 ± 0.53	92
18:6 (H)	359.9 ± 20.8	13.40 ± 0.41	100
18:6 (L)	435.5 ± 29.2	14.03 ± 0.54	96
6:18 (H)	414.3 ± 27.9	14.07 ± 0.44	100
6:18 (L)	465.4 ± 25.6	14.46 ± 0.45	100
DD	512.2 ± 34.3	15.41 ± 0.49	100
Initial sample	28.5 ± 1.5	5.75 ± 0.12	

Table 5. Results of significance tests between treatment dry weight means of juveniles cultured under different combinations of photoperiod and light intensity.

Ranked treatments	LL (L)	DD	6:18(L)	18:6(L)	6:18(H)	LL(H)
LL(L)						
DD	NS					
6:18 (L)	$p<0.05$	$p<0.05$				
18:6 (L)	$p<0.01$	$p<0.05$	NS			
6:18 (H)	$p<0.01$	$p<0.01$	$p<0.05$	NS		
LL (H)	$p<0.01$	$p<0.05$	$p<0.05$	NS	NS	
18:6 (H)	$p<0.01$	$p<0.01$	$p<0.01$	$p<0.01$	$p<0.05$	NS

Figure 2. A relationship between the quantity of light received each day and the mean dry weight of juvenile lobsters after 12 weeks growth under different light regimes.

Regression equation Y = 35.43 log X + 525.7.

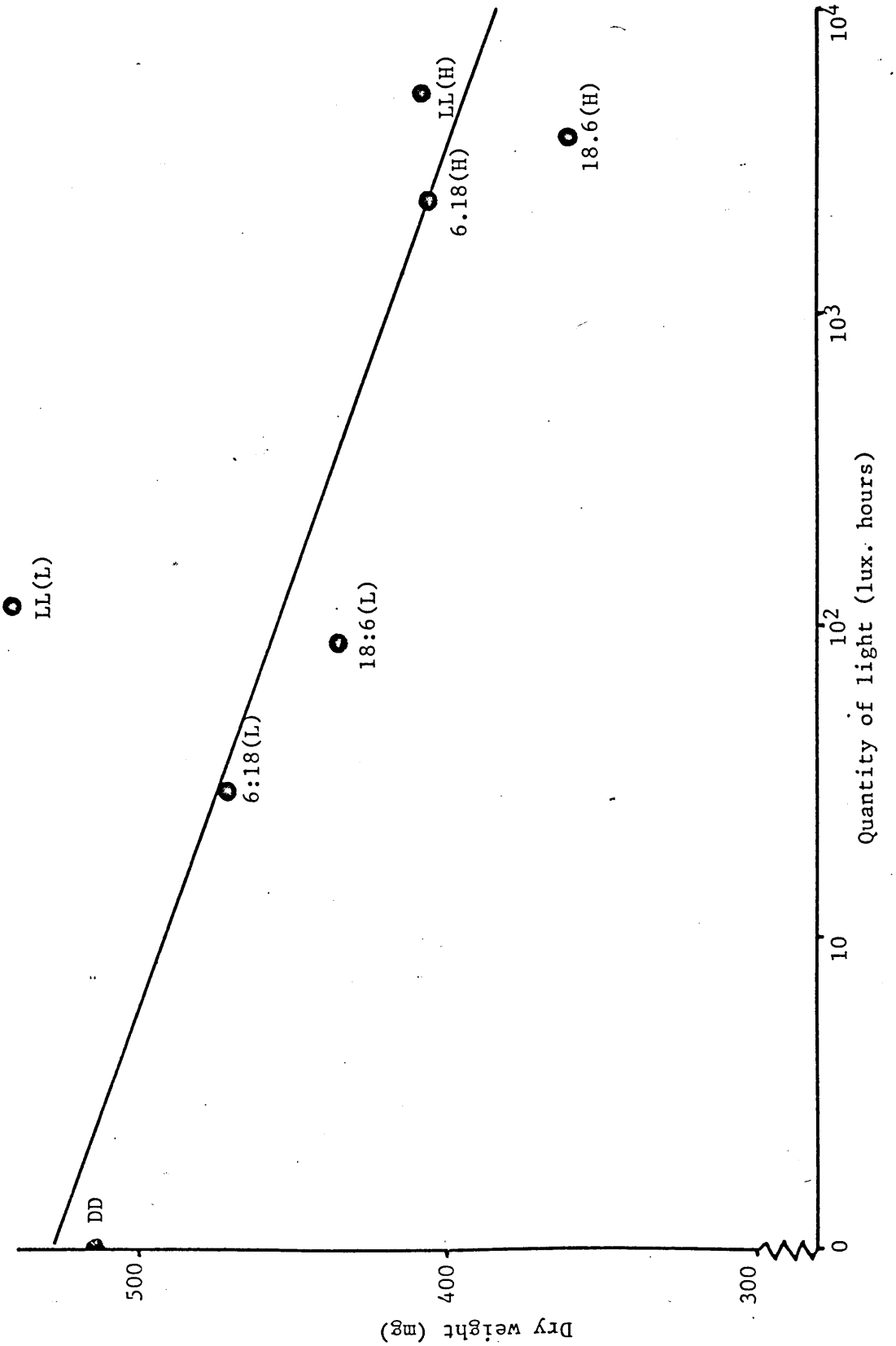


Table 6. Carapace length (mm) of each moult stage of juveniles cultured under different combinations of photoperiod and light intensity.

Treatment	Stage 7	8	9	10	11
LL (H)	8.20 ± 0.45	10.00 ± 0.51	11.73 ± 0.31	13.46 ± 0.36	15.36 ± 0.64
LL (L)	8.25 ± 0.13	10.05 ± 0.22	12.23 ± 0.17	14.36 ± 0.22	16.66 ± 0.43
18:6 (H)	8.00 ± 0.49	9.62 ± 0.16	11.39 ± 0.25	13.07 ± 0.27	14.81 ± 0.42
18:6 (L)	8.47 ± 0.41	9.85 ± 0.39	11.62 ± 0.58	13.57 ± 0.35	15.71 ± 1.70
6:18 (H)	8.23 ± 0.26	9.58 ± 0.31	11.25 ± 0.45	13.18 ± 0.33	14.81 ± 0.80
6:18 (L)	8.28 ± 0.47	9.80 ± 0.40	11.66 ± 0.39	13.82 ± 0.33	15.63 ± 0.98
DD	8.41 ± 0.39	10.16 ± 0.29	11.92 ± 0.39	14.20 ± 0.31	16.12 ± 0.53

Duration (days) of each moult stage.

	Stage 7	8	9	10
LL (H)	12.8 ± 0.4	15.4 ± 0.9	18.3 ± 0.7	20.2 ± 1.1
LL (L)	12.8 ± 0.4	14.7 ± 0.6	17.6 ± 0.7	21.0 ± 1.2
18:6 (H)	14.0 ± 1.1	16.8 ± 3.5	19.2 ± 0.9	21.8 ± 0.5
18:6 (L)	14.2 ± 2.5	15.5 ± 1.4	20.0 ± 1.5	21.5 ± 1.8
6:18 (H)	13.7 ± 0.8	15.1 ± 0.6	19.4 ± 0.9	19.7 ± 1.5
6:18 (L)	13.3 ± 0.7	14.7 ± 0.5	18.5 ± 0.7	20.0 ± 0
DD	13.2 ± 0.6	14.4 ± 0.5	18.3 ± 1.0	21.5 ± 0.8

Discussion

The results obtained from both trials were similar in many ways, but there was a difference in survival and the effect of light intensity. The poor survival in the first trial seems to have been due to factors other than the experimental variables, although aLD regimes are thought to have contributed to reduced survival in Orconectes (Aiken, 1969) and Penaeus duorarum (Bishop, 1970). The effect of light intensity is best compared by reference to the growth under DD which is a conveniently duplicated baseline condition. In the first trial, the intensity of 340 lux was less inhibitory to growth than the 220 lux used in the second trial despite the generally enhanced growth at lower intensities. The significance of this result is not apparent, it may be a result of natural variation in response or more likely associated with interference from other factors during the first trial.

The most significant aspect that has emerged is that circadian LD cycles are not necessary to achieve good growth and survival in juvenile lobsters. A specific nLD treatment was not included in this study, but while the gradual changes in light intensity associated with nLD cycles may be important, the length of the photoperiod is not. The growth rates obtained in the best treatments were, in fact, the fastest ever recorded at the Conwy laboratory, and many hundreds of juveniles have been reared for other experimental purposes under nLD photoperiods. Constant conditions of darkness or low intensity illumination, therefore, represent a real improvement over circadian LD cycles, while the total amount of light each day is, apparently, one limiting factor.

The ability of juvenile lobsters to adapt to light regimes that give no photoperiod cue to a circadian cycle, indicates that any circadian organisation of physiological processes is either independent of the lighting

conditions or poorly developed. This conclusion is similar to that obtained from activity studies (Section 3). Endogenous rhythms of both locomotor and feeding activity can be demonstarted under constant conditions, but in general, there is no overt circadian pattern to either activity. This is probably a juvenile characteristic which provides for an opportunist existence, although Branford (1979) has demonstrated that even the adult is not so strongly nocturnal as is commonly believed. The only clear physiological rhythm so far identified in H. gammarus is that of egg hatching (Ennis, 1973a).

In contrast, the American lobster displays a pronounced nocturnal activity pattern in both the juvenile and adult stages (Zeitlin-Hale and Sastry,1978; Weiss,1970). Endogenous rhythmicity has not been recorded in the juvenile, but adult lobsters from inshore populations (but not offshore populations) do show a weak endogenous activity pattern (Cobb,1969). Circadian organisation does not, therefore, seem to be a marked feature in the lobster and the light regimes favoured by the juvenile may be suitable for culture up to a marketable size.

There is some evidence that circadian light-dark cycles are necessary for complete development. As in Rhithropanopeus and Crangon (Bomirski and Klek, 1974), vitellogenesis in H. americanus occurs in two stages separated by a resting phase which occurs during the low temperatures of winter. At elevated culture temperatures ovary resorption can occur because vitellogenesis development does not respond to temperature in the same way as the processes controlling the moult cycle (Aiken and Waddy, 1976). Co-ordination of the ovarian and moult cycles may, therefore, be under photoperiodic control and Van Olst and Carlberg (1979) have reported that both temperature and photoperiod need to be manipulated to ensure successful reproduction.

Co-ordination of physiological processes through photoperiodic responses does not, however, seem to account for the observed effects of light regime on the growth of juvenile H. gammarus. A more likely explanation is that

the growth rate is affected indirectly by the influence of light schedule on patterns of behaviour, as well as by direct stress reactions to unfavourable conditions. Results presented in Section 3 indicate that the enhanced growth under DD and LL(L) results from unrestricted locomotor and feeding activity. Rapid changes in light intensity are disturbing especially at high intensity photoperiods, while longer photoperiods restrict activity. Reduced food consumption under LL may reflect a lower energy expenditure, but this advantage is probably outweighed by an increased stress. Long photoperiods of 18-24 hours light are, however, suitable for communal rearing where less aggressive behaviour occurs when activity is supressed and individuals remain inside shelter (Van Olst and Carlberg, 1979).

Differences in the growth rate achieved under the various lighting regimes were mainly a result of differences in the size of the moult increment and Dalley (1980) found that this was also the reason for poorer growth of Palaemon elegans held under non-circadian light regimes. Light regime affects both intermoult period and moult increment in Carcinus (Adelung, 1971) and Orconectes (Armitage et al., 1973), but only the intermoult period is affected in Cambaroides (Kurata, 1962) and Panulirus (Chittleborough, 1975). There is, however, a general lack of reliable data on factors affecting the moult increment due to the difficulty of measurement, particularly in communally reared animals, and effects on moult frequency are often the only sign of unsuitable conditions for growth. In H.gammarus lighting conditions exert a greater effect on the moult increment and this strongly suggests that the hormones responsible for water uptake at moult are under nervous control. If the reduced growth was solely due to differences in locomotor and feeding activity, the intermoult period would be more affected because of limitation on the rate of tissue growth.

The measured light intensity may not accurately reflect the amount of light actually perceived by the lobster. The spectral distribution of light

emitted from incandescent bulbs is such that some 50% of the radiant power is of wavelengths greater than 500nm., and lobster rhodopsin does not respond to these longer wavelengths (Kampa et al., 1963). The light intensities used in this study were, therefore, considerably less than those normally experienced in the wild, and this may explain why nocturnal activity is not pronounced in activity studies (Section 3).

A light intensity threshold of activity has not been determined, but low intensity LL may be effectively indistinguishable, from DD. Under laboratory conditions considerable activity occurs at intensities up to 400 lux, and adult lobster have been observed actively foraging on the sea bed at 137 lux (Howard, pers.comm.). H.americanus seem to be generally more photopathic, juveniles are more generally entrained to the light-dark cycle (Zeithin-Hale and Sastry, 1978) and adults in the wild return to shelter 'before sunrise' (Weiss, 1970). The duration of the fourth stage is, however, unaffected under nLD cycles at intensities from less than one to 200 - 300 lux (Cobb, 1970).

The wavelength of light has been found to be important in Palaemon serratus (Van Wormhoudt and Ceccaldi, 1975), where blue and green light was found to be more favourable for growth than red and orange light. Long photophases are also preferred to shorter photophases. If the rhodopsin found in Palaemon has a similar sensitivity to lobster rhodopsin, the reduced growth under red and orange light may be because the longer wavelengths are insufficient to register the length of the photophase.

In vitro studies of lobster rhodopsin have shown an increased sensitivity in the ultra-violet range (Wald and Hubbard, 1957) and ultra-violet light sensitivity also apparently exists in Penaeus duorarum because growth under continuous ultra-violet light is less than that under DD (Bishop, 1970).

The effect of light wavelength on photoperiod responses may, therefore, be significant and studies made under artificial light should be cautiously interpreted. Despite this fact, DD and low intensity LL probably represent the most suitable light regimes for juvenile culture. Further studies on the effect of light wavelength and photoperiod may help to explain the underlying mechanisms, but improvements in the growth rate are unlikely.

The differences in growth rate found in this study indicate that the correct choice of light regime will be an important factor in achieving the high growth rates necessary for the commercial culture of marketable sized lobsters. If the growth rates of the lobsters in the first trial were maintained, marketable size would be attained six weeks sooner under DD than either of the other treatments. From the second trial, marketable size would be reached in 100 and 103 weeks under LL(L) and DD, but 113 weeks would be required under the next best treatment of low intensity 6:18LD.

Long term trials are required to confirm these estimates, but without doubt the selection of an unsuitable light regime will adversely affect the economics of lobster culture.

Summary

1. The effect of light regime and light intensity on the growth and survival of juvenile lobsters was recorded over the first three months of post-larval life.

2. The most suitable light regimes were constant darkness and low intensity constant illumination.

3. Differences in the growth rate were a result of variations in the size of the moult increment rather than an effect on the intermoult period.

4. The total amount of light each day appears to be more important in growth regulation than a direct photoperiodic response of the moult control processes. The best growth occurred under light regimes that allowed unrestricted feeding and locomotor activity and imposed a minimum of disturbance.

5. Observations on the food consumption confirmed that differences in food utilisation could be attributed to the effect of light regime on the level of activity.

6. On the basis of the growth rates achieved during the 12 week experimental period, selection of an inappropriate light regime would result in a considerable increase in the age at marketable size, and hence on the profitability of a commercial culture operation.

SECTION 2.4

THE EFFECT OF SHELTER AVAILABILITY ON THE GROWTH AND SURVIVAL OF JUVENILE LOBSTERS.

Introduction

Shelter selection and occupancy has been most extensively studied in Homarus americanus, but observations on H.gammarus indicate that both species have similar requirements. Lobsters exhibit a clear preference for some form of shelter, and are found in greatest abundance on rocky or stony areas of the sea bed (Cobb, 1969; Dybern, 1973). Lobsters will rapidly colonise suitable artificial reefs placed on otherwise unfavourable flat sand or mud areas (Scarratt, 1968; Sheehy, 1976), and all stages can be found after a few years (Scarratt, 1973). When the amount of shelter is limited, two or more individuals may share the same shelter, although sharing between similar sized individuals is rare (Dunham, 1972; Sheehy, 1976).

Lobsters generally prefer a low profile shelter with a height equal to about half the width, and there is a good relation between the shelter dimensions and the carapace length of the lobster (Cobb, 1971). If suitable crevices are not available, lobsters will excavate under or around rocks or other suitable objects to create a refuge, usually with an opening at each end (Cobb, 1977). When the substrate is suitable, burrows may be constructed, particularly by juveniles (Berrill and Stewart, 1973; Dybern, 1973) and these may be complex with several openings and blind ending chambers (Howard and Bennett, 1979). Burrowing activity begins in both species during the fourth and fifth stages (Berrill, 1974; Berrill and Stewart, 1973), and up to 45mm carapace length H. americanus spends almost the entire time within the burrow system (Pecci et al., 1978). This may explain why H.gammarus is also rarely observed below this size (Howard and Bennett,

1979).

Lobster behaviour is influenced by shelter availability. Juvenile H. americanus exhibit a more pronounced nocturnal activity pattern and less light period activity when shelter is provided (Zeitlin-Hale and Sastry, 1978). H.gammarus is not so responsive, but activity patterns are less irregular when shelter is available, and there is less disturbance at the beginning of each light period (Section 3). The expression of activity rhythms in burrowing species is often affected by the experimental conditions (Atkinson and Naylor, 1973) and when a suitable substrate is unavailable random or irregular high activity occurs in for example, Penaeus monodon Fabricius (Möller, 1974), Crangon (Hagerman, 1970b) and Praunus (Wallesby, 1973).

The shelter related behaviour of lobsters in the wild helps to ensure protection from predators, especially of the newly moulted individuals, as well as from other adverse environmental influences such as current speed (Howard, 1980). It is not, however, known whether shelter is a necessary requirement for lobster growth, although lower growth rates have been observed in populations of crayfish (Flint and Goldman, 1977) and rock lobsters (Newman and Pollock, 1974) from grounds with restricted cover or high population density. Food supply doubtless has an effect, but laboratory studies have demonstrated that growth rates can be affected by other environmental conditions even when the food supply is plentiful.

This study was designed to establish the effect of shelter on the growth of juvenile H.gammarus under optimum temperature and food conditions, and to determine whether some form of shelter will be required in systems for intensive lobster culture.

Materials and Methods

Forty juvenile lobsters were reared for a period of 12 weeks in individual containers, in half of which black semi-circular plastic shelters were provided. Shelter shape was based on the observations of Cobb (1971), with the length of each shelter approximately 1.5 times the total length of the lobster, and the initial diameter 9.5mm. These shelters were replaced with larger shelters of 19.1mm and 25.4mm diameter as the lobsters grew and became able to overturn the shelter. All shelters were open at each end. Juveniles were fed daily throughout on pieces of fresh mussel tissue together with a supplement of frozen Artemia every seven days, any uneaten food was removed the following day.

Experimental stock was obtained from the progeny of a wild caught berried female, and the larvae were reared to the fourth stage by the mass culture techniques described in Section 1. Sufficient juveniles were retained to allow selection of suitable individuals (Section 1) and were transferred to $64cm^2$ individual containers in a shallow fibre-glass tray.

Water circulation and aeration were maintained by a siphon device, the temperature of the water kept at 20±1°C by air heating of the laboratory, and salinity kept at 30±1ppt by the addition of deionised tap water or artificial seawater salts as appropriate. Water quality was preserved by biological filtration in conjunction with a replacement of 50% of the system volume each week.

Ambient lighting conditions were allowed from southfacing windows, together with supplementary laboratory lighting between about 0830

and 1800 hours of up to 400 lux. Photoperiod (sunrise to sunset) at mid point of experiment 11:13 LD.

Fifty juveniles were selected during stage 4 at 10 days old. Ten were sacrificed for an initial sample and the remainder randomly assigned to each treatment with shelters provided in the appropriate containers. During the following 12 weeks, daily observations of shelter occupancy were made, moult dates were recorded and the carapace length of cast exuviae measured. At the end of the trial the final carapace length was recorded and surviving juveniles sacrificed for dry weight measurement.

Results

Shelter occupancy was not immediate, but by the eighth day of the trial and throughout the remainder of the experimental period over 90% of the shelters were occupied at each observation period (0900-1000h) except when the shelters had been overturned.

Juveniles provided with shelter had a higher growth rate than those without shelter and were significantly larger after 12 weeks growth (Table 1). The difference between treatment mean dry weights was significant at $p<0.01$, and for mean carapace length (CL) at $p<0.05$. Survival was unaffected in either treatment.

The differences in growth rate were mainly due to an effect on the moult increment. The lengths of the intermoult period at each stage were very similar in both treatments (Table 2), and there was no significant difference in the mean period between stages 5 and 9. The shorter intermoult periods of juveniles with shelter at stages 5 and 7 was, however, statistically distinguishable from those without.

The size of the moult increment, as shown by the increase in mean stage CL (Table 3) was larger in those lobsters provided with shelter. The difference between treatment mean stage CL increased with moult stage and became pronounced at stage 8 ($p<0.05$) and stage 9 ($p<0.02$). Treatment means did not differ at stage 10 because only a proportion of juveniles in each treatment achieved this stage, and the individuals that did reach this stage were generally the smallest (because intermoult period is inversely proportional to CL). This can be demonstrated by the CL of ninth stage juveniles provided with shelter. The mean CL of individuals

that reached stage 10 was 11.84±0.25mm, while the mean CL of those that did not reach the tenth stage was 12.17±0.50mm.

The improved growth rate of juveniles provided with shelter would, if sustained, yield considerable advantages in the long term. On the basis of the growth rate (CL increase) achieved in this study, lobsters provided with shelter would reach marketable size of 80mm CL in 107 weeks, while 117 weeks would be required with no shelter. The difference may in fact be greater because CL data is not as accurate an estimate of growth as dry weight records but there are no reliable estimates available for the dry weight of marketable sized animals.

Table 1 Mean dry weight, carapace length and survival of juvenile lobsters cultured for 12 weeks with or without shelter.

Treatment	Dry weight (mg)	Carapace length (mm)	Survival (%)
Initial sample	15.8 ± 2.4	4.64 ± 0.19	
Shelter	341.6 ± 31.0	13.13 ± 0.47	100
No shelter	281.5 ± 29.1	12.36 ± 0.66	95

Table 2 Duration (days) of successive moult stages and mean period (days) between stage 5 and stage 9 of juveniles cultured with or without shelter.

Treatment	Stage 5	6	7	8	9	5-9
Shelter	12.1±0.7	12.5±0.6	14.9±1.0	19.2±1.1	20.7±1.0	58.1±3.1
No shelter	13.8±0.9	13.1±0.6	16.7±1.1	18.6±0.9	21.0±0.8	60.6±1.9

Table 3 Mean carapace length (mm) of successive moult stages of juveniles cultured with or without shelter.

Treatment	Stage 5	6	7	8	9	10
Shelter	5.47±0.14	6.83±0.31	8.50±0.25	10.26±0.23	12.00±0.26	13.92±0.21
No shelter	5.48±0.15	6.83±0.17	8.37±0.26	9.83±0.31	11.55±0.23	13.66±0.50

Discussion

The influence of shelter or substrate on behaviour is well documented, but there are fewer records available of effects on the growth rate although some research has been directed towards improving survival and increasing the stocking density of communally reared species. Among the penaeids, P.japonicus Bate has a pronounced tendency to burrow, and growth is reduced in bare tanks (Wickins and Beard, 1978). Other species including P.monodon and P.orientalis (= P. chinensis (Osbeck) have less of a burrowing habit and good yields can be achieved in the absence of a suitable substrate (Forster and Beard, 1974). Research on prawn culture tends to be concentrated on species that can tolerate bare tanks, because substrate provision is unsuitable for intensive culture systems (Wickins, 1976).

Stocking density is usually limited by the area available for each individual, and can be increased by enlarging the effective floor area. This can be achieved by providing shelves or layers of substrate which help to reduce the incidence of fighting and cannibalism (Ling, 1969; Rickards, 1971). Survival of communally reared juvenile Homarus americanus can also be increased with a suitable substrate, and survival after six months is markedly better on stone substrates than on flat sand (Van Olst, Carlberg and Ford, 1975). Further improvements in survival can be achieved by providing surplus shelter together with a long photoperiod (18h or more light each day) which encourages the juveniles to spend most of their time inside the shelter (Van Olst and Carlberg, 1979).

The growth rate is often less important in communally reared species than the final yield, which includes survival effects.

The lobster is one of the few species cultured individually on a routine basis, and Cobb (1969) demonstrated that under a natural photoperiod, shelter provision slightly increased the growth rate in H. americanus. Lighting conditions were, however, more important, and a significant improvement in growth was found under constant darkness compared to that under a normal photoperiod. The less pronounced effect of shelter on H.americanus compared to that on H.gammarus may have been because the light intensity in Cobb's study was only 50-150 lux and perhaps insufficient to stimulate shelter occupancy.

The response of H.americanus to light intensity is not known, but in the wild, shelter seeking generally begins a little before sunrise (Weiss, 1970) although an intensity of 525-600 lux was used by Zeithin-Hale and Sastry (1978) to demonstrate the influence of shelter on juvenile activity. Adult H.gammarus can be observed actively foraging in the sea bed at 137 lux (Howard, pers. comm.) although 200 lux is sufficient to stimulate crevice seeking in the juvenile (Howard and Bennett, 1979). Activity studies on the juvenile have shown that shelter effects are more noticeable at 400 lux than at 250 lux (Section 3).

Shelter requirements are intimately connected with the lighting conditions. Cobb (1971) demonstrated that negative phototaxis is more important than positive thigmotaxis, although transparent shelters are occupied if none other is available. H.gammarus will invariably sit backed against tank corners when no shelter is available (pers.obs.) and this presumably generates a sense of security. Juveniles will rapidly select naturally occurring crevices in stone substrates ($> 7 \leqslant 20$mm diameter) under constant light of 200 lux, but in constant darkness no clear preference is apparent and an equal proportion

remain on the sediment surface (Howard and Bennett, 1979).

The improvement in the growth rate of the lobsters provided with shelter might be expected to arise through lower activity levels while residing inside the shelter but if this were the case a greater proportion of energy could be directed towards tissue growth and the intermoult period would be affected. The main effect of shelter was on the size of the moult increment and this is usually related to the size of the animal and, therefore, the potential amount of water uptake at moult. Reduced moult increments when no shelter is available indicate that water uptake is actively limited, probably through a central nervous system influence on the release of the hormones responsible for water uptake. This same response is also evident under unfavourable conditions of other environmental factors, and these are discussed in other sections of this thesis.

Selection of a suitable light regime may be a more practical technique of enhancing the growth rate than sheltering the lobster from adverse lighting conditions, and constant darkness or low intensity constant illuminations seem to be the most favourable for growth (Section 2.3). Nevertheless, the shelter requirement of individually reared lobsters is unlikely to be solely influenced by responses to light, for in the wild there may be a greater adaptive pressure on locating a safe refuge, particularly for the protection of newly moulted individuals, than to prevent exposure to adverse light conditions. Further studies are required to determine whether shelter has a more fundamental influence, and this might be demonstrated by observing the effect of shelter under constant darkness.

Summary

1. Juvenile lobsters were reared for 12 weeks with or without a semi-circular shelter inside each individual container.

2. Juveniles provided with shelter attained a significantly greater weight, mainly as a result of larger size increments at moult.

3. The influence of shelter on the moult increment shows that sensory responses to shelter availability may be more important in growth regulation than the effects of shelter on activity and energy expenditure.

SECTION 2.5

THE EFFECT OF FREQUENCY OF FEEDING ON THE GROWTH AND SURVIVAL OF JUVENILE LOBSTERS

The food supply is a potentially limiting factor to lobster growth, but in the natural environment it is almost impossible to measure the availability of suitable food or the daily food consumption. In the laboratory, nutritional status has been shown to be an important factor in the regulation of moulting is many crustaceans. A certain amount of tissue growth and reserve storage is necessary before ecdysis, and at a given temperature food supply may be the major determinant of growth (Adelung, 1971).

Although temperature and food supply exert the most obvious effects on the rate of tissue growth, moulting can also be influenced by more subtle factors. The effect of variables such as shelter availability, amount of living space, and lighting conditions are described elsewhere in this thesis, but the mechanism by which these factors influence growth is not clear. Moulting may be directly affected by sensory mediated control over hormone production, or there may be an indirect influence over the rate of tissue growth. Unfavourable conditions can lead to behavioural changes in feeding and locomotor activity, which together with stress reactions may have adverse effects on food intake and energy expenditure.

The extent to which nutrition alone influences moulting is still not well established. In many species reduced rations predictably lead to a lengthening of the intermoult period, for example Cambaroides (Kurata, 1962), Carcinus (Adelung, 1971) and Palaemon lamarrei (Milne Edwards) (Shakuntala and Reddy, 1976). The moult increment may also be affected as in Panulirus (Chittleborough, 1975) and Nephrops (Klein-Breteler, 1975a). When food supplies are very restricted, negative moult increments can occur in Crangon,

(Meixner, 1968), while zero growth or shrinkage also occurs under other adverse conditions - Penaeus monodon on a low protein diet (Lee, 1971), Palaemon serratus cultured in litre beakers at 20°C (Reeve, 1969), and Panulirus under crowded conditions (Marshall, 1945). Adelung (1971) reported that no moulting occurred in starved Carcinus.

The effect of food availability on the growth of Homarus gammarus is also relevant to the intensive culture of this species. Studies on the food consumption of juvenile H.gammarus at the Conwy laboratory have shown that while there is a general pattern of daily food intake related to the stages of the moult cycle, the food consumed by individuals varies considerably from day to day, and no food is eaten on the days immediately before and after ecdysis (Munford, pers.comm.). Because of this variation it is not possible to predict an appropriate daily ration, and in practice, to ensure that growth is not limited by the food supply, a ration equivalent to the maximum daily intake is usually provided. This results in a considerable amount of uneaten food which has to be removed manually to prevent excessive pollution of the water, although the toxic products of decomposition could be treated by complex filtration apparatus. The use of throughflow systems to maintain water quality is generally ruled out by the cost of water heating and a susceptibility to deterioration in the quality of the seawater supply.

Until adequate artificial foods have been developed in a form suitable for automatic feeding, the daily feeding of fresh food diets and the removal of uneaten food represents a major cost area. A priority, therefore, is to determine whether daily feeding is necessary, and whether reduced rations give the same benefits of food utilisation found in the penaeid prawns (Sedgewick, 1979; Venkataramaiah, Lakshmi and Gunter, 1974).

For individually reared animals periodic starvation is a more practical method of limiting the food supply than daily feeding of smaller rations

and may be a better technique. Studies on the penaeids have shown that feeding every third day can result in better growth of 10g animals than daily feeding, although smaller animals require more frequent feeding (Lee, Liang and Liao, 1976).

The following experiments were designed to assess the effect of periodic starvation on growth, moulting and food consumption in juvenile H.gammarus.

Materials and methods

Groups of ten juveniles were reared for 12 weeks at three frequencies of feeding - daily, every two days and every three days, designated as rations 1, 2 and 3 respectively. At each feed an amount of mussel tissue was provided in excess of that required for the 24h period, and uneaten food removed the following day. In a second trial groups of 15 juveniles were reared under the same conditions as above for six weeks and the amount of food consumed measured over the last 31 days of the experimental period. The ages of the juveniles at the end of each trial were 98 and 68 days respectively. Both trials were exposed to a natural photoperiod supplemented by laboratory lighting during daylight hours (maximum 300 lux).

Experimental stock for each trial were obtained from the progeny of a separate wild caught ovigeous female and the larvae reared to the fourth stage by the mass culture techniques described in Section 1, sufficient juveniles were retained to allow subsequent selection of suitable individuals (see Section 1). Juveniles for the first trial were held individually in $64cm^2$ containers placed inside two shallow interconnected plastic tanks with a total system volume of 62l and water was circulated and aerated by an overhead sprinkler system which delivered 0.17 $l.min^{-1}$ to each container. A temperature of $20 \pm 1^{o}C$ and salinity of 32 ± 1 p.p.t.was maintained throughout and the water changed twice weekly to preserve water quality. All juveniles were fed daily on fresh mussel tissue with a dietary supplement of frozen Artemia every seven days.

At 12 days old, 34 juveniles were selected, an initial sample of six sacrificed and the remainder assigned equally to the three treatments with treatment containers randomly distributed in the plastic tanks. An Artemia supplement was added to the ration every sixth day to coincide with the days on which all three treatments received food.

In the second trial water circulation and aeration were maintained by a siphon system as described in Section 1. Juveniles were held in 64 cm^2 containers in a shallow fibreglass tray at the same levels of temperature and salinity as in the first trial. A biological filter was incorporated into the system and water replacement reduced to a 50% change once a week. Forty-five juveniles were selected at 26 days old and randomly assigned to the three treatments. An Artemia supplement was not provided because of the difficulty in collecting and measuring the uneaten fragments.

The amounts of food consumed in each treatment were recorded from the eleventh to the forty-second day of the trial, and the wet weight of juveniles measured at the beginning and end of this period. The food consumption was determined from the total amount of food eaten by each group of juveniles on each feeding day. A known quantity of mussel flesh in excess of the daily requirement was distributed equally between the lobsters in each treatment. The amount uneaten the next day was measured and values corrected for losses due to decomposition and leaching (see Section 1). Values for the food consumption of juveniles that died during this study were excluded from the analysis. Wastage was estimated at 25%, but the amount lost during feeding could not be estimated. In both trials moult dates and carapace length (CL) were recorded, while at the end of the first trial the final CL of survivors was measured before sacrificing for dry weight and biochemical analysis by methods described in Section 1.

Results

In the first trial the growth rate was proportional to the frequency of feeding with the greatest dry weight and CL attained by juveniles fed daily. Some mortality occurred in all three treatments during the first two weeks of the trial, but survival was unaffected by the ration level (Table 1). There was no statistically significant difference between the dry weight or CL of juveniles fed rations 1 and 2, but juveniles fed at ration 3 were significantly smaller than those fed daily (dry weight difference $p<0.01$, CL difference $p<0.02$).

The growth rate was not apparently affected by the influence of ration level on the length of the intermoult period (Table 2). There were no significant treatment differences although juveniles fed at ration 3 had a shorter average intermoult period at stages 8 and 9 than juveniles fed daily. The proportion of juveniles in each treatment that attained stage 10 showed that the mean intermoult period values did not fairly reflect the frequency of moulting. At ration 1, 77% attained stage 10, at ration 2, 50%; and at ration 3, 40%. The difference between the frequency of moulting predicted from the average intermoult periods, and that indicated by the numbers of juveniles attaining stage 10,was due to the amount of variation around the mean values for intermoult period. Treatment differences between the average CL of each stage were no more pronounced than effects on the intermoult period (Table 3). Juveniles fed at ration 3 were, however, consistently smaller at each stage, although those fed daily were no larger than those fed at ration 2. Biochemical analyses revealed little difference between treatments (Table 4). The only component showing marked variation was the non-protein nitrogen which was notably higher at ration 3 than at ration 1. The differences in growth rate between treatments were, therefore, due to a combination of small variations in both moult frequency and moult increment.

In the second trial the pattern of juvenile growth and moulting bore a more consistent relation to the frequency of feeding. There was little difference between the wet weight or CL of juveniles fed at rations 1 and 2, but significant reductions were found at ration 3 (weight difference $p<0.01$ CL difference $p<0.05$). Survival was slightly reduced at ration 3, but not by a significant amount (Table 5).

A larger sample size, together with less variation about the mean values, allowed the effect of feeding frequency on moulting to be more clearly differentiated (Tables 6 and 7). At rations 1 and 2 the durations of each stage were very similar, but at ration 3 a significantly longer intermoult period occurred at stages 6 and 7 ($p<0.01$) and at stage 8 ($p<0.05$). As with the intermoult period, there was no difference in the stage carapace length at ration 1 and 2, but juveniles fed at ration 3 were significantly smaller at stage 7 ($p<0.01$) than those fed daily and smaller than both other treatments at stage 8 ($p<0.01$).

The effect of feeding frequency on the food consumption is shown in Table 8. Juveniles fed every three days had the highest rate of food consumption per feed, expressed as either total weight, or percentage of the body weight. The total amount of food eaten over the trial period was, however, only half that of juveniles fed daily. Daily feeding resulted in the greatest total food consumption and weight gain, but the 9% lower weight gain at ration 2 was achieved at a considerably lower level of food intake.

The food conversion ratio at rations 2 and 3 was very similar, but poor utilisation of food at ration 1 resulted in a 30% increase in the FCR (wet weight basis). At the expense of only slight reductions in the growth rate, considerable improvements in the efficiency of food utilisation can, therefore, be achieved by feeding lobsters every other day.

Table 1. Mean dry weight, carapace length and survival of juvenile lobsters cultured for 12 weeks at three ration levels.

Ration	Dry weight (mg)	Carapace length (mm)	Survival (%)
1	264.7 ± 35.6	12.54 ± 0.53	80
2	242.3 ± 43.0	12.03 ± 1.03	90
3	189.7 ± 31.0	11.16 ± 0.94	90
Initial sample	16.39 ± 4.09	5.31 ± 0.25	

Table 2. Duration (days) of successive moult stages of juvenile lobsters cultured at three ration levels.

Ration	Stage 6	7	8	9
1	13.7 ± 3.8	14.8 ± 2.3	19.0 ± 4.3	19.6 ± 2.1
2	13.7 ± 6.3	17.4 ± 2.9	18.3 ± 2.4	20.3 ± 3.5
3	14.2 ± 2.0	17.3 ± 2.7	16.8 ± 1.9	19.0 ± 3.4

Table 3. Carapace length (mm) of successive moult stages of juvenile lobsters cultured at three ration levels.

Ration	Stage 6	7	8	9	10
1	6.41 ± 0.62	7.97 ± 0.43	9.26 ± 0.63	11.00 ± 0.78	12.62 ± 0.59
2	6.13 ± 0.55	7.98 ± 0.24	9.46 ± 0.43	11.09 ± 0.41	12.98 ± 1.48
3	6.42 ± 0.72	7.50 ± 0.44	9.16 ± 0.42	10.64 ± 0.50	12.13 ± 1.48

Table 4. Proximate analysis of juvenile lobsters cultured for 12 weeks at three ration levels. Estimates as a percentage of the ash-free dry weight.

Ration	Ash	Lipid	Carbohydrate	Protein	Non-protein nitrogen
1	31.2	7.4	4.5	39.6	1.9
2	32.5	10.1	4.1	43.0	2.1
3	33.2	8.6	3.5	44.8	3.6
Initial sample	33.6	8.6	1.3	35.9	4.2

Table 5. Mean wet weight, carapace length and survival of juveniles at the beginning and end of period of measured food consumption.

Ration	Wet weight (g)		Carapace length (mm)		Survival (%)	
	Day 11	Day 42	Day 11	Day 42	Day 11	Day 42
1	0.16 ± 0.02	0.44 ± 0.03	6.88 ± 0.38	9.30 ± 0.27	100	87
2	0.16 ± 0.02	0.42 ± 0.03	6.76 ± 0.27	9.22 ± 0.23	100	87
3	0.15 ± 0.01	0.36 ± 0.03	6.67 ± 0.20	8.94 ± 0.17	100	67

Table 6. Duration (days) of successive moult stages of juvenile lobsters cultured for 6 weeks at three ration levels.

Ration	Stage 6	7	8
1	14.8 ± 1.0	18.5 ± 1.1	20.3 ± 1.5
2	16.1 ± 0.5	19.1 ± 0.8	20.5 ± 1.4
3	18.9 ± 1.9	20.5 ± 0.6	22.4 ± 1.2

Table 7. Carapace length (mm) of successive moult stages of juvenile lobsters cultured at three ration levels.

Ration	Stage 6	7	8
1	6.68 ± 0.14	8.00 ± 0.18	9.30 ± 0.24
2	6.65 ± 0.13	7.94 ± 0.30	9.25 ± 0.20
3	6.59 ± 0.13	7.73 ± 0.10	8.89 ± 0.15

Table 8. Food consumption and weight gain of juveniles fed at three ration levels for 31 days.

	Ration 1	Ration 2	Ration 3
Total food eaten. lobster $^{-1}$ during trial period.(g)	1.80	1.19	0.98
Average food consumption. lobster^{-1}.feed^{-1}. (g)	0.06	0.07	0.09
Percent body weight eaten. lobster^{-1}.meal^{-1}.	20.7	26.9	42.4
Mean wet weight increase during trial period.(g)	0.29 ± 0.03	0.26 ± 0.03	0.22 ± 0.03
Food conversion ration (wet:wet).	6.2:1	4.6:1	4.5:1

Discussion

In the juvenile lobster both the intermoult period and the moult increment are adversely affected by reduced rations, although frequent feeding of sub-satiation amounts might evoke a different response to that caused by infrequent feeding of satiety level quantities. The juvenile adapts to infrequent food supplies by consuming large quantities of food, and by improvements in food utilisation,and this is consistent with the predatory feeding habit necessary to capture the crabs, starfish,sea urchins and molluscs which constitute a major proportion of the diet (Weiss, 1970). A large amount of animal tissue is required in artificial diets and 60% protein may be necessary (Castell and Budson, 1974), while a large quantity of calcareous material is consumed after ecdysis (Weiss, 1970).

The Natantia, in comparison, are more usually browsing feeders or omnivorous scavengers, algal material is also included in the natural diet (Wickens, 1976) and these species would be expected to be more suited to frequent feeding. Studies on Penaeus merguiensis De Man have shown that feeding on artificial diet 4 times each day gives better growth than the same ration fed once a day, while the best growth at either regime is at the highest daily ration of 13-14% body weight.day $^{-1}$ (Sedgewick, 1979). The adverse effect of once daily feeding may have resulted from nutritional deterioration of the diet after prolonged water exposure and the nutritional value of the diet has been shown to affect the feeding efficiency of P.japonicus which is proportional to the amount of crude protein in the diet (Deshimaru and Shigueno, 1972). Gut clearance times also indicate that more frequent feeding may be required on poor diets. Gut clearance in Palaemonetes varians (Leach) takes 4-6h after a detritus meal and 27h after an animal protein meal (Snow, 1969).

In pond culture, periodic feeding of Penaeus japonicus is beneficial (Lee,

Liang and Liao, 1976). Daily feeding sustained the best growth of 2.9g prawns, two days feeding out of every three days was best for 5.2g prawns, and 9.6g prawns grew fastest when fed every three days. A similar result was observed in the red prawn, an unspecified penaeid, by Liao and Lee (1972), but these results have not yet been demonstrated under intensive culture and other food substances may have been available in the ponds.

Shleser (1974) reported on the growth of juvenile H.americanus at feeding frequencies similar to those of this study, but did not include moult data. Significant reductions in growth were found at less than daily feedings, but this was partly because the rations fed to all treatments were the satiety amount for daily fed animals and juveniles fed every two or three days were, therefore, only provided with half or a third of the total ration fed to the daily fed animals.

The lowest ration levels generally result in the best food conversion ratio (FCR) among prawn species and as there was no difference between the FCR of H.gammarus reared at rations 2 or 3, the minimum FCR may have been achieved. FCR is more often expressed as the ratio between the dry weight of food fed to the wet weight increase, and on this basis the FCR at rations 2 and 3 were less than 1:1, although this result should be treated with caution because of the small quantities involved. Juvenile H.americanus have returned a FCR of 2.3:1 on an artificial diet (Gallagher, Conklin and Brown, 1976), while Jahnig (1973) and Hughes, Sullivan and Shleser (1972) calculated a FCR for long term culture of 3-4:1. An estimate of 3.6:1 has been made for Panulirus (Chittleborough, 1975) while values of less than 2:1 have been achieved in Penaeus merguiensis even at high ration levels (Sedgewick, 1979).

The most extensive investigations of crustacean food requirements have been made on the commercially important prawn species which are generally reared in mass culture and moult details rarely recorded. Some penaeids have, however,

been noted to exhibit slightly reduced moult increments at less frequent feeding levels (Liao and Lee, 1972), although among decapods in general, the intermoult period is usually more affected. This may be due to the degree of rationing imposed, Adelung (1971) found that half the daily ration did not affect the moult increment in Carcinus, but a lower ration did have an effect (Klein-Breteler, 1975a). Ration level has been shown to influence the moult increment in H.americanus larvae where the greatest mean CL at stage 4 was found in larvae reared on the largest quantities of Artemia (Carlberg and Van Olst, 1976).

There was no significant difference between the intermoult period or the moult increment in juvenile H.gammarus reared at rations 1 and 2, but both components were adversely affected at ration 3. The effect of food supply of the intermoult period presumably arises through a limit on the availability of suitable nutrients to achieve the necessary tissue growth before ecdysis, but this does not satisfactorily account for the effect on the moult increment. Water uptake at ecdysis depends primarily on the size of the animal, for the correlation between premoult and postmoult CL is always high. In the lobster 91% of the ingested seawater appears in the haemolymph 2.5h after ecdysis (Mykles, 1980) and this water uptake seems to be under hormonal control because eyestalk ablation results in enlarged moult increments (Mauviot and Castell, 1976). The mechanisms of hormone regulation have not been established, but sensory mediation is likely and nervous inhibition of growth by reduced water uptake may have occurred in response to an adverse food supply, in addition to direct effects on tissue growth. Adverse levels of other environmental factors are known to affect the moult increment in juveniles even when food is plentiful, and these are discussed in other sections of this thesis.

Changes in behaviour at reduced rations may be partly responsible for the improved food utilisation. Activity studies (Section 3) show that the normal pattern of feeding activity is altered when juveniles are fed

every three days with rationed individuals showing a restricted period of activity. In addition, starved animals do not exhibit such a marked nocturnal pattern of locomotor activity. Similar modifying effects of food availability on activity have also been recorded in Nephrops (Möller and Naylor, 1980) with the presence of food enhancing the endogenous nocturnal activity pattern as well as inducing more diurnal activity. The general activity level of Crangon (Weinberg, 1975) and Rhithropanopeus larvae (Cronin and Forward, 1980) are also induced by starvation, as is oxygen consumption in Cancer (Ansell, 1973) and Carcinus (Klein-Breteler, 1975b).

Although daily feeding is not necessary for the lobster, there is a 12h cycle to the secretion of digestive enzymes following a meal (Barker and Gibson, 1977) which probably reflects the normal nocturnal feeding activity (Section 3). Studies by Van Wormhoudt and Malcoste (1976) have shown the presence of an endogenous circadian component to digestive enzyme secretion in Palaemon serratus but this feature has not been demonstrated in the lobster and could be a disadvantage to a species that does not rely on a regular food supply.

It is unlikely that types of feeding regime other than daily feeding would result in better growth of juvenile lobsters, but the improved utilisation of food found at reduced rations warrants further investigations on frequency of feeding for the deterioration in food quality is a major problem in feeding dead or artificial foods, and frequent feeds of small food quantities would help preserve food quality. Feeding every two days is, however, a more practical solution to reduce feeding costs and improve food utilisation,because frequent feeding of smaller quantities would be prohibitively expensive. On the basis of the growth rates achieved in this study, lobsters fed every two days would only require an extra 10 weeks to reach marketable size, with a further 20 weeks if fed every three days. From studies on other species it is also likely that even longer periods of starvation would be adequate for larger animals.

Summary.

1. Juvenile lobsters were fed daily, every other day or every three days and the effect on growth, moulting and food consumption recorded.

2. Juveniles fed daily achieved the fastest growth rates but there was no statistically significant reduction in the growth rate of juveniles fed every two days, although feeding every three days gave poor growth. Differences in the growth rate were due to effects on both the length of the intermoult period and the size of the moult increment.

3. The total amount of food consumed by juveniles over a 31 day trial was directly proportional to the frequency of feeding and the average daily intake as a percentage of the body weight was inversely proportional to the frequency of feeding.

4. The slightly higher weight gain of juveniles fed daily was at the expense of a greater food intake and the food conversion ratio was consequently worse than that of lobsters fed every two days.

5. Periodic starvation may be beneficial in intensive lobster culture because food utilisation is improved at the expense of only slight reductions in growth rate and the cost of both feeding and wasted food is reduced.

SECTION 3

OBSERVATIONS ON THE LOCOMOTOR AND FEEDING ACTIVITY OF JUVENILE LOBSTERS.

Introduction

The juvenile lobster Homarus gammarus is rarely observed in the wild and there are very few records of individuals less than about 40 mm carapace length from either the baited traps used in the lobster fishery or scientific sampling techniques. Underwater observations by Howard and Bennett (1979) yielded only two juveniles of 37 and 52 mm carapace length after 20 man-hours of diving in several habitats, while Pecci et al. (1978) have reported that juvenile H.americanus spend almost the entire time within a tunnel system or other refuge. Consequently, little is known of the natural behaviour of the juvenile.

Adult H.americanus are nocturnally active (Cobb, 1969; Weiss, 1970). Activity begins as the light intensity decreases and includes food searching for a variety of marine animals (Weiss, 1970) and shelter acquisition. Some social behaviour may occur, for dominance hierarchies have been observed in captive populations (Cobb and Tamm, 1975; Douglis, 1954) and a reduction in aggressive behaviour has been noted in communally held animals (Dunham, 1972). A chemical sense evokes responses to other lobsters (McLeese, 1973a) as well as to food odours (Mackie, 1973; McLeese, 1973b) and sound production may also play a role in communication (Fish, 1966).

Adult H. gammarus are predominantly nocturnal, although the proportion of dark period activity varies through the year (Branford, 1979). There is no evidence of an endogenous component to locomotor activity but Ennis (1973a) has recorded a persistent rhythm of larval

release by ovigerous females. A weak endogenous rhythm of locomotor activity has been identified in H. americanus from inshore populations but this is not apparent in offshore populations (Cobb, 1969).

Shelter seems to be a general requirement for the lobster. Juveniles will rapidly seek shelter and utilise naturally occuring crevices between small stones (Howard and Bennett, 1979) or excavate below and around suitable objects (Berrill, 1974; Berrill and Stewart, 1973). Burrows may be made in suitable sediments (Dybern, 1973) and can be of complex design (Howard and Bennett, 1979). The distribution of adult lobsters is affected by the availability of suitable shelter (Cobb, 1969) and artificial reefs placed on otherwise unfavourable grounds are rapidly colonised (Scarratt, 1968; Sheehy, 1976). The shelter requirement is mainly due to negative phototactic responses, although positive thigmotaxis is also apparent (Cobb, 1971) and a safe refuge is particularly important for newly moulted individuals. Lighting conditions and shelter availability are therefore fundamental influences on lobster behaviour and this study was designed to investigate the effect of these two factors on the locomotor activity of mid-moult juveniles. The intermoult period of the experimental stock could only be predicted on the basis of size and date of last moult and was only reliable to within 20 days (95% confidence limits of mean intermoult period) so selected individuals could have been some 10 days from the mid-moult point.

Activity patterns are liable to be influenced by the moult stage for the moult cycle exerts a profound influence over the life of

all crustaceans, and variations in a number of physiological and behavioural processes associated with the moult stage have been recorded. These include biochemical composition (Glynn, 1968; Heath and Barnes, 1970; Hepper, 1977; Spindler-Barth 1976), respiration (Lewis and Haefner, 1976) and aggression (Tamm and Cobb, 1978). The composition of the lobster's diet also changes with moult stage (Ennis, 1973b; Weiss, 1970), as does the daily food consumption (Munford, pers. comm.) and shelter selection would be expected to be more critical around ecdysis. Observations were therefore made on changes in activity occurring during the moult cycle.

In many activity studies experimental animals are not fed, to prevent possible entrainment by the feeding schedule and to amplify responses which are partly concerned with food search. At the same time, food availability is known to affect activity in some species, for example Crangon (Hagerman, 1970b), Nephrops (Möller and Naylor, 1980) and Rhithropanopeus (Cronin and Forward, 1980) while respiration is clearly affected by the feeding level in Carcinus (Klein-Breteler,1975b) and Cancer (Ansell, 1973). It was therefore relevant to consider the effect of food on juvenile activity to more fairly reflect the situation under culture conditions.

An understanding of the pattern of feeding activity is essential to define a feeding strategy for lobster culture. Among the decapods, nocturnal locomotor activity is very common and so, therefore, is feeding activity, although feeding may occur during light periods in post-moult Jasus (Fielder, 1965), presumably when food demand is greatest. A bimodal dawn and dusk pattern of locomotor activity is apparent in some species and this may be

associated with an optimum light intensity, e.g. Nephrops (Arechiga and Atkinson, 1975) and a bimodal feeding pattern has been demonstrated in Crangon septemspinosa Say (Wilcox and Jeffries, 1974). An endogenous rhythm of digestive enzyme secretion, with a 12 hour period, has been found in Palaemon (Van Wormhoudt and Malcoste, 1976) but there is no evidence for such a rhythm in Homarus gammarus, although there is a 12 hour cycle of enzyme secretion in response to a meal (Barker and Gibson, 1977). The final series of experiments was therefore designed to establish the pattern of feeding activity and the effect of light schedule.

These investigations were primarily designed to study behavioural responses in the context of intensive lobster culture and analysed laboratory reared animals maintained at temperatures suitable for optimum growth (18-22°C). This potentially limited the extent to which particular ecological significance could be attached to the results, although there is evidence that in other species, activity rhythms can persist through many generations reared under constant conditions, whilst temperature independence is a characteristic feature of physiological rhythms (Bunning, 1964).

Materials and methods.

Recording of locomotor activity.

A photo-electric method was used whereby movement of the lobster interrupted a light sensitive receiver. The electrical resistance of the receiver was altered by changes in illumination, and the accompanying variations in current were amplified to activate a relay drive circuit and event recorder. Two types of recording system were used. In the first experiments a visible red light beam and light sensitive photocell were connected to an event recorder, while in later experiments an infra-red light source and sensor were coupled to an electronic counter and printer.

A visible red light beam was produced from a 2.5v penlight bulb and red filter (Kodak Wratten No.92) and directed across the experimental chamber onto a photo-resistive cell. The wavelength of the transmitted light was greater than 600 nm and was chosen to cause minimum disturbance, based on the work of Kampa et al. (1963) and Kennedy and Bruno (1961), who demonstrated that lobster rhodopsin was not sensitive to these longer wavelengths. The photocell units were connected to an amplifier designed at the Marine Science Laboratory, University College of North Wales, and the output fed into a 4-channel event recorder (Rustrak Instrument Division, Model 292-4). Passage of the lobster across the light beam was recorded by marks on pressure sensitive paper and a time base was fitted from the chart speed of 1.27 mm h^{-1}. Activity was estimated from the number of events each hour.

This system had three major disadvantages:

(1) Although the red light beam was considered to be effectively invisible, substitution of an infra-red source ensured reduced disturbance.

(2) The sensitivity of the apparatus allowed frequent small movements, such as chelae waving, to be recorded as events, and these could not be distinguished from locomotor activity. A delay circuit was therefore incorporated to minimise the effect of such actions.

(3) Visual counting of events from pressure sensitive paper was a time-consuming and potentially inaccurate operation, for even with a fast chart speed it was extremely difficult to reliably identify events separated by a few seconds. An electronic counter and printout machine was therefore substituted in place of the Rustrak recorder, which automatically recorded and printed the number of events. This more accurate counting method inevitably led to higher hourly activity values.

Light from an infra-red transmitter was directed through a collimator to form a narrow beam across the experimental chamber, and onto an infra-red sensor. Interruption of the light beam caused small current changes in the sensor circuit and these operated a relay in a sensor control unit, designed at the M.A.F.F. Electronics Laboratory, Lowestoft. The control unit innervated an event counter which consisted of a modified A.F.T.E.R. (Automatic Fishing Time Electronic Recorder) originally designed at Lowestoft for recording trawling time. The A.F.T.E.R. units consisted of a minute pulse generator and timer and Sodeco impulse printing counter (Model PL208). Impulses from the sensor control were automatically accumulated in the A.F.T.E.R. and totals printed every 30 minutes. After each printout the device

automatically cleared and re-set for the next count.

Animals were housed in opaque perspex tanks 42 x 10 x 12 cm deep during recording. A water flow of 1-2 l.min-1 was supplied at a temperature of 20±2°C and ambient salinity of 30-34 p.p.t. In most cases a throughflow system was operated but in later experiments closed system recirculation was combined with periodic water changes. The tanks were placed in a lightproof compartment and lighting provided when necessary by incandescent bulbs controlled by a time clock and rheostat. Constant dim red light (wavelength >600 nm) was used in the constant dark treatments. Light intensity was measured with an E.E.L. photometer. Shelters provided in some experiments were hemicylindrical cement structures 10 cm long by 8 cm diameter determined from the relation between shelter size and lobster size observed by Cobb (1971). Juveniles were not routinely fed during most experiments but when required pieces of mussel flesh were provided daily to excess (at 0900-1000 h) and uneaten food removed the following day.

Experimental stock were laboratory bred and reared up to 12 months old (stage 17-19, 30-44mm carapace length) in a closed recirculation system as described in Section 1, at a temperature of 20±2°C and under an artificial light regime of 12:12 LD (0800-2000 h, 200-300 lux). Juveniles were removed from the rearing system four days before experimentation and maintained in a tank system similar to that used during recording.

Analysis of results.

In each experiment up to four individuals of similar size and moult stage were simultaneously recorded over a period of at least five days. The first day's record was excluded from the analysis. Hourly

activity values were recorded for each individual and the group mean hourly activity (MHA) estimated. These results were analysed both graphically and by Periodogram analysis (Enright, 1965). In the graphical illustrations MHA values exceeding 60 were arbitrarily given the same values, but the exact values were used in calculations. A horizontal bar is shown on each graph and shaded to indicate times of darkness. Periodograms are shown as plots of the standard deviation (SD) of form estimate against hour frequency. MHA values were compared where appropriate by calculating the statistic 'd', the ratio of the difference between the mean and the root of the sum of sample variances (Bailey, 1959).

Feeding activity

A mechano-electric recording system was used. A half shell of Mytilus was clamped to the lower end of a rod suspended in a plastic tank and allowed to move freely just off the bottom. An electrical impulse was generated from an amplifier unit by the closure of two brass contacts at the upper end of the rod each time the food was moved. Events were recorded by either Rustrak or A.F.T.E.R. unit.

Accidental innervation of the circuit by 'non-feeding' movements were minimised by the position of the food in the centre of a large tank (40 x 40 x 10 cm deep) full of static water and a shelter was provided for the subjects. Fresh food was provided each day between 0830 and 1000 h. The water was lightly aerated by airstones and changed every three days. The tank was placed under a lightproof cover inside which the lighting conditions could be controlled. Experimental stock were the same as for the locomotor activity studies.

Analysis of results

Records of individual animals were taken over a number of days and the mean hourly activity calculated. The number of events each hour were analysed graphically to demonstrate the pattern of activity, although the amounts of food consumed could not be estimated.

Design of experiments.

In the first series of experiments the locomotor activity was recorded under a number of different light schedules to establish the importance of light in regulating activity. The extent to which these responses were modified by shelter availability and light intensity was also tested. The influence of moult stage on locomotor activity was recorded by monitoring the activity of juveniles through the intermoult period, and was designed to determine whether observations on mid-moult animals fairly reflected the overall activity pattern. A comparison was also made between the activity of fed and starved animals, to illustrate the situation under culture conditions. The effect of light schedule on feeding activity of mid-moult animals was recorded at both daily feeding and at reduced rations, and the changes in feeding activity from pre-moult to post-moult monitored.

The conditions in each trial are shown in full in Table 1 and are briefly repeated before each set of results.

Table 1 Experimental treatments

	Light regime	Photoperiod (h)	Light Intensity (lux)	Shelter	Food	Lobsters Treatment^{-1}	Duration (d)
			Locomotor activity				
1.	12:12	0800-2000	250	-	-	4	4
2.	12:12	0800-2000	250	+	-	4	4
3.	12:12	0800-2000	400	+	-	4	4
4.	DD	-	<1	-	-	4	4
5.	DD	-	<1	+	-	4	4
6.	LL	24h	250	+	-	2	4
7.	LL	24h	400	+	-	4	4
8.	LL	24h	400	-	-	4	4
9.	DD	-	-	-	-	2	4 a
10.	6:6	1800-2400 0600-1200	250	-	-	4	4
11.	12:12	2100-0900	250	-	-	4	4
			Moult stage				
12.	12:12	0800-2000	250	-	+	2	47 and 56 b
	12:12	0800-2000	250	-	+	1	12 c
			Food availability				
13.	12:12	0800-2000	250	-	+/-	2+2	4
			Feeding activity				
14.	12:12	0800-2000	200	+	+	1	22 d
15.	DD	-	<1	+	+	1	5
16.	LL	24h	200	+	+	1	11
17.	20:4	2400-2000	200	+	+	1	4
18.	20:4	1400-1000	200	+	+	1	4
19.	12:12	0800-2000	200	+	1/3 e	1	10

Notes:

a Lobsters chilled to 4°C for 7 h before recording
b Activity through complete intermoult period
c Activity through portion of intermoult period
d Feeding activity from premoult to post moult
e Feeding every three days

Results

1. 12:12 LD, 250 lux, no shelter.

Under conditions similar to those in a typical culture system, the most conspicuous features of juvenile activity were peaks at the beginning of both light and dark phases (Figure 1a). There was no evidence that the MHA progressively increased to these peaks, although in some cases activity was high for the following one or two hours. No other activity pattern was apparent except for a slight decline in total daily activity over the experimental period. The sizes of the standard deviations of the form estimates shown in the periodogram analysis (Figure 1b) reflected these activity peaks at frequencies of 12 and 24 hours and an otherwise constant level of activity is evident in the 24h form estimate (Figure 1c). There was no significant difference between MHA in light and dark periods.

2. 12:12 LD, 250 lux, with shelter.

Peak activity at the beginning of light and dark phases was again the most obvious feature (Figure 2a). The overall activity level was less irregular, with periods of high and low activity persisting for several hours, but there was no consistent pattern. Periodogram analysis showed greater variation than in experiment 1, although the peaks at frequencies of 12 and 24 hours were still apparent (Figure 2b). Generally higher activity during the light period is apparent in the 24h form estimate (Figure 2c).

3. 12:12 LD, 400 lux, with shelter.

There was noticeably less activity during the light period over the first three days at the higher light intensity (Figure 3a). Activity peaks were present at the beginning of the dark phase but not at the beginning of the light phase. Periodogram analysis

(Figure 3b) indicated rhythmicity at frequencies of over 21h and was probably due to high activity during the first hours of darkness (Figure 3c). MHA was generally higher during darkness.

4. Constant darkness

There was slight evidence of rhythmic activity under constant conditions during the first 48 h, but subsequent activity was apparently random (Figure 4a). Periodogram analysis indicated rhythmicity at frequencies of 12-13h and 24-26h (Figure 4b) and there was generally higher activity during the first seven hours of expected darkness (Figure 4c).

5. DD, with shelter.

A more regular pattern of activity occurred when shelter was provided. The MHA tended to reach peaks by gradually increasing over a number of hours and activity decline was more gradual, giving irregular cycles of low and high activity (Figure 5a). Periodogram analysis (Figure 5b) indicated rhymicity associated with frequencies of 12-13 and 24-26 h which seemed to be due to activity peaks around 1100 and 2300h (Figure 5c).

6. Constant illumination, 250 lux, with shelter.

A pronounced pattern of activity was evident with high activity centred around expected darkness and extending through to 1200-1500 h (Figure 6a). Activity was generally low around 1200-2400 h and there was a noticeable drift in the time of onset of high activity, beginning at 1900h on the first day and 2400h on the fourth day. Rhythmic activity was indicated at frequencies of 13-14h (Figure 6b) but large standard deviations

masked the response at higher frequencies.

7. LL, 400 lux, with shelter.

The level of activity at a higher light intensity was very low after the first 12h (Figure 7a) but there was no evidence of the rhythmicity found in experiment 6 (Figure 7 b, c).

8. LL, 400 lux, no shelter.

Activity levels were only slightly higher when no shelter was available and there was little fluctuation around the mean value (Figure 8a). There was no discernible pattern to activity in either the periodogram analysis or 24h form estimate (Figures 8 b, c.).

9. Constant darkness following chilling.

The locomotor activity was apparently random after chilling for 7 hours (0900-1600 h) at 4°C (Figure 9a). The only conspicuous feature was a rise in the general activity level after the first 48 hours but there was no evidence of rhythmic activity (Figures 9 b, c). The activity of a second juvenile exposed to the same condition was also apparently random (Figures 10a, b, c).

10. 6:6 LD, 250 lux, no shelter.

The locomotor activity showed the characteristic activity peaks at the beginning and end of each light period but the MHA was otherwise unaffected by either light or dark phase (Figure 11a). Rhythmicity was indicated at frequencies of 6, 12, 18 and 24 h (Figure 11b). A lower MHA was evident during expected day with activity increasing from 1700 h into the period of expected darkness (Figure 11c).

11. Reversed 12:12 LD, 250 Lux, no shelter.

After a progressive decline in activity during the first light period, the only obvious feature was the high activity at the beginning and end of each light period (Figure 12a). During the last 48h high activity was evident during expected darkness and was followed by low activity between 1100 and 1900h. Periodogram analysis confirmed rhythmicity at 12 and 24h frequencies (Figure 12b) which corresponded to the activity peaks seen in Figure 12c, and there was some secondary rhythmicity at frequencies of 16 and 20h.

In all the above trials there was considerable variation in the responses of individual juveniles but a comparison of 'd' values for hourly activity in light or dark periods, or expected periods under constant conditions, showed that differences were rarely significant because of high variances. A crude analysis was therefore based on an arbitrary difference of 5 events. h^{-1} and revealed that 62% of test animals had a similar activity level throughout the day, 28% were generally dark active and 10% were mainly light active.

12. Activity through the inter-moult period, under 12:12 LD, 250 lux, no shelter.

The daily MHA values for nocturnal and diurnal activity of two juveniles are shown in Figures 13 and 14. In the first juvenile activity decreased after ecdysis and during this period was predominantly nocturnal. A minimum activity level occurred around 20 days after ecdysis (equivalent to 30% of the intermoult period) after which activity increased to a relatively constant, mainly diurnal pattern, with considerable daily fluctuation in total activity. Nocturnal activity became more apparent in the days preceding ecdysis.

A second lobster exhibited a similar pattern of daily activity, with an activity minimum 33% of the way through the intermoult period, but nocturnal activity predominated throughout. Activity during a portion of the intermoult period was recorded in a third individual (Figure 15), where the activity minimum occurred 35% of the way through the intermoult period and largely nocturnal activity predominated both before and after.

13. Effect of food availability under 12:12 LD, 250 lux, no shelter.

A clear nocturnal activity pattern was evident in daily fed lobsters (Figure 16a). Activity increased immediately after the onset of darkness, remained at a high level until 0300 h and then decreased to a constant low level during the light phase. A transient activity peak occurred at the beginning of the light period. Periodogram analysis indicated rhythmicity at around 12 and 24h frequencies (Figure 16c). The activity of unfed lobsters showed less difference between dark and light periods and activity peaks at light-dark transitions were lower. A slightly higher amount of nocturnal activity was however apparent and rhythmicity indicated at frequencies of 12 and 24h (Figure 16d).

14. Feeding activity around ecdysis under 12:12 LD, 200 lux, with shelter.

The feeding activity was recorded over a 22 day period and the proportions of nocturnal and diurnal feeing each day are shown in Figure 17. Feeding activity was further characterised by calculating the average daily pattern over four stages around ecdysis.

These were:

Figure 18a 11-5 days before ecdysis Stage C4 (Drach, 1939).

18b 4-1 days before ecdysis D

18c 1-4 days after ecdysis A+B

18d 5-10 days after ecdysis B+C1

The MHA was irregular during the first seven days with feeding confined almost entirely to the dark periods. In the days preceding moult, the MHA was more constant and equally divided between nocturnal and diurnal activity. Following ecdysis MHA dropped to a minimum and there was only a little nocturnal activity during the next three days. Activity then increased up to a maximum eight days after ecdysis and became more irregular with feeding during both day and night (figure 17).

The pattern of feeding within each day is clearer in Figures 18a-d. During the late intermoult period, feeding began after the onset of darkness and reached a maximum level some three hours later. Negligible activity occurred between 0400 and 1900h. Just before ecdysis this pattern was augmented by light period feeding with a secondary peak at 1100h. During the postmoult phase there was only a little feeding activity confined almost entirely to the dark period. Feeding activity subsequently increased, especially during the night and light period activity also increased.

15. Feeding activity under constant darkness.

No discernible pattern was evident apart from a tendency towards low activity around 0600h (Figure 19a). Periodogram analysis showed no overt rhythmic component to the activity but high standard deviations were present at frequencies of 10, 14 and 23h (Figure 19b). In general, periods of low activity occurred between

0400 and 1000h, and rose to a maximum between 2000 and 2400h (Figure 19c) which indicated an endogenous component to feeding activity.

16. Feeding activity under constant illumination of 200 lux. Throughout most of the experimental period the highest activity was recorded around 2400h and this feature was especially noticeable for a period of six days when activity was at other times negligible (Figure 20a). Periodogram analysis did not however confirm this observation (Figure 20b) and it seems that daily variations in the time and intensity of peak feeding masked what was at times an overt rhythm. There was no noticeable drift in the time of peak feeding but the duration of feeding varied from day to day. On an average daily basis, most feeding occurred between 2000 and 2200 h and was constantly low at other times (Figure 20c).

17 and 18. Feeding activity at long day photoperiods 20:4 LD, 200 lux. When only four hours darkness was provided each day, feeding activity remained confined to the hours of darkness, irrespective of the time of the dark period (Figure 21). Activity appeared to be more intense when the dark period occurred at night than when the dark period was provided around 1200h.

19. Feeding activity at reduced rations under 12:12 LD, 200 lux. When a juvenile was fed every three days the amount of feeding activity gradually decreased (Figure 22). The activity after continuous daily feeding (Day 1) extended throughout the dark period after a peak during the first few hours. After two days starvation some feeding began immediately after food presentation but most activity was confined to the first eight hours of

darkness. After a further period of starvation the activity was further decreased and mainly confined to the dark. By the tenth day feeding was confined to two short periods, 5 and 13-16h after food presentation.

Figure 1a. Mean locomotor activity (events. h^{-1}) of juvenile lobsters in 12:12 LD, 250 lux, no shelter.

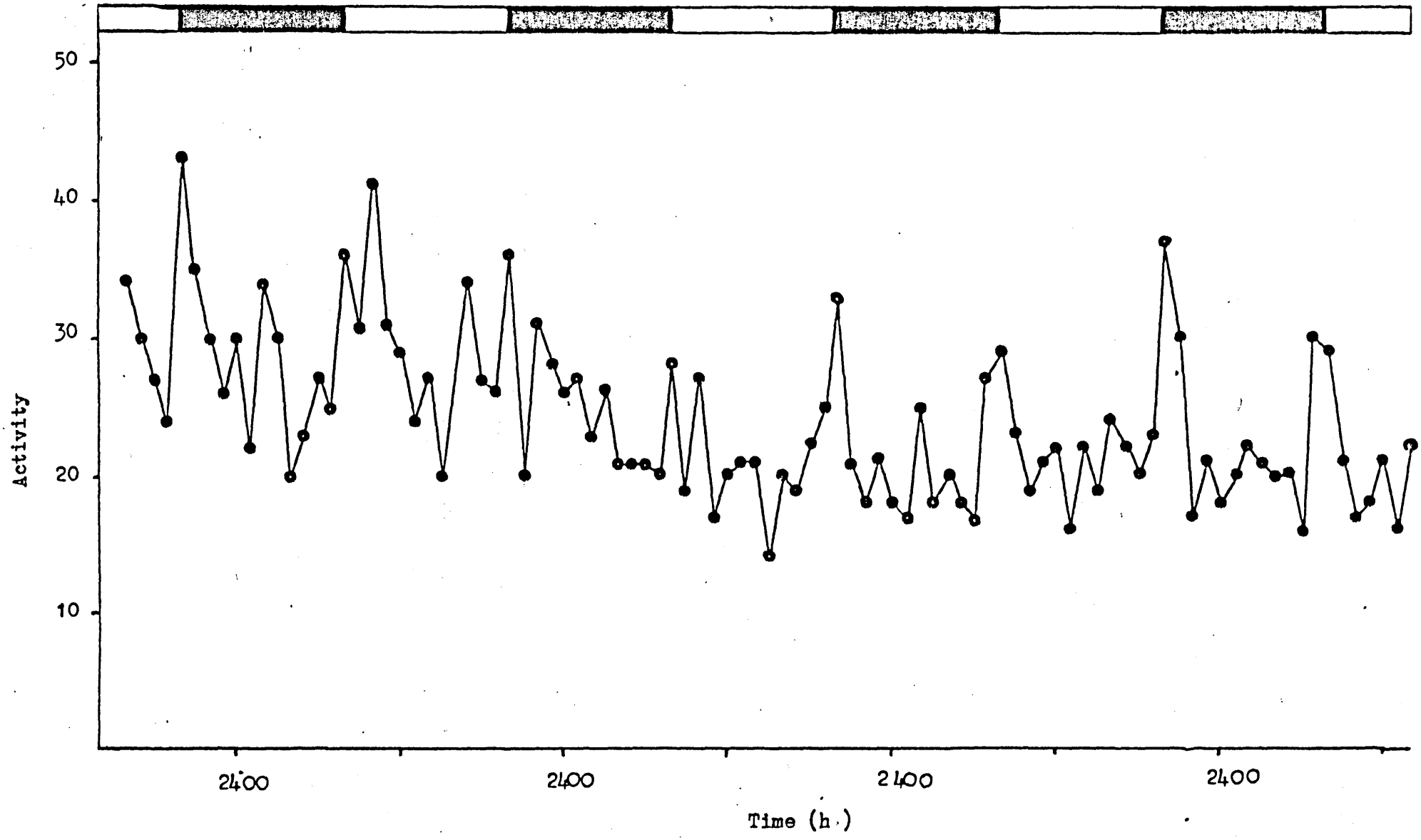
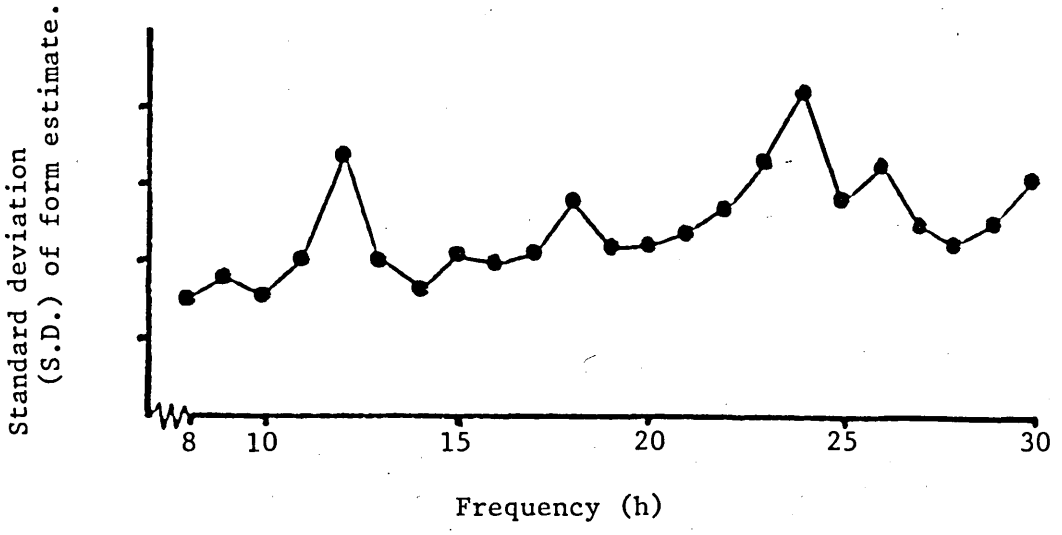

50
40
30
20
10
Activity
2400
2400
2400
2400
Time (h)

Figure 1b Juvenile activity in 12:12 LD, 250 lux, no shelter. Periodogram of mean hourly activity values for frequencies of 8-30h.

Figure 1c 24h form estimate (mean events.h^{-1})


Standard deviation
(S.D.) of form estimate.
8
10
15
20
25
30
Frequency (h)

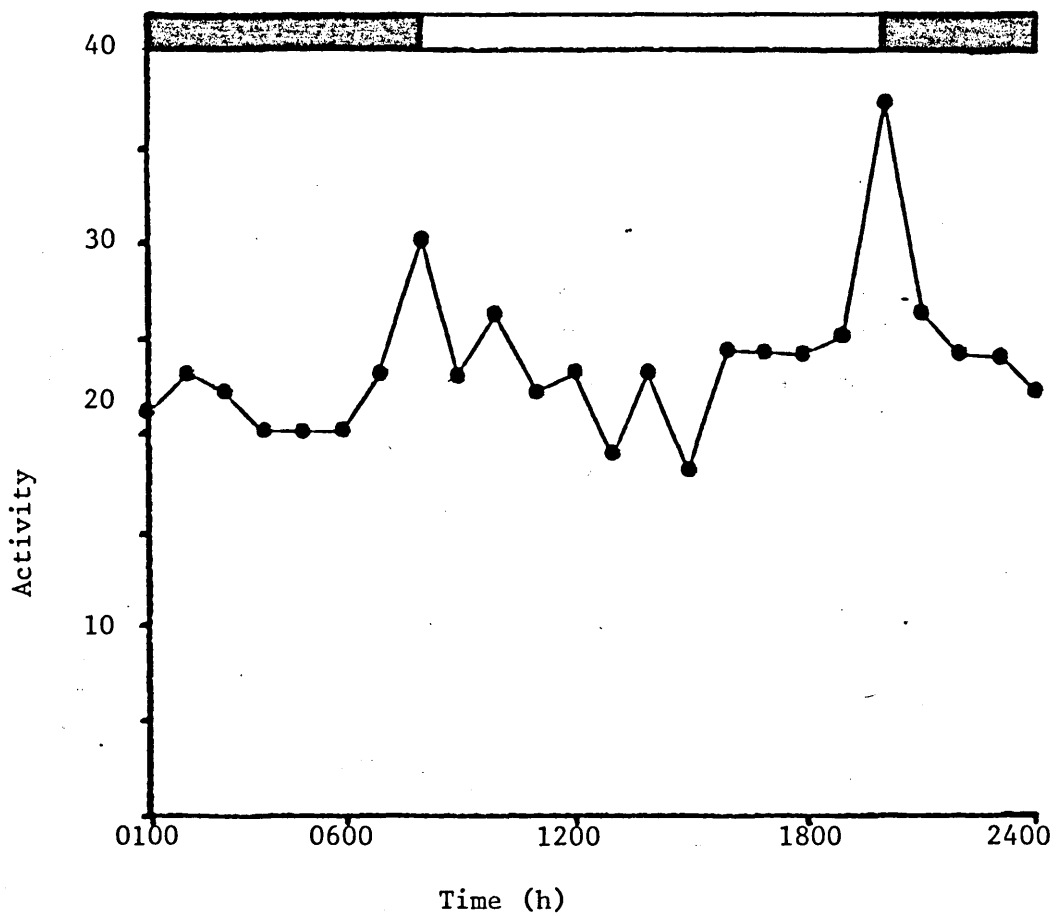

40
30
20
10
Activity
0100
0600
1200
1800
2400
Time (h)

Figure 2a Mean locomotor activity (events.h^{-1}) of juvenile lobsters in 12:12 LD, 250 lux, with shelter.

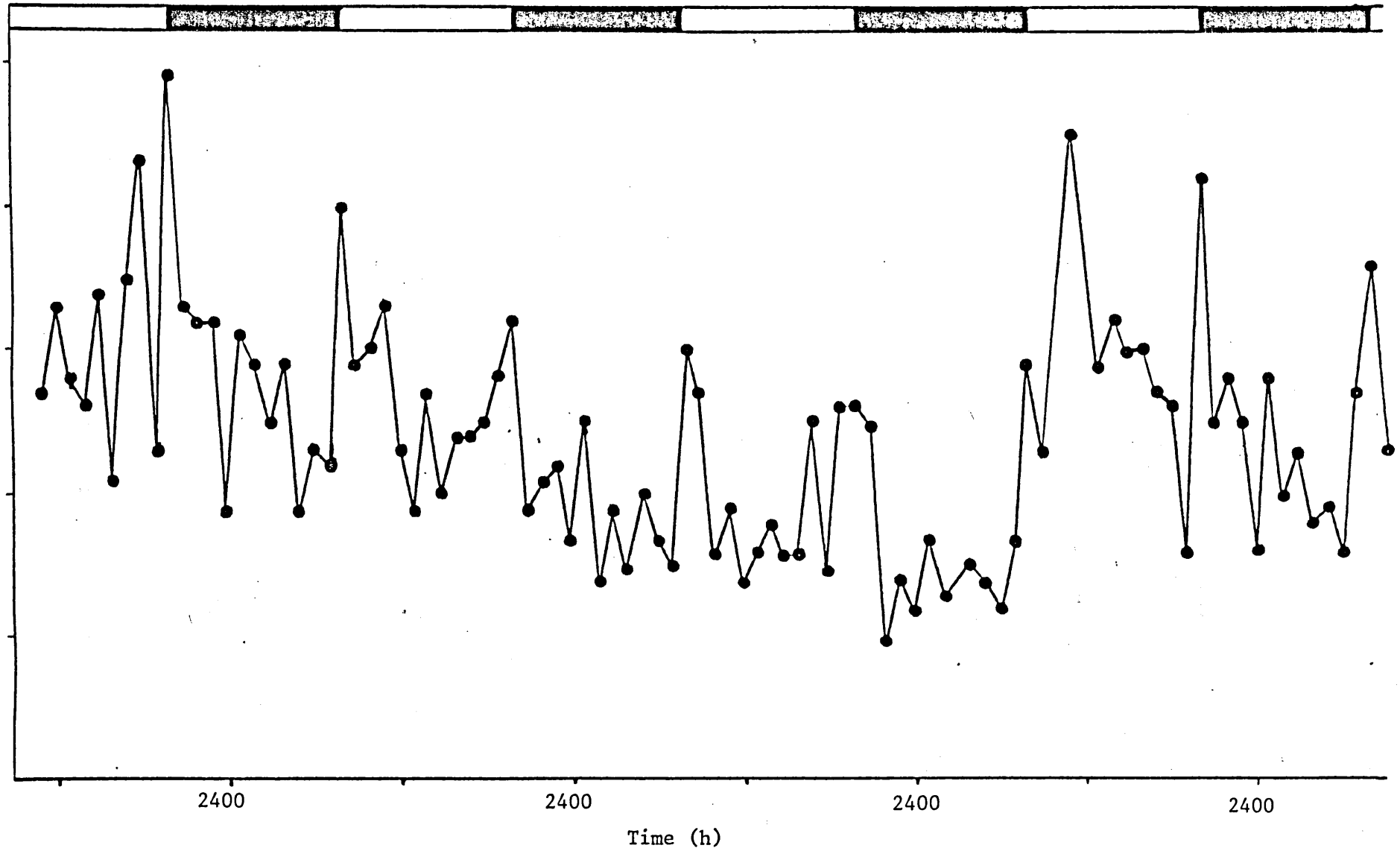
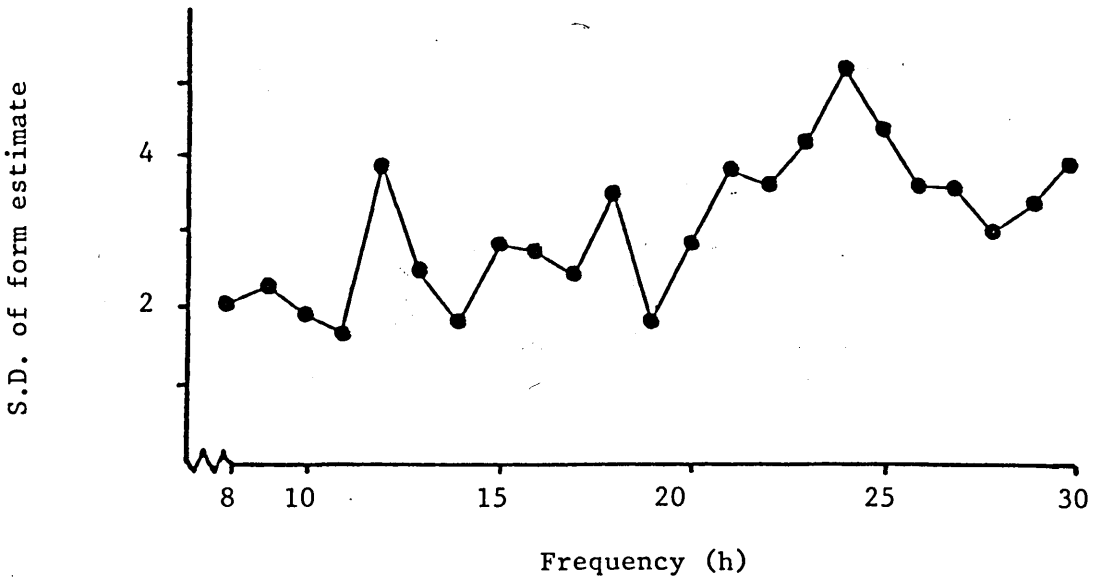

50
40
30
20
10
I39
Activity
2400
2400
2400
2400
Time (h)

Figure 2b Juvenile activity in 12:12 LD, 250 lux, with shelter - Periodogram of mean hourly activity values for frequencies of 8-30h.

Figure 2c 24h form estimate (mean events.h^{-1})


S.D. of form estimate
4
2
8
10
15
20
25
30
Frequency (h)

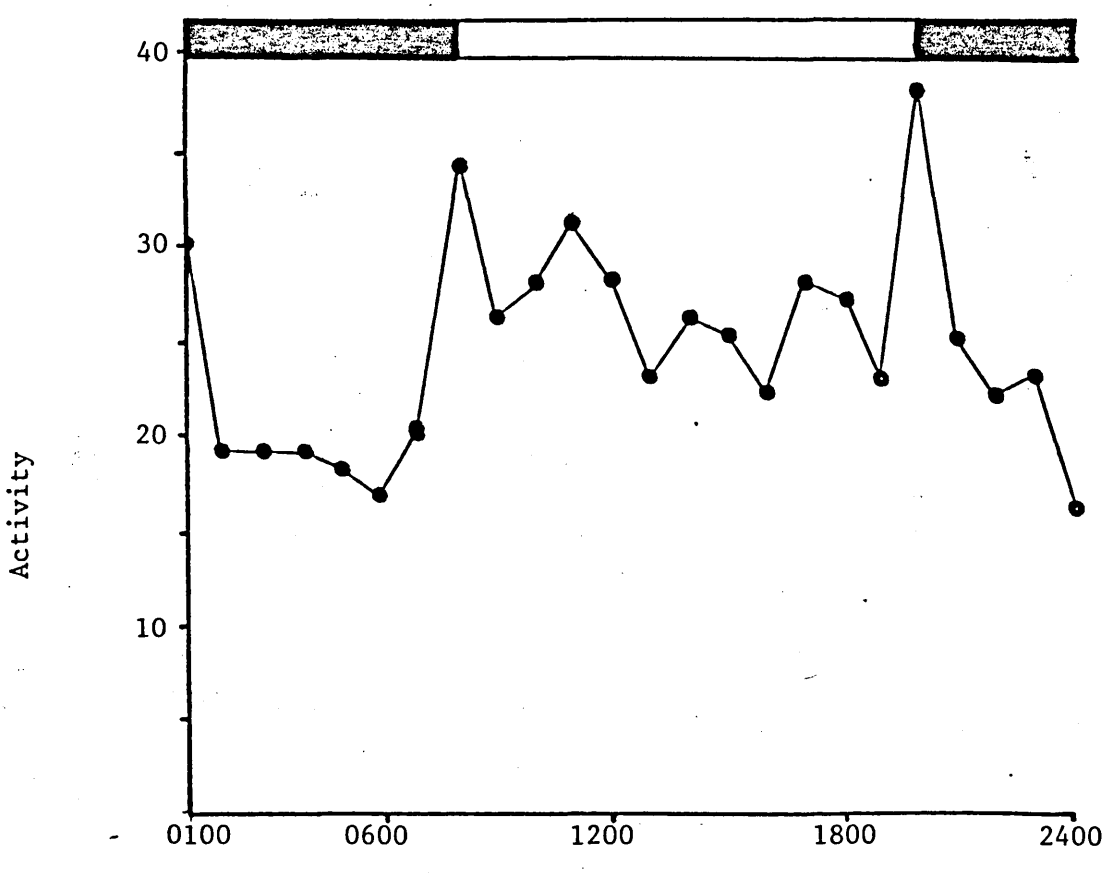

Activity
40
30
20
10
0100
0600
1200
1800
2400
Time (h)

Figure 3a Mean locomotor activity (events.h^{-1}) of juvenile lobsters in 12:12 LD, 400 lux, with shelter.

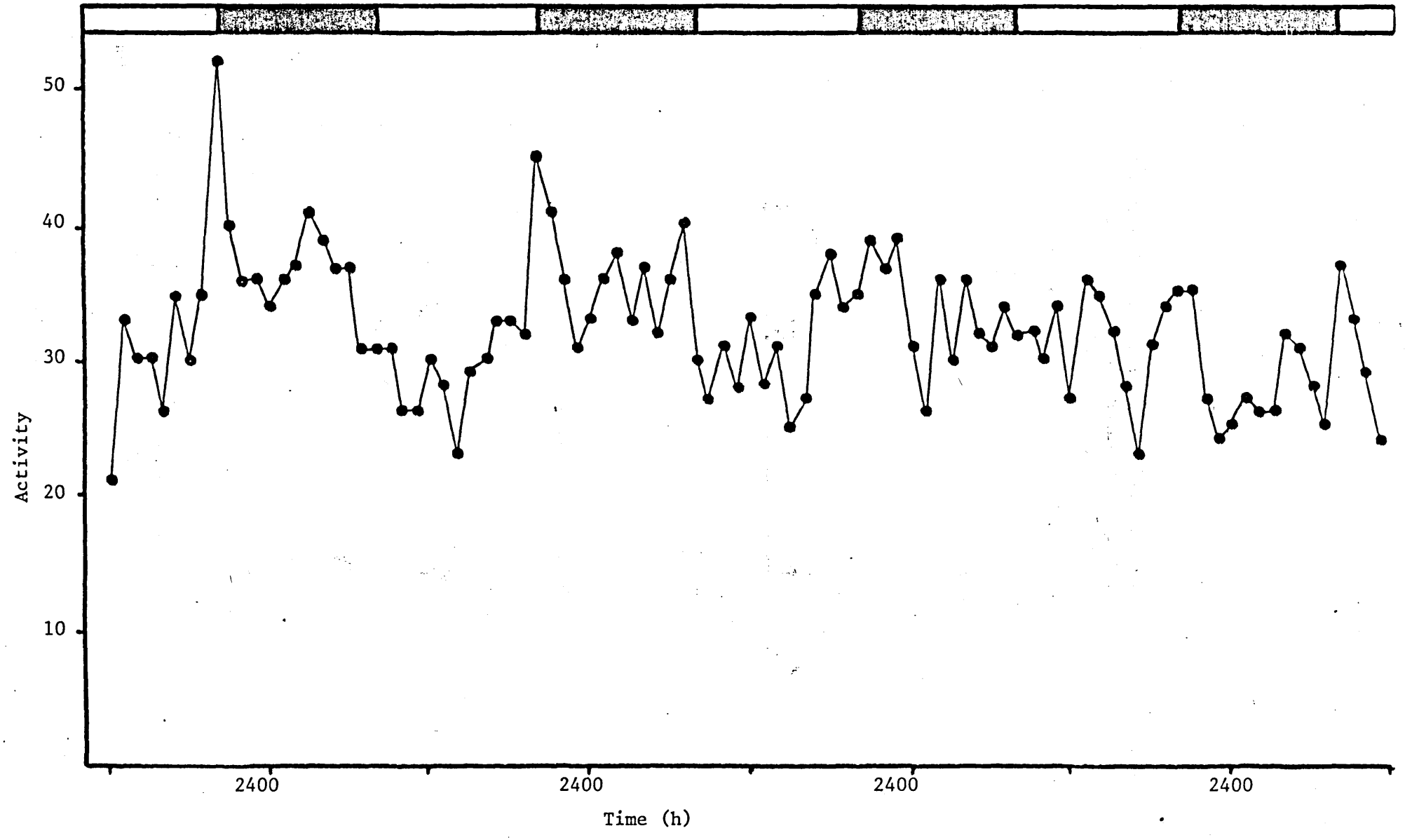

50
40
30
20
10
Activity
2400
2400
2400
2400
Time (h)

Figure 3b. Juvenile activity in 12:12 LD, 400 lux, with shelter. Periodogram of mean hourly activity values for frequencies of 8-30 h.

Figure 3c 24h form estimate (mean events.h^{-1})

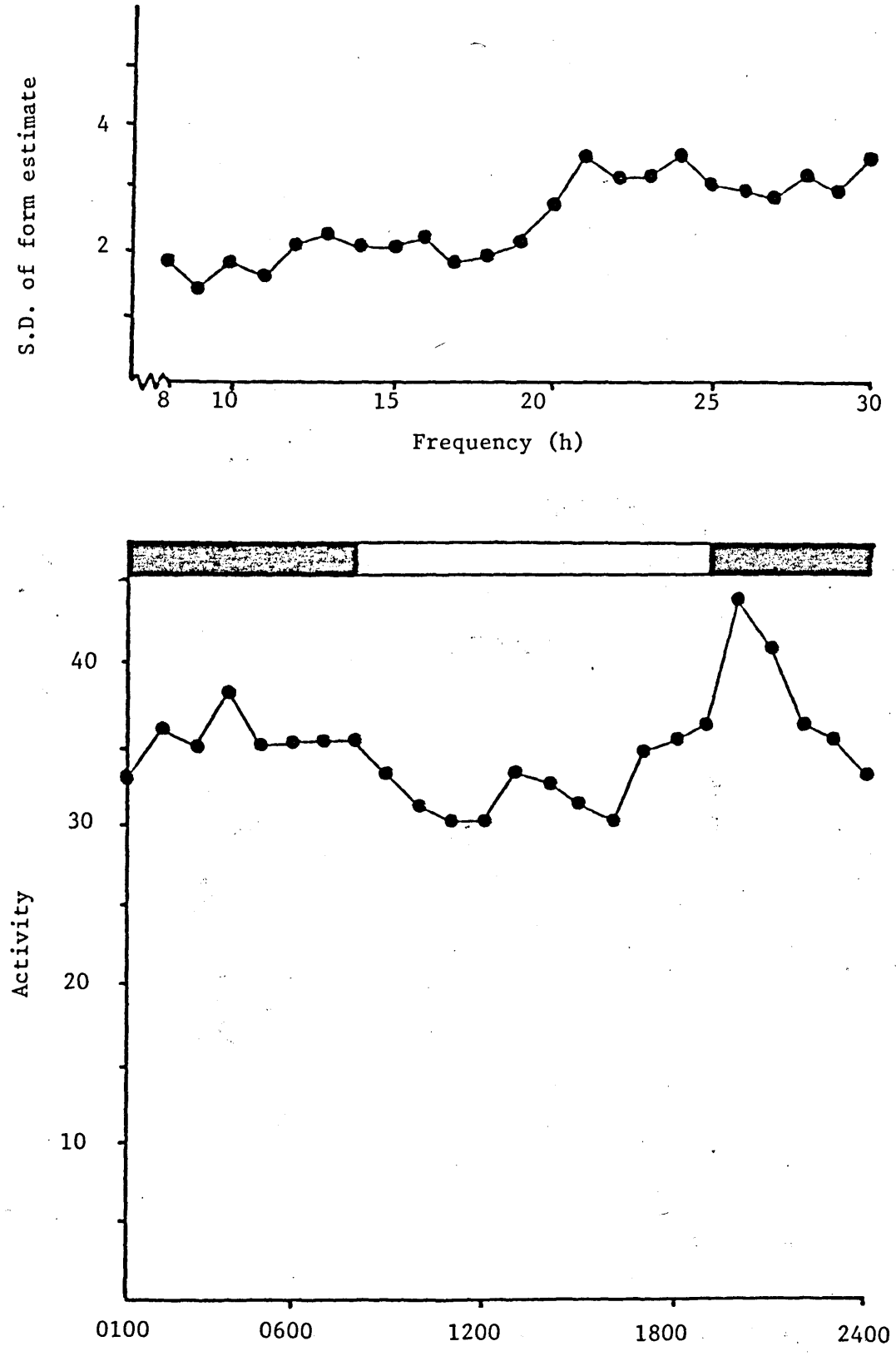

S.D. of form estimate
4
2
8
10
15
20
25
30
Frequency (h)
Activity
40
30
20
10
0100
0600
1200
1800
2400
Time (h)

Figure 4a Mean locomotor activity (events.h^{-1}) of juvenile lobsters in DD, no shelter.

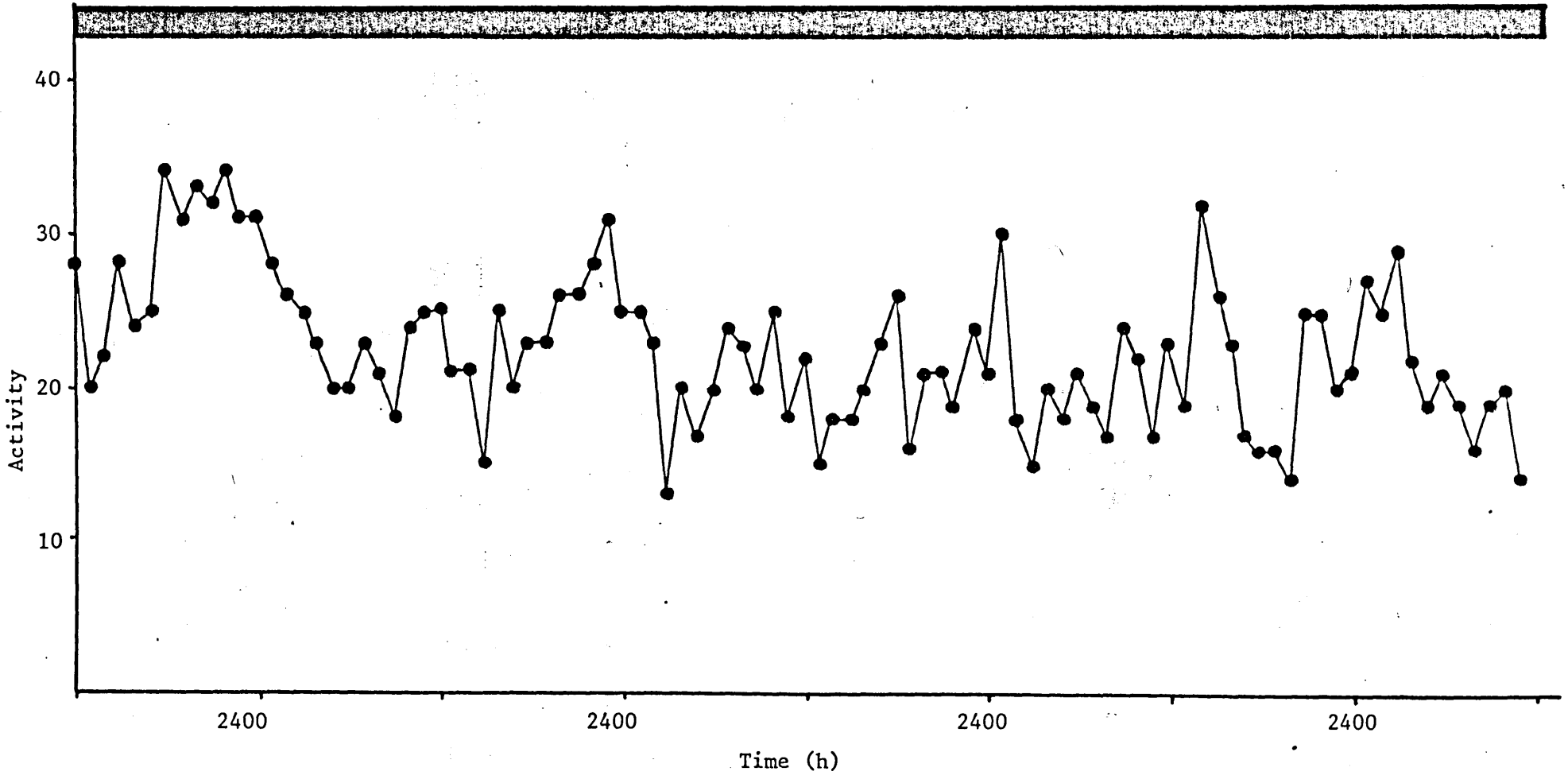
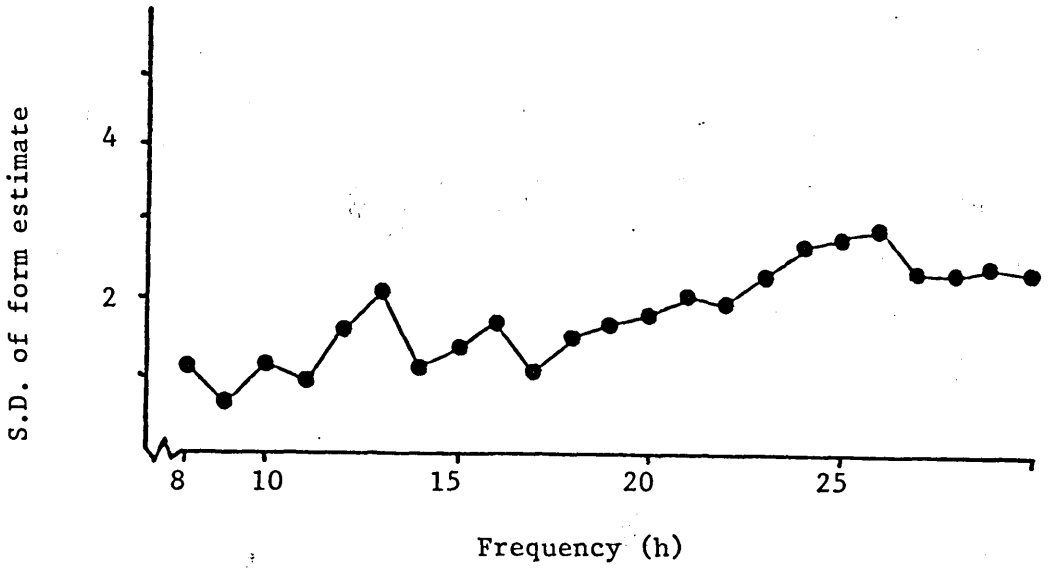

40
30
20
10
Activity
2400
2400
2400
2400
Time (h)

Figure 4b Juvenile activity in DD, no shelter - Periodogram of mean hourly activity values for frequencies of 8-30h.

Figure 4c 24h form estimate (mean events.h^{-1})


S.D. of form estimate
4
2
8
10
15
20
25
Frequency (h)

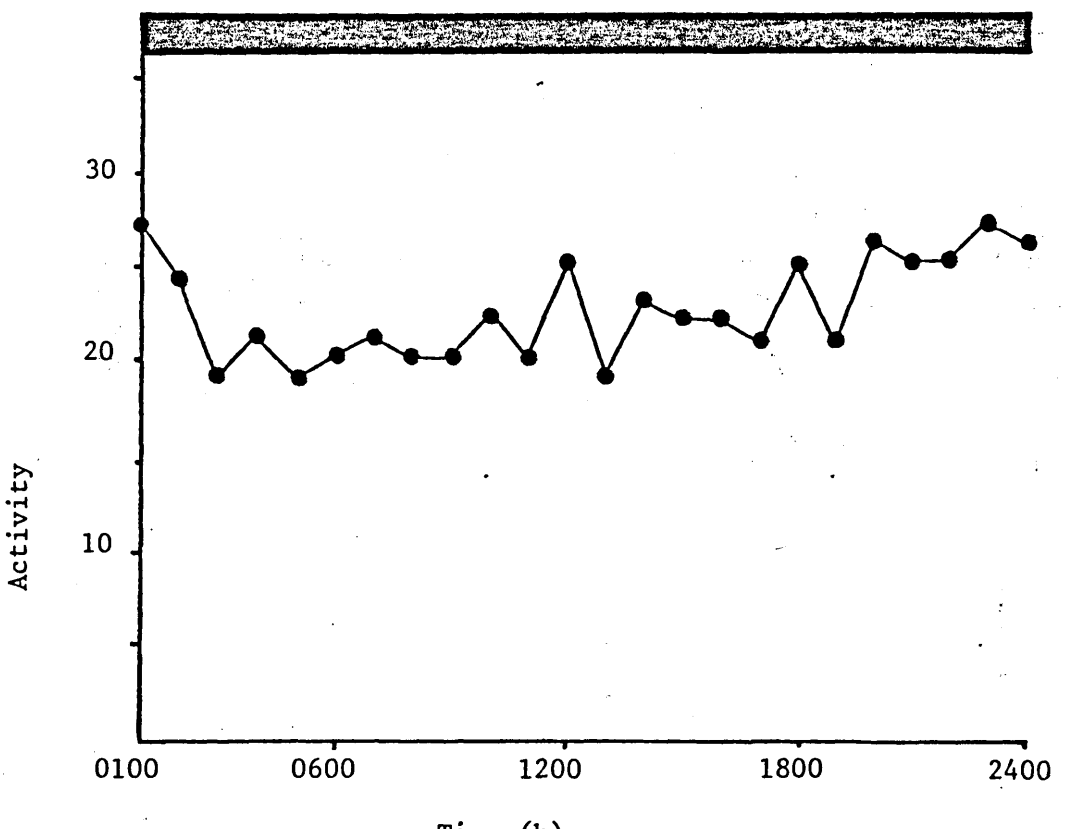

Activity
30
20
10
0100
0600
1200
1800
2400
Time (h)

Figure 5a Mean locomotor activity (events h^{-1}) of juvenile lobsters in DD, with shelter.

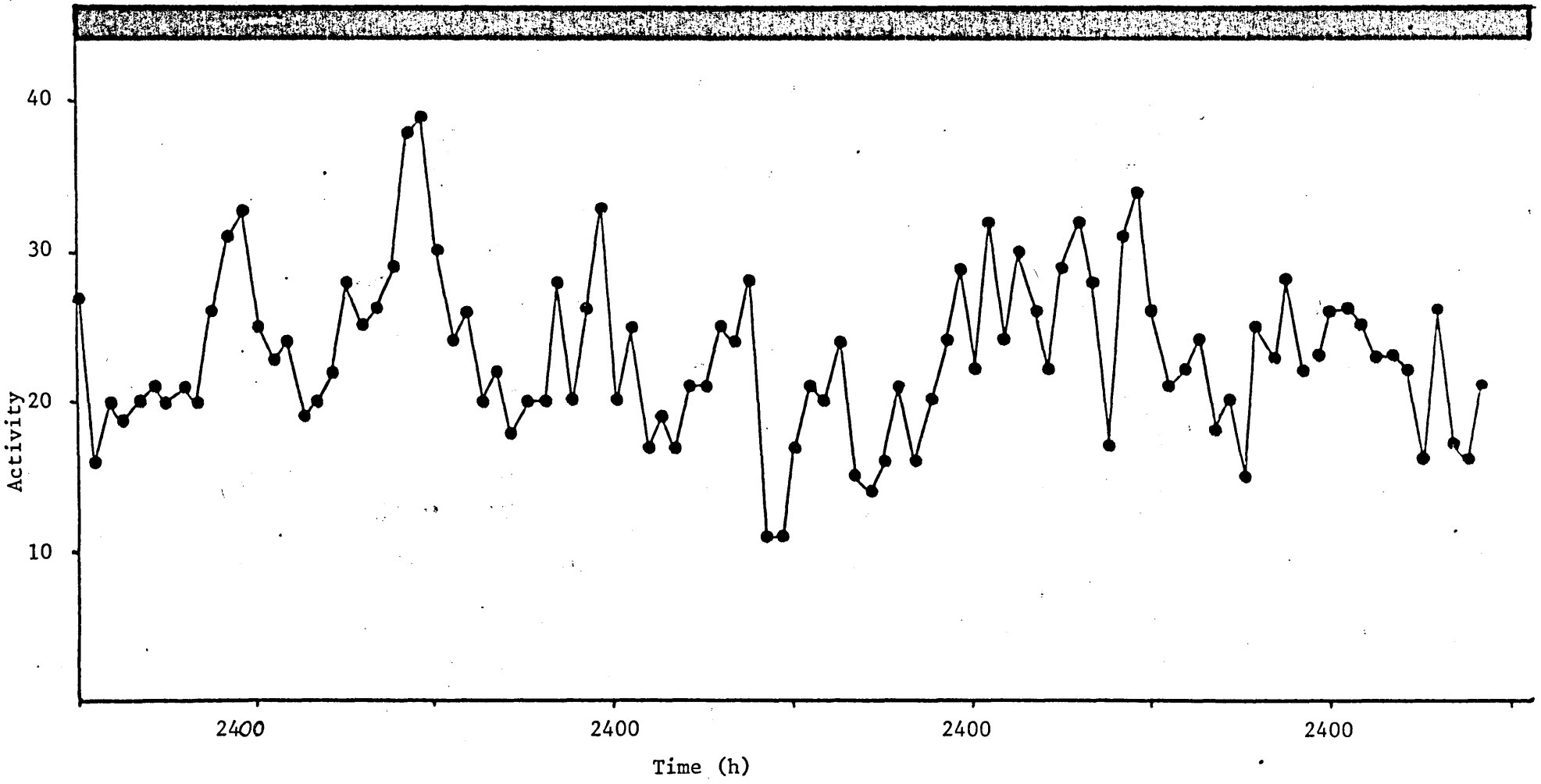
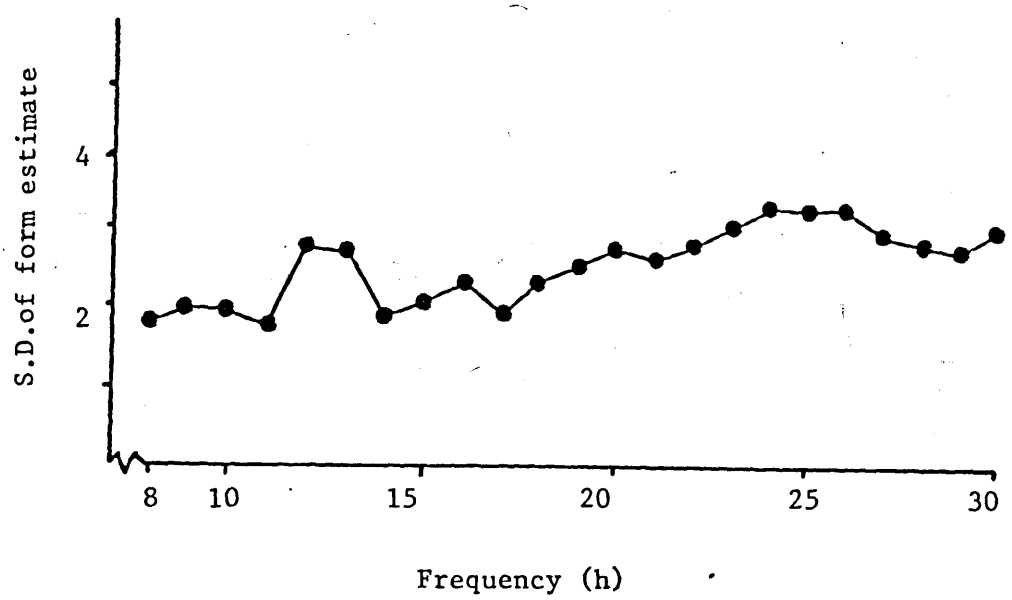

40
30
20
10
Activity
2400
2400
2400
2400
Time (h)

Figure 5b Juvenile activity in DD, with shelter. Periodogram of mean hourly activity values for frequencies of 8-30h.

Figure 5c 24h form estimate (mean events.h^{-1})


S.D.of form estimate
4
2
8
10
15
20
25
30
Frequency (h)

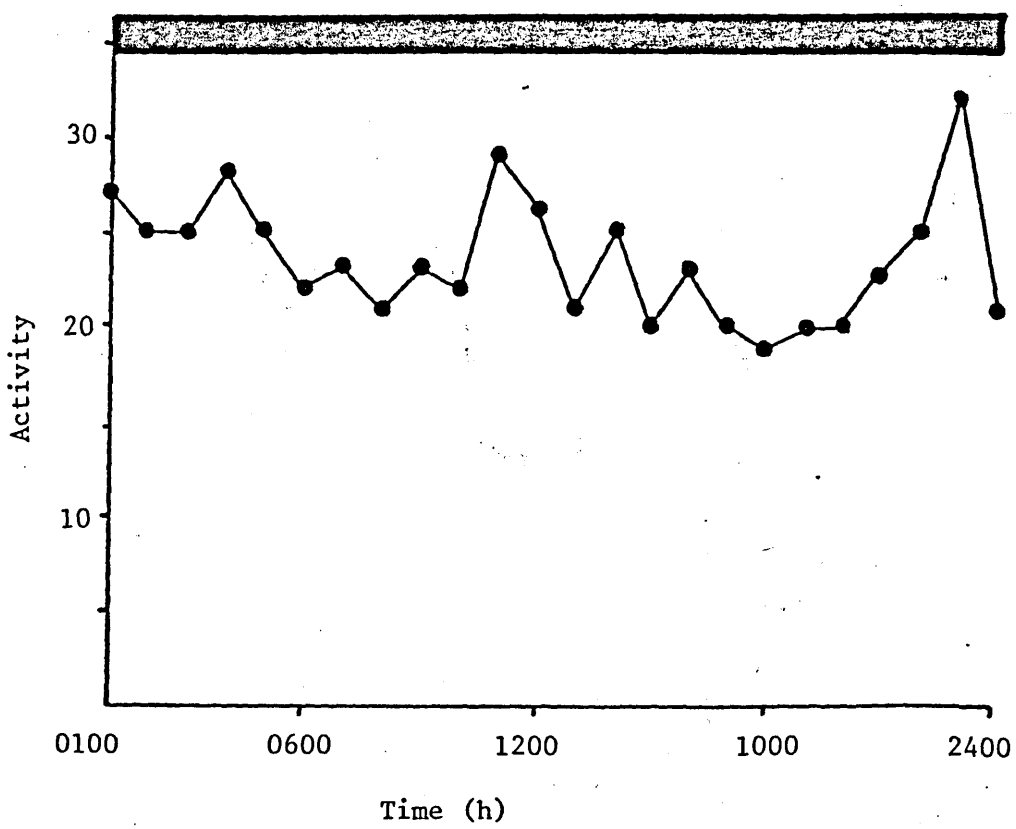

Activity
30
20
10
0100
0600
1200
1000
2400
Time (h)

Figure 6a Mean locomotor activity (events.h^{-1}) of juvenile lobsters in LL, 250 lux, with shelter.

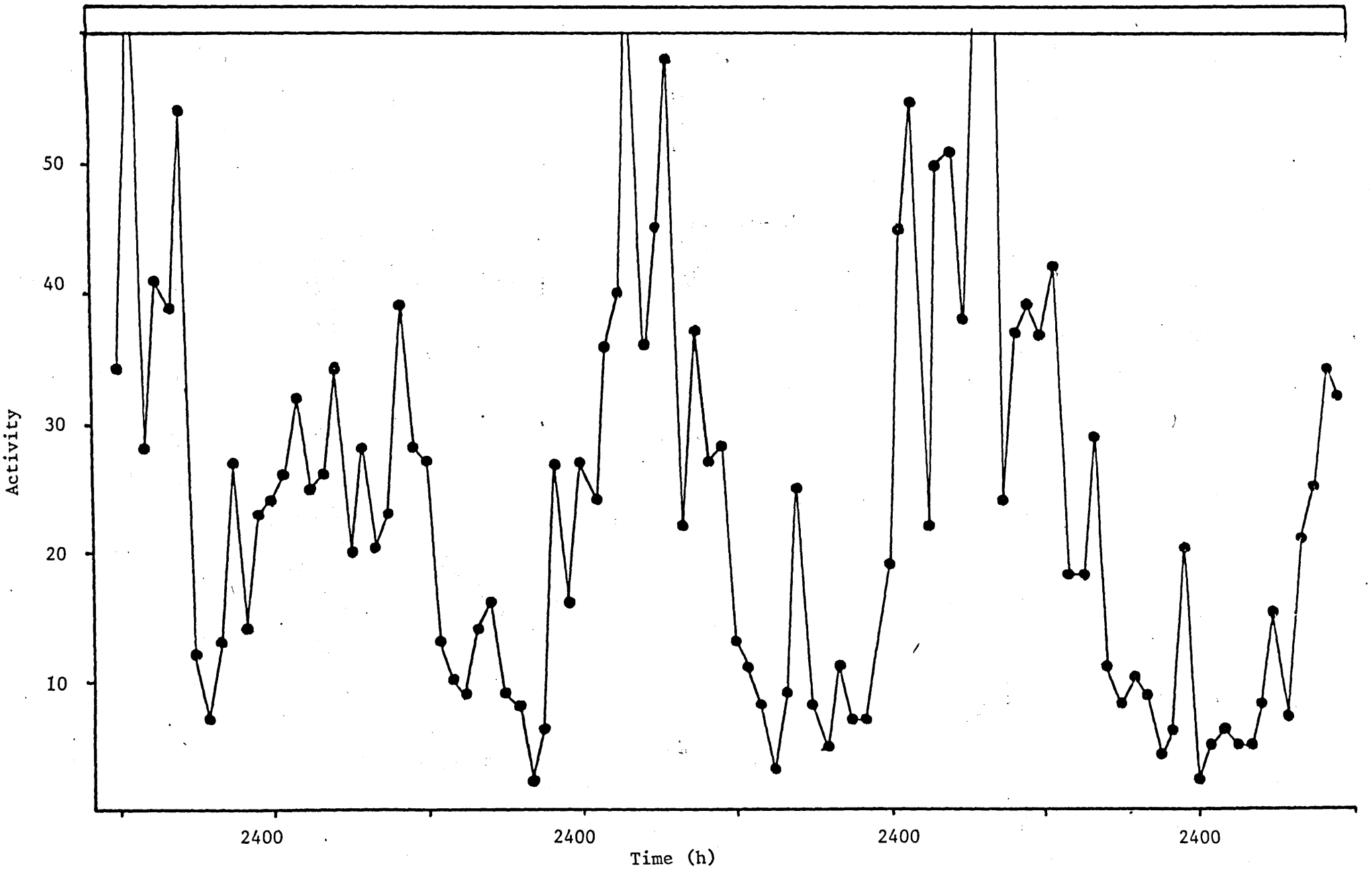
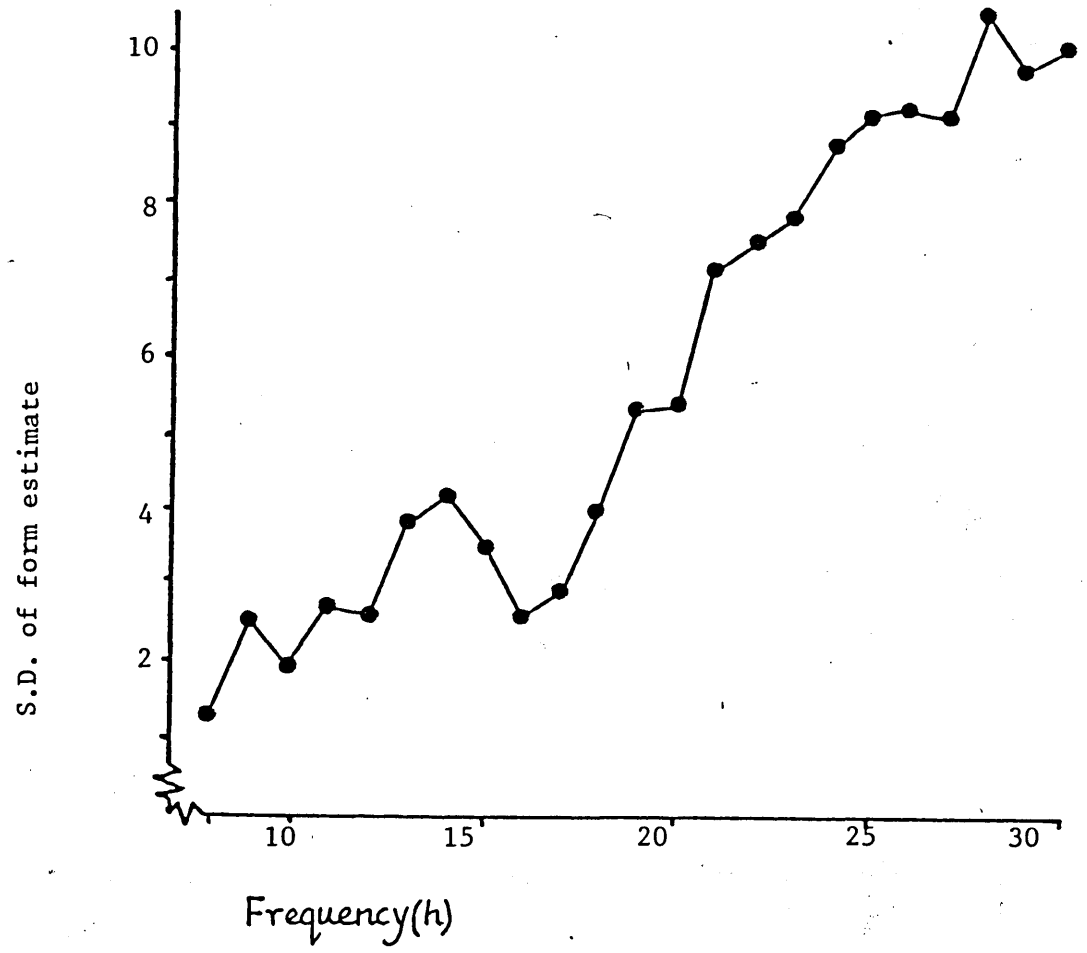

50
40
30
20
10
Activity
2400
2400
2400
2400
Time (h)

Figure 6b 24h form estimate (mean events $.h^{-1}$)

Figure 6c Juvenile activity in LL, 250 lux,with shelter. Periodogram of mean hourly activity values for frequencies of 8-30h.


S.D. of form estimate
10
8
6
4
2
10
15
20
25
30
Frequency(h)

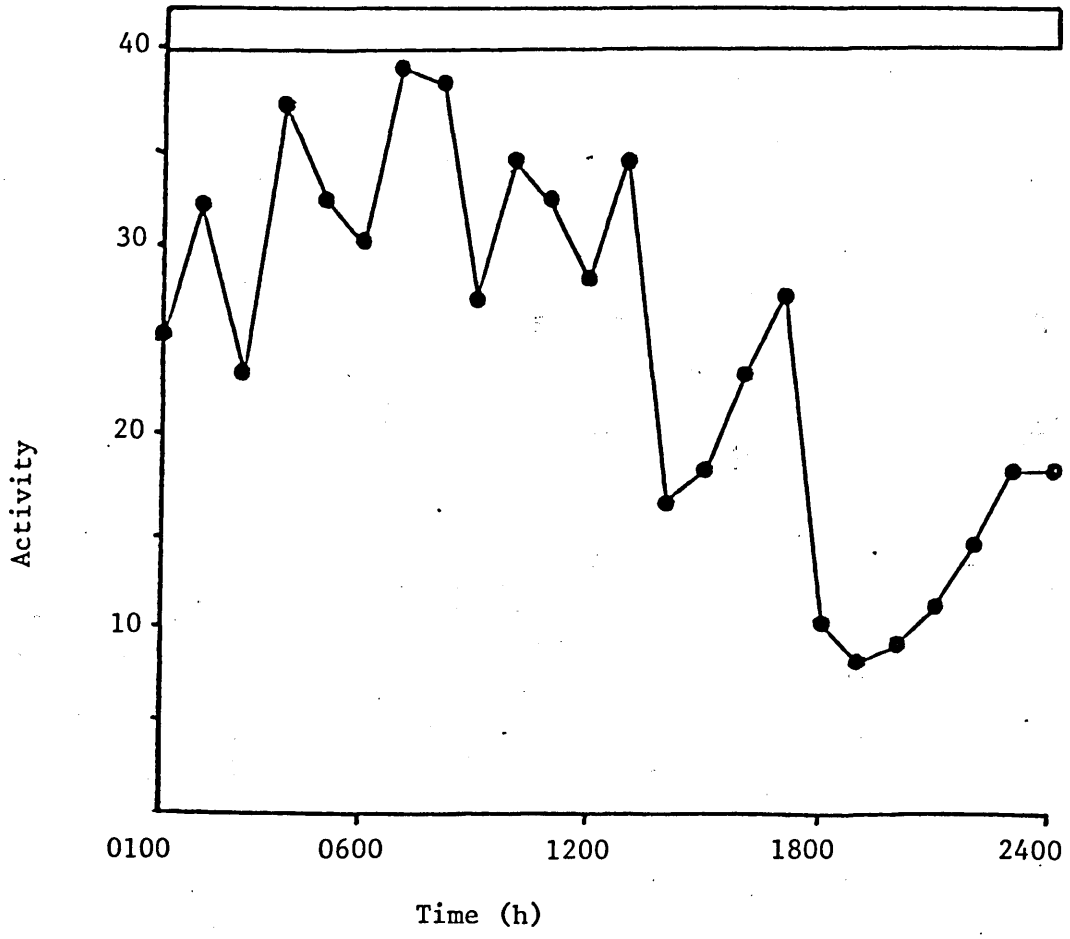

Activity
40
30
20
10
0100
0600
1200
1800
2400
Time (h)

Figure 7a. Mean locomotor activity (events. h^{-1}) of juvenile lobsters in LL, 400 lux, with shelter.

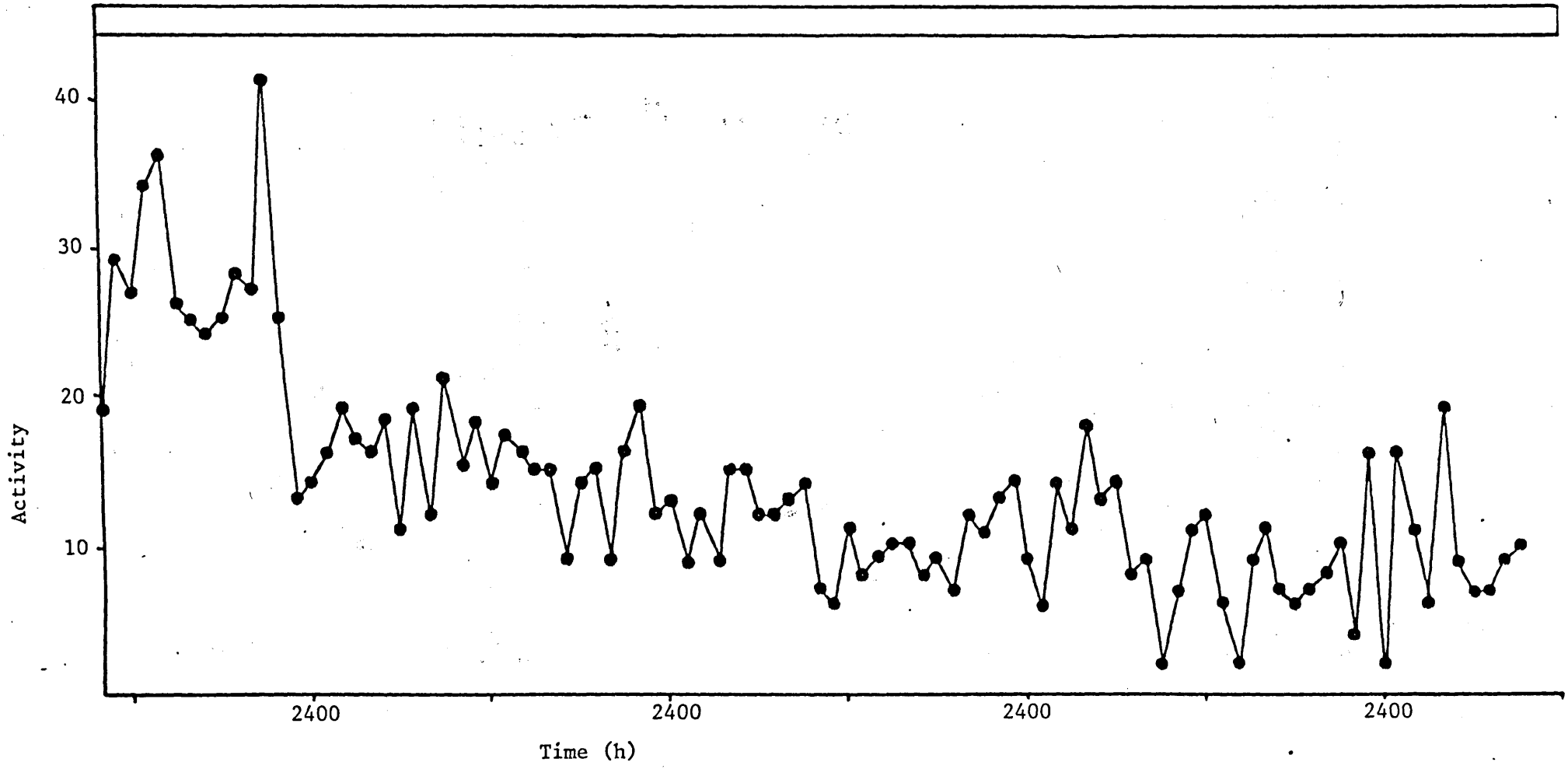
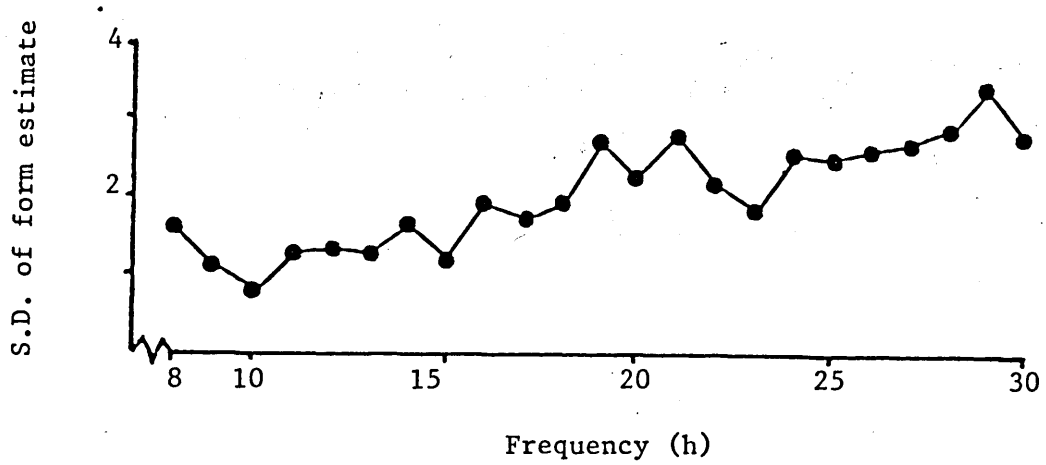

40
30
20
10
Activity
2400
2400
2400
2400
Time (h)

Figure 7b Juvenile activity in LL, 400 lux, with shelter.

Periodogram of mean hourly activity values for frequencies of 8-30h.

Figure 7c 24h form estimate (mean events.h^{-1}).


S.D. of form estimate
4
2
8
10
15
20
25
30
Frequency (h)

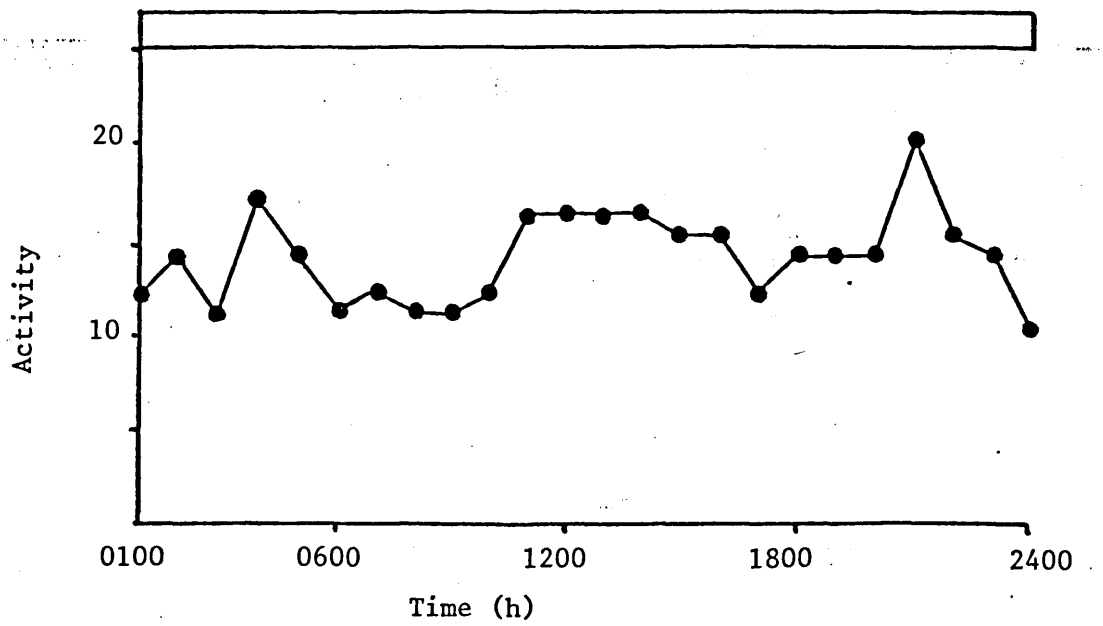

Activity
20
10
0100
0600
1200
1800
2400
Time (h)

Figure 8a Mean locomotor activity (events h^{-1}) of juvenile lobsters in LL, 400 lux, no shelter.

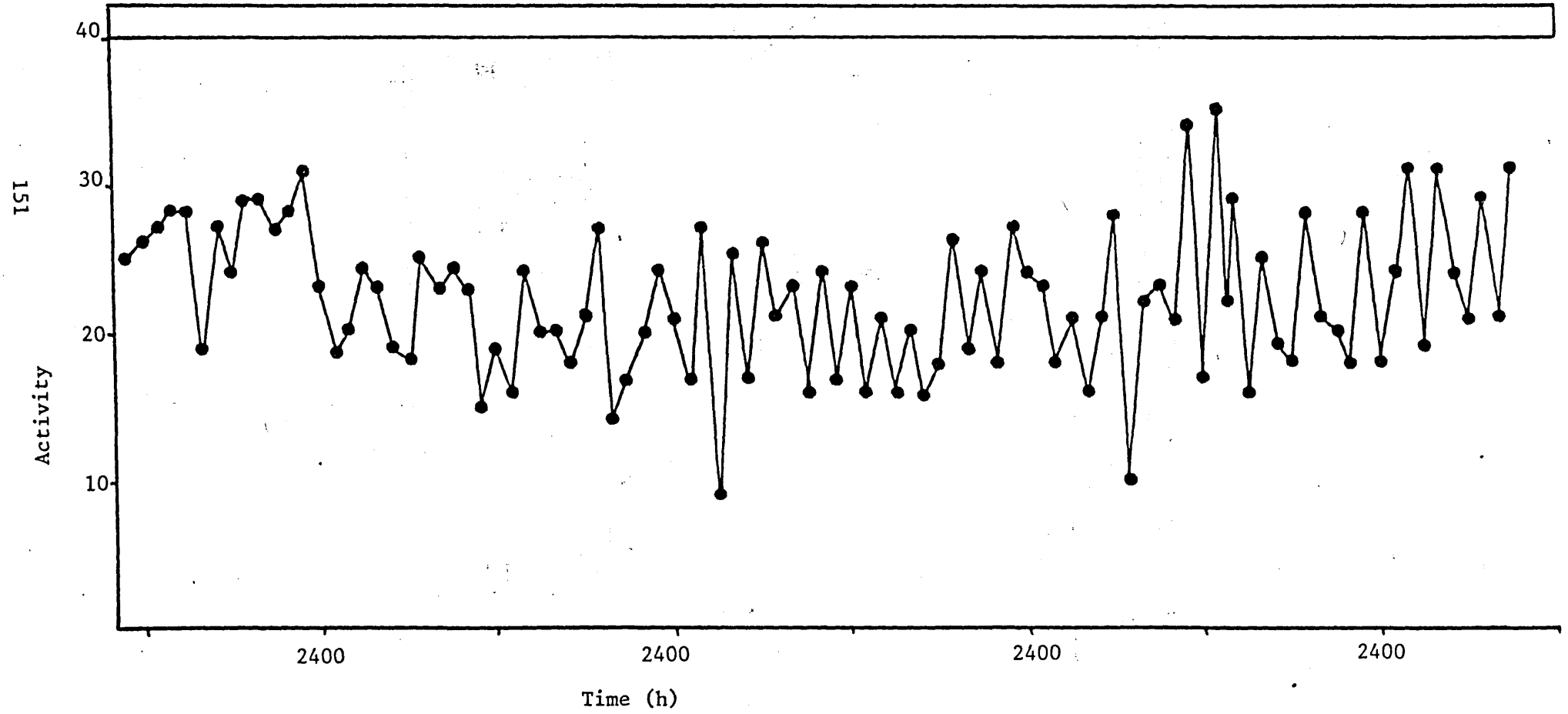
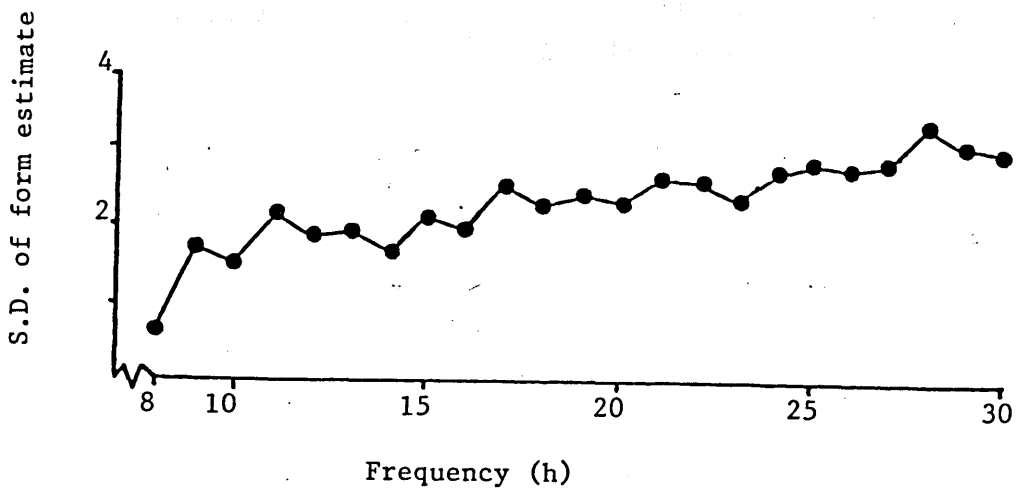

151
40
30
20
10
Activity
2400
2400
2400
2400
Time (h)

Figure 8b Juvenile activity in LL, 400 lux, no shelter. Periodogram of mean hourly activity values for frequencies of 8-30h.

Figure 8c 24h form estimate (mean events.h^{-1})


S.D. of form estimate
4
2
8
10
15
20
25
30
Frequency (h)

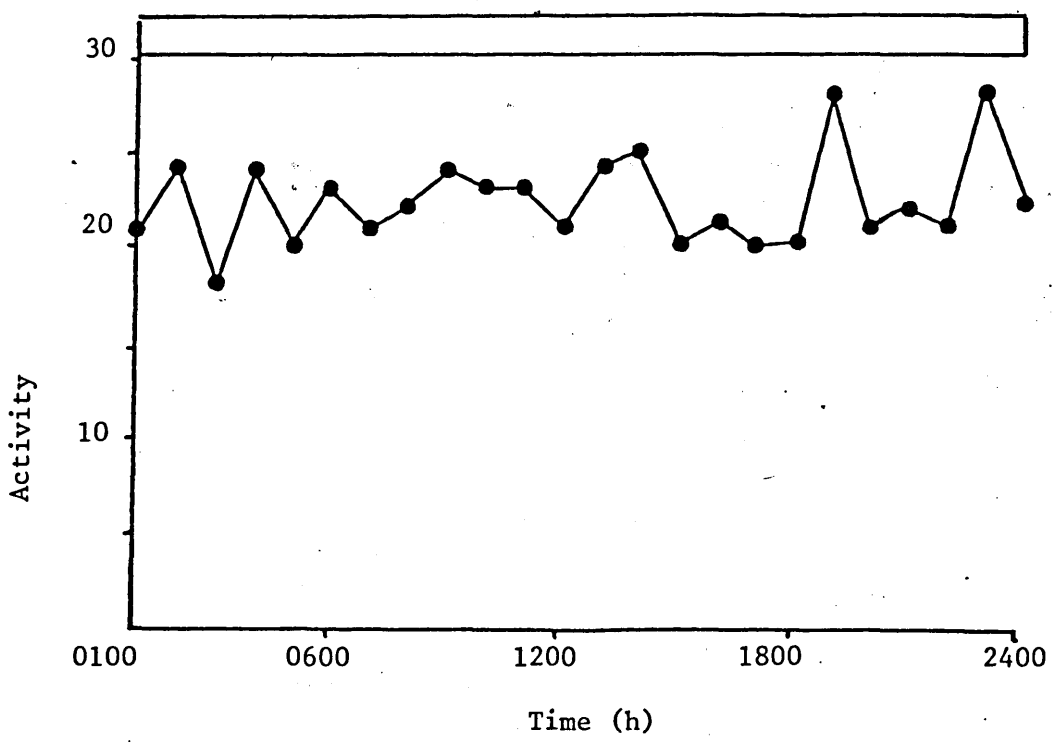

30
20
10
Activity
0100
0600
1200
1800
2400
Time (h)

Figure 9a Locomotor activity (events.h^{-1}) of a juvenile lobster in DD, no shelter, after chilling at 4°C for 7h.

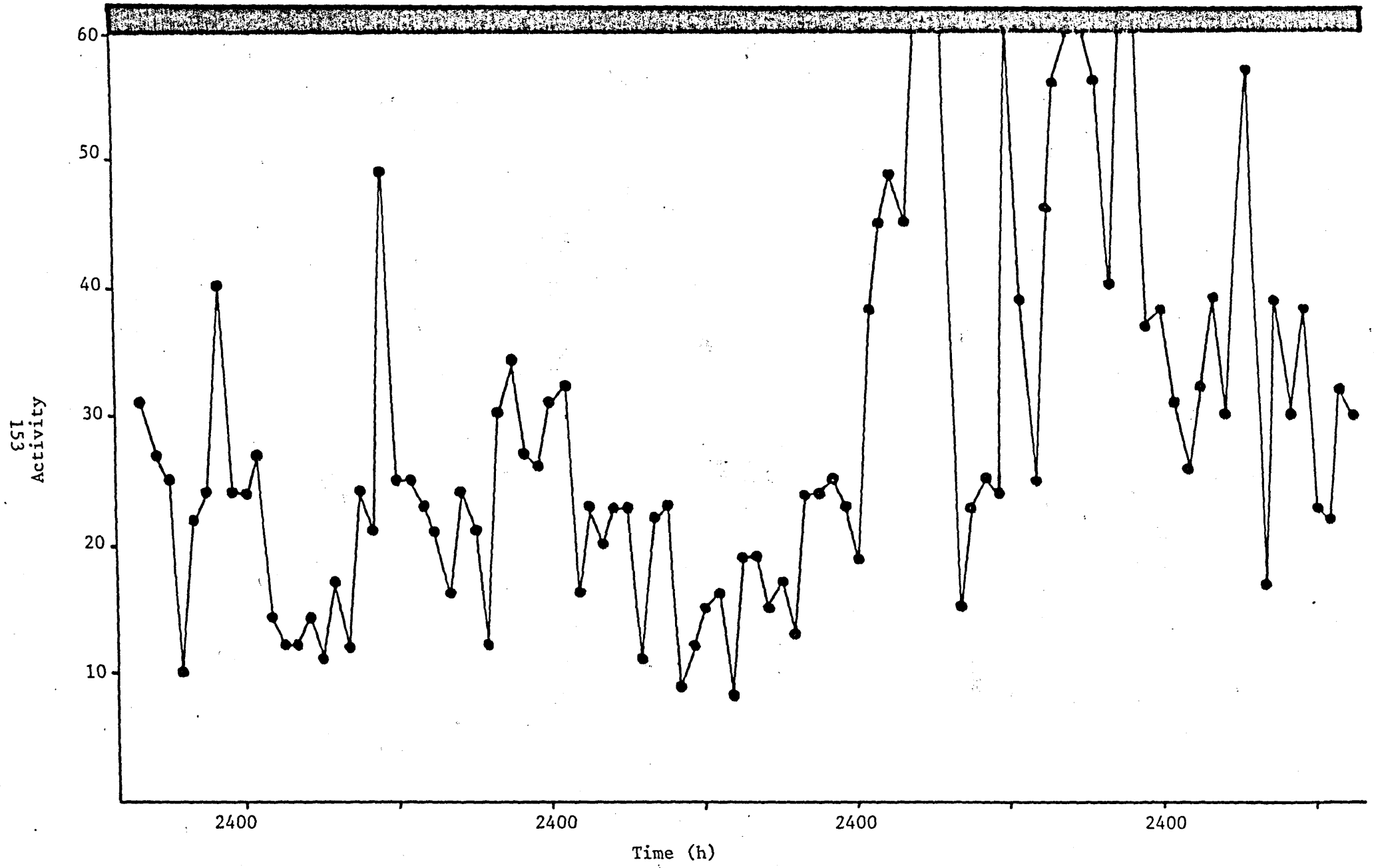
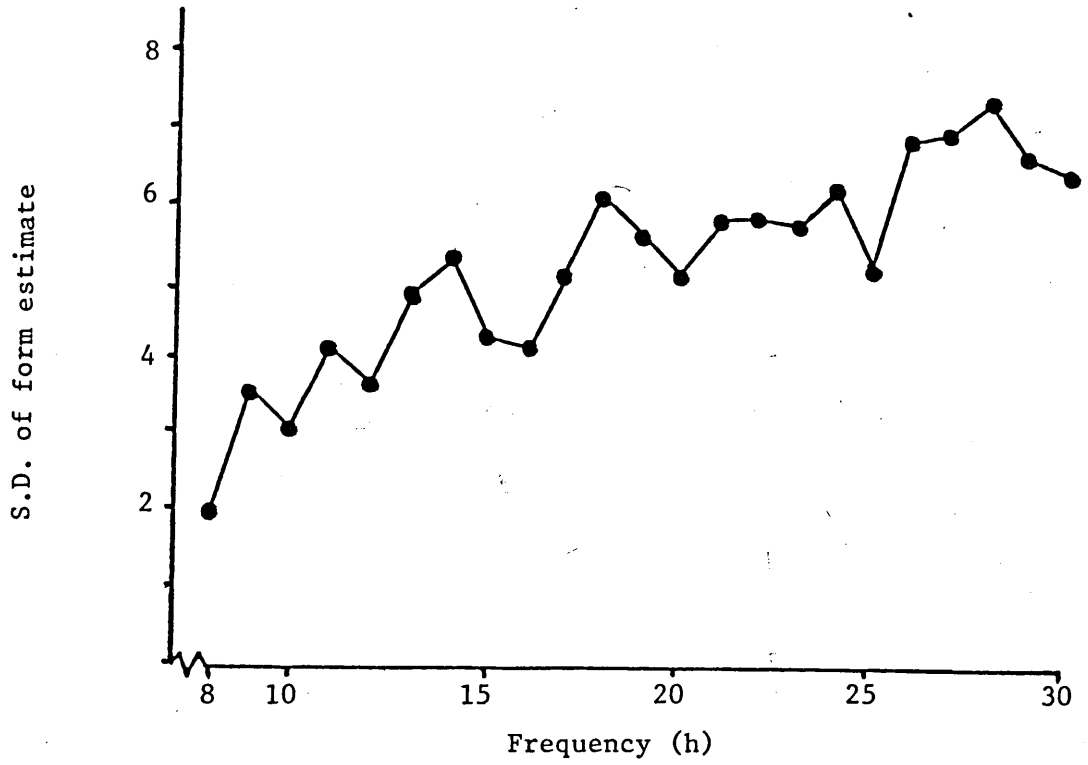

60
50
40
30
20
10
153
Activity
2400
2400
2400
2400
Time (h)

Figure 9b Juvenile activity in DD, no shelter, after chilling. Periodogram of hourly activity for frequencies of 8-30h.

Figure 9c 24h form estimate (mean events.h^{-1})


S.D. of form estimate
8
6
4
2
8
10
15
20
25
30
Frequency (h)

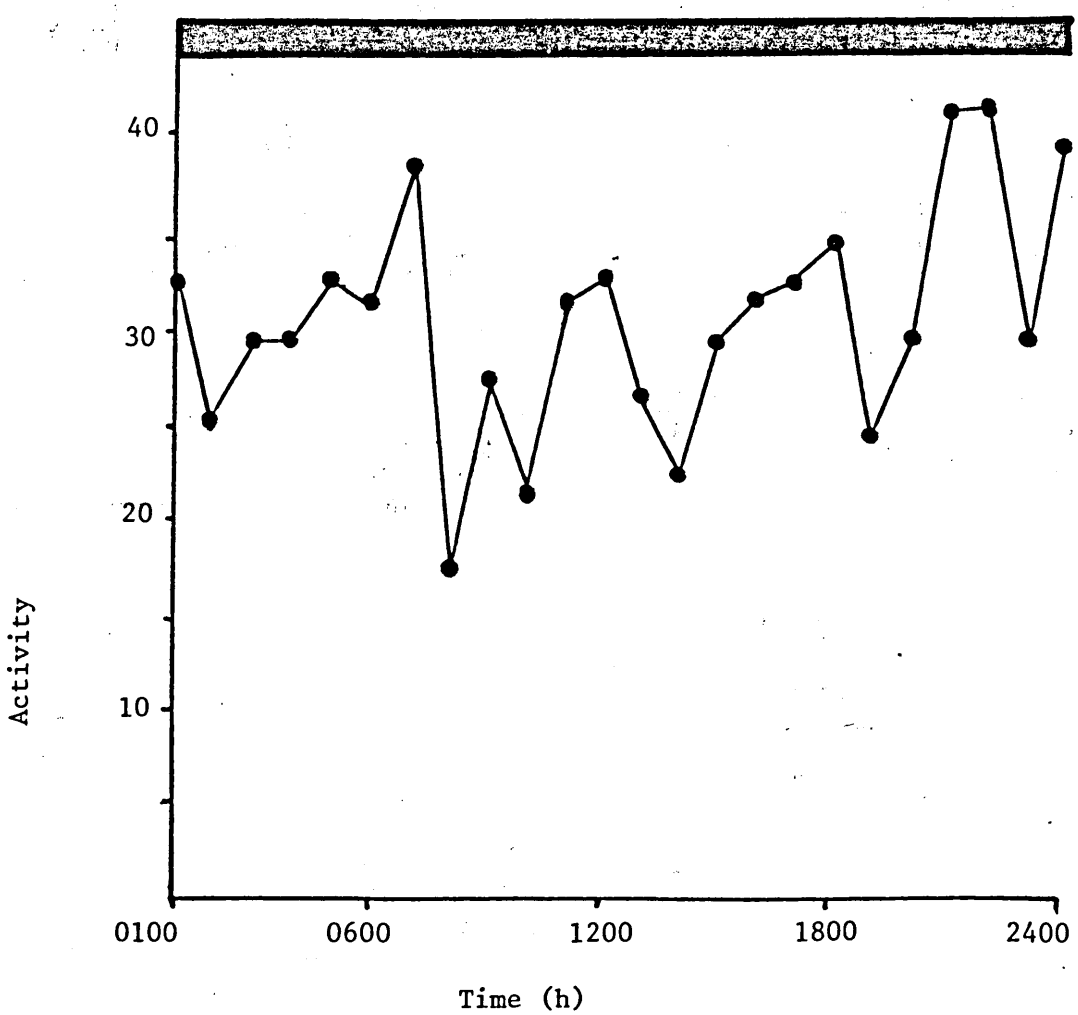

Activity
40
30
20
10
0100
0600
1200
1800
2400
Time (h)

Figure 10a. Locomotor activity (events. h^{-1}) of a juvenile lobster in DD, no shelter, after chilling at $4^{o}C$ for 7h.

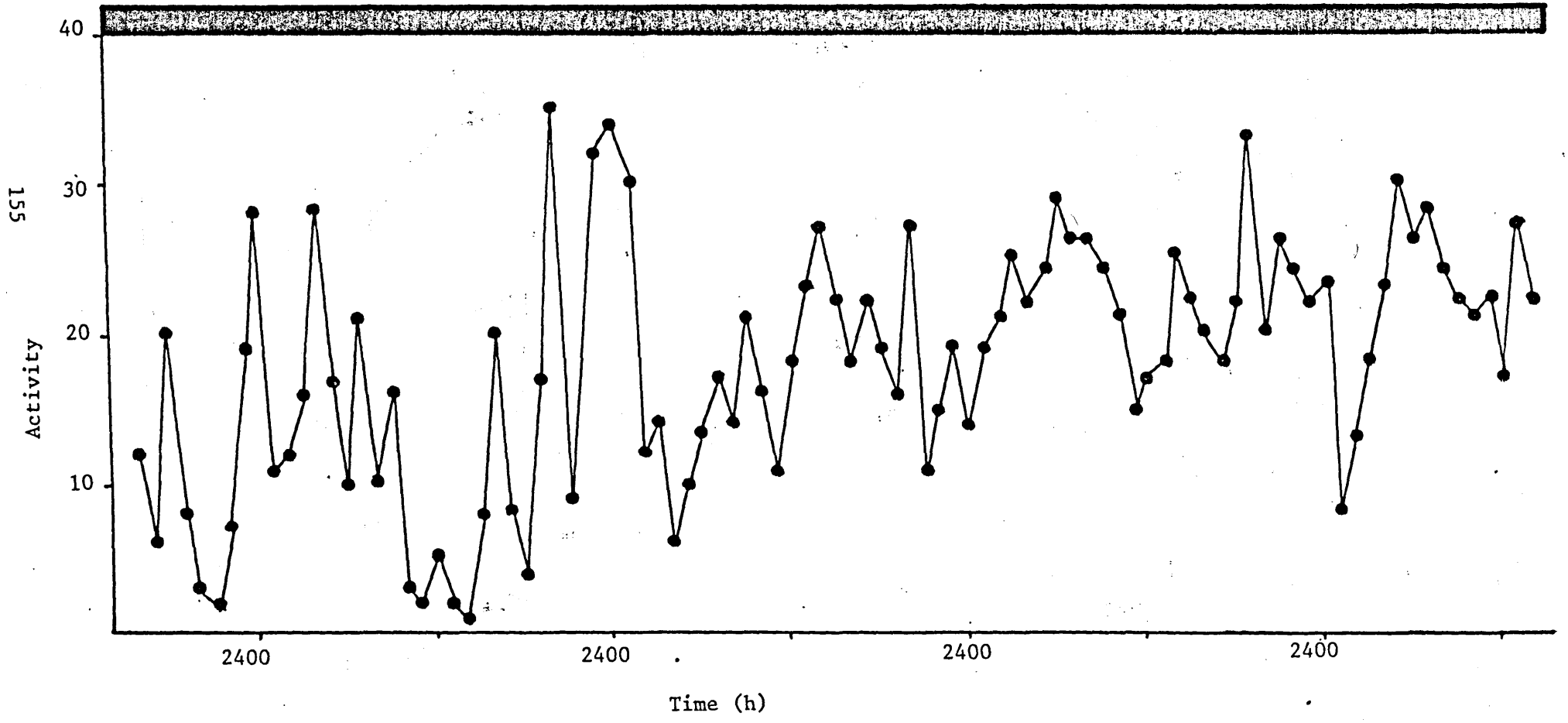
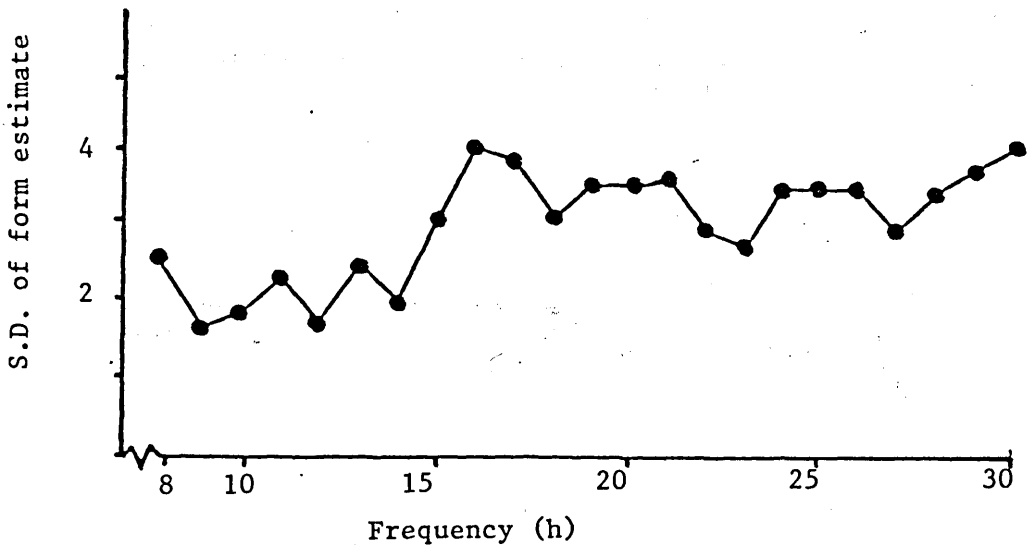

40
30
20
10
Activity
2400
2400
2400
2400
Time (h)

Figure 10b Juvenile activity in DD, no shelter, after chilling. Periodogram of hourly activity for frequencies of 8-30h.

Figure 10c 24h form estimate (mean events.h^{-1})


S.D. of form estimate
4
2
8
10
15
20
25
30
Frequency (h)

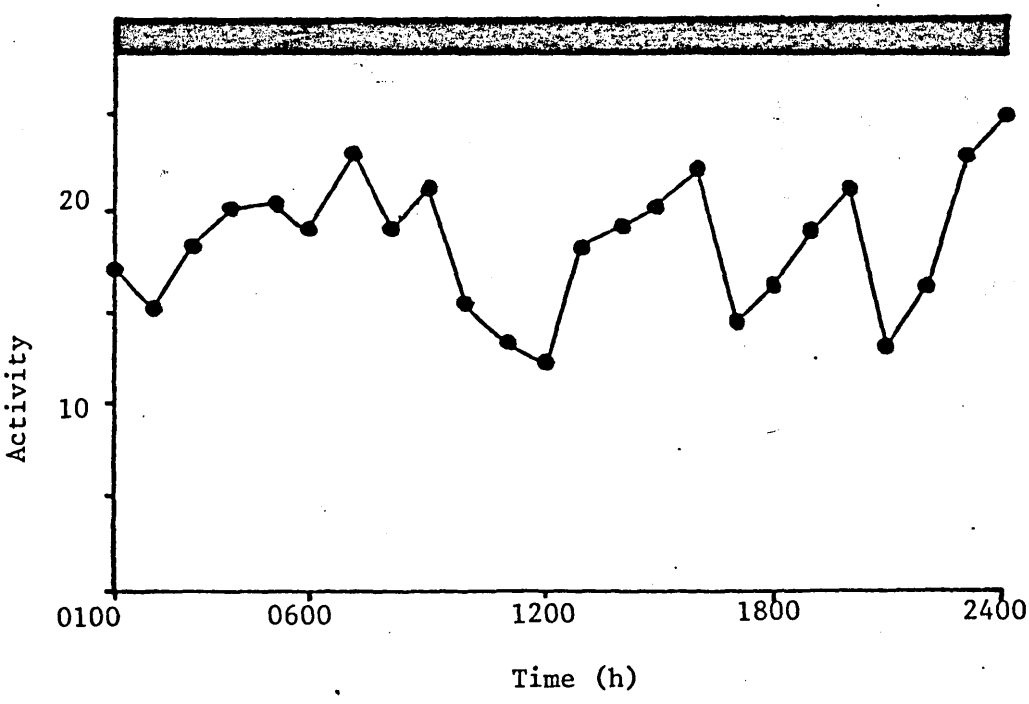

Activity
20
10
0100
0600
1200
1800
2400
Time (h)

Figure 11a Mean locomotor activity (events.h^{-1}) of juvenile lobsters in 6:6 LD, 250 lux, no shelter.

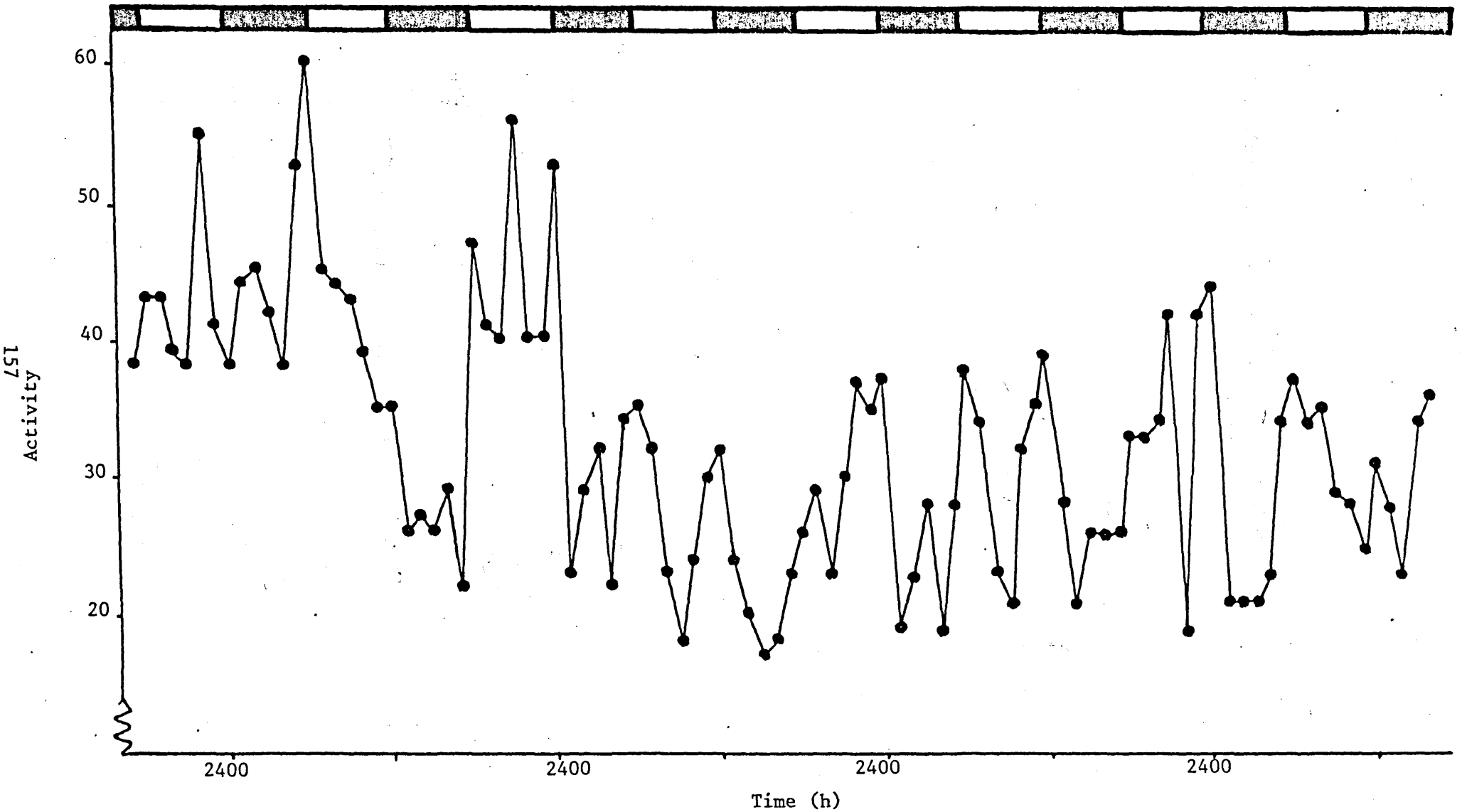
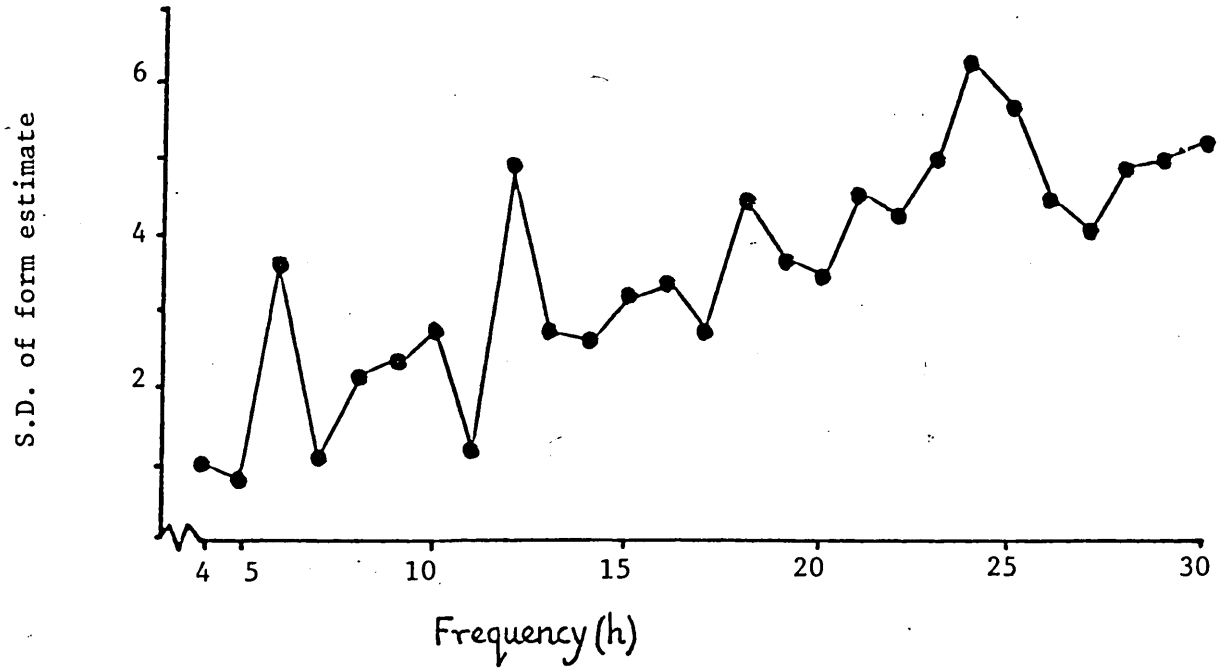

60
50
40
30
20
Activity
157
2400
2400
2400
2400
Time (h)

Figure 11b Juvenile activity in 6:6 LD, 250 lux, no shelter. Periodogram of mean hourly activity values for frequencies of 4-30h.

Figure 11c 24h form estimate (mean events.h^{-1}).


S.D. of form estimate
6
4
2
4
5
10
15
20
25
30
Frequency (h)

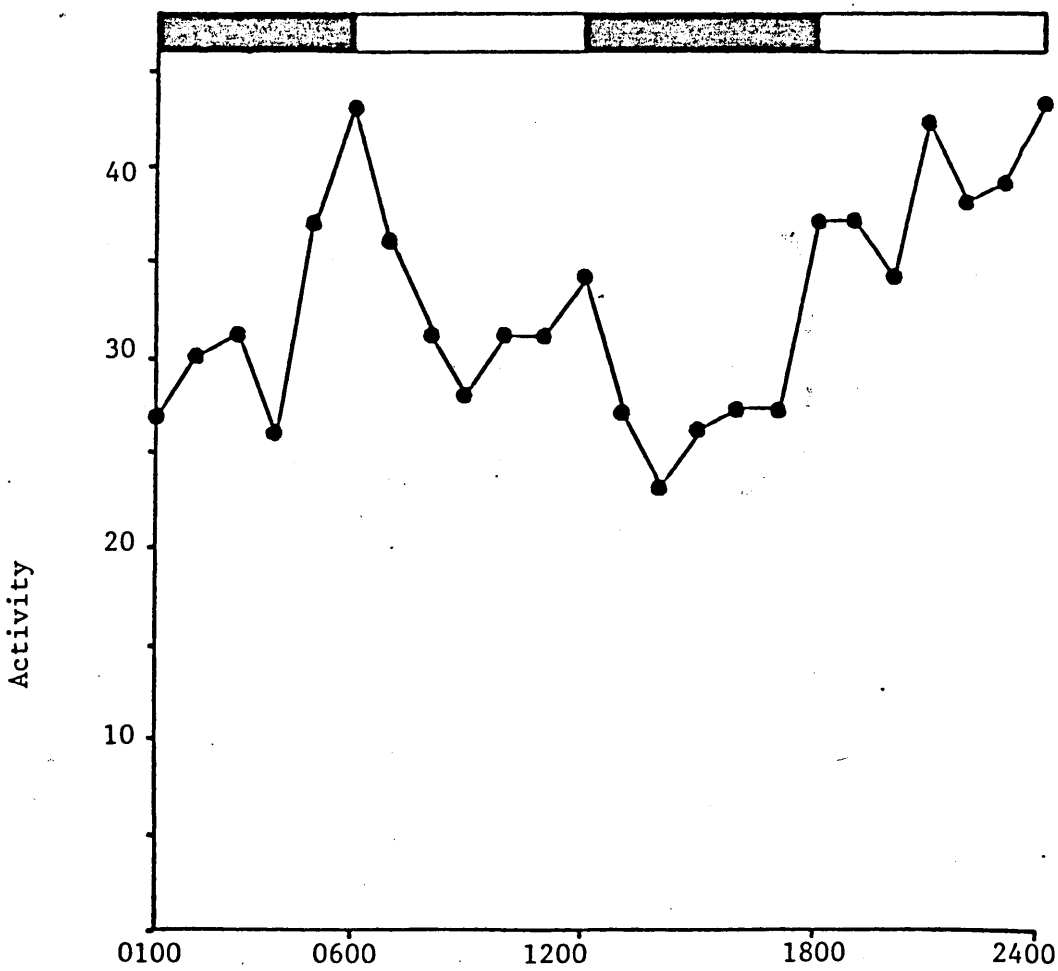

Activity
40
30
20
10
0100
0600
1200
1800
2400
Time (h)

Figure 12a Mean locomotor activity (events.h^{-1}) of juvenile lobsters in reversed 12:12 LD, 250 lux, no shelter.

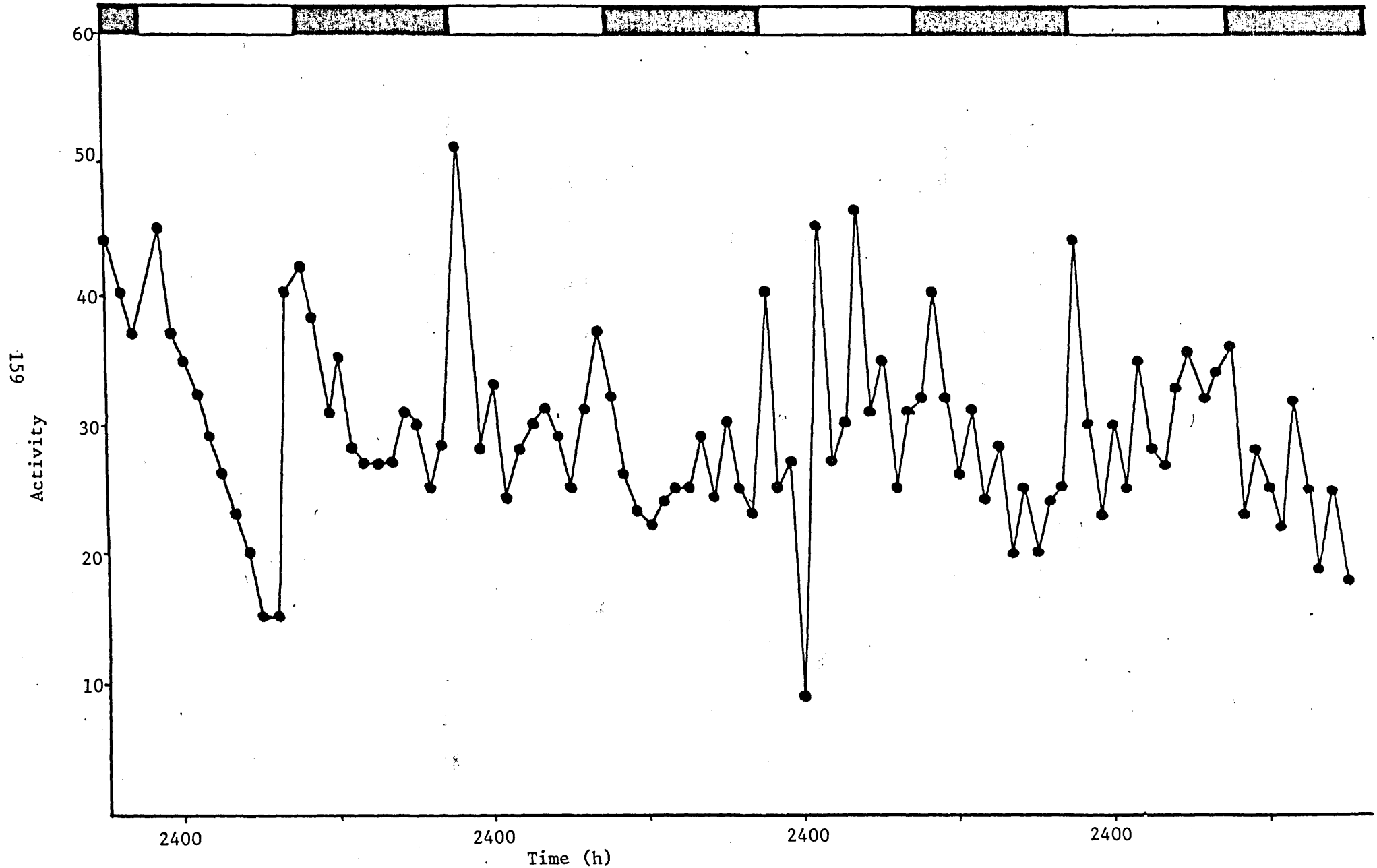
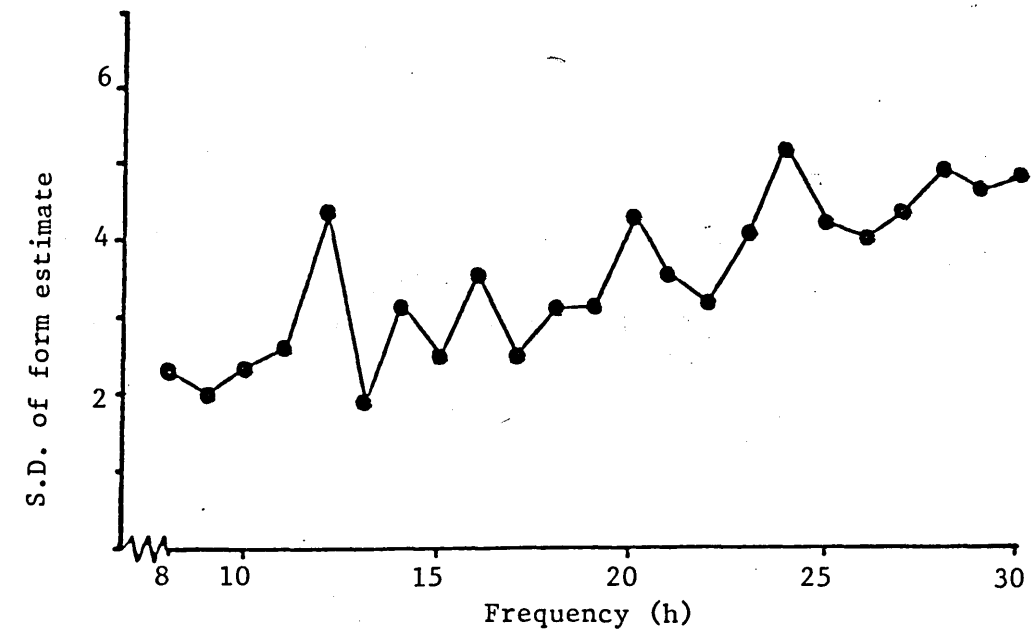

60
50
40
30
20
10
Activity
159
2400
2400
2400
2400
Time (h)

Figure 12b Juvenile activity in reversed 12:12 LD, 250 lux, no shelter. Periodogram of mean hourly activity values for frequencies of 8-30h.

Figure 12c 24h form estimate (mean events.h^{-1}).


S.D. of form estimate
6
4
2
8
10
15
20
25
30
Frequency (h)

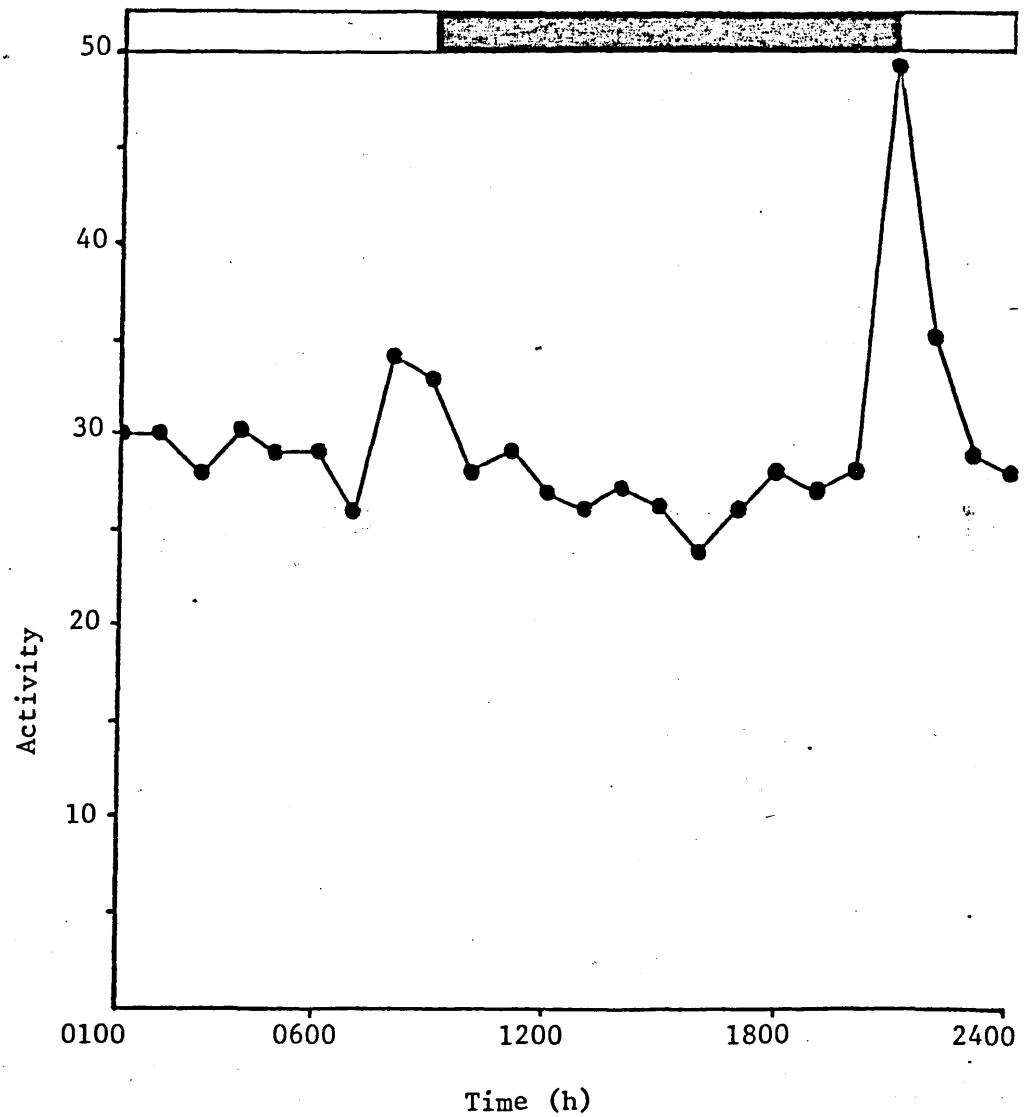

50
40
30
20
10
Activity
0100
0600
1200
1800
2400
Time (h)

Figure 13. Juvenile activity during intermoult period in 12:12 LD, 250 lux, no shelter.

Open circles diurnal activity, closed circles nocturnal activity. (Events.h^{-1}).

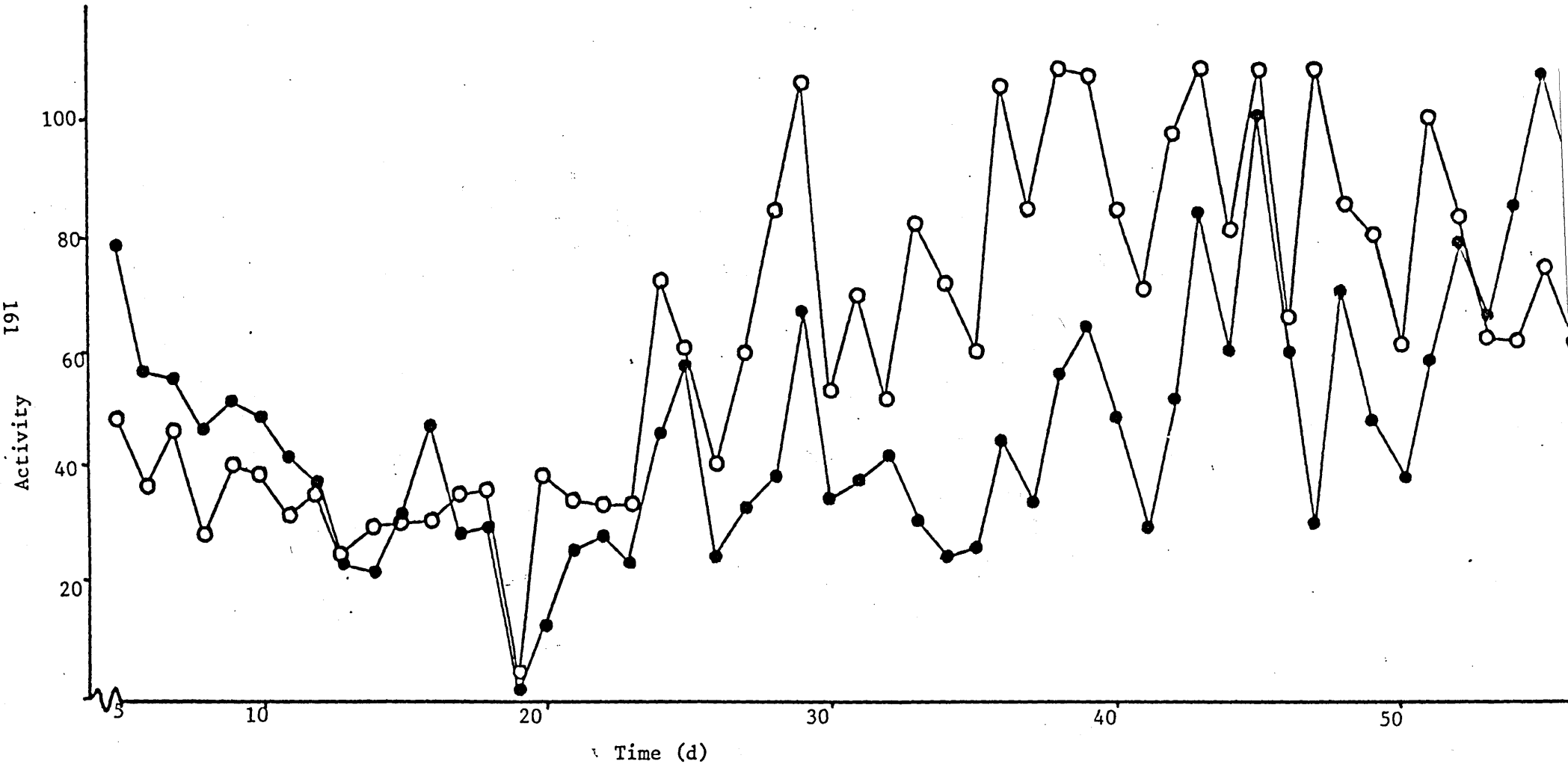

Activity
100
80
60
40
20
5
10
20
30
40
50
Time (d)

Figure 14 Juvenile activity during intermoult period in 12:12 LD, 250 lux, no shelter.

Open circles diurnal activity, closed circles nocturnal activity (events.h^{-1}).

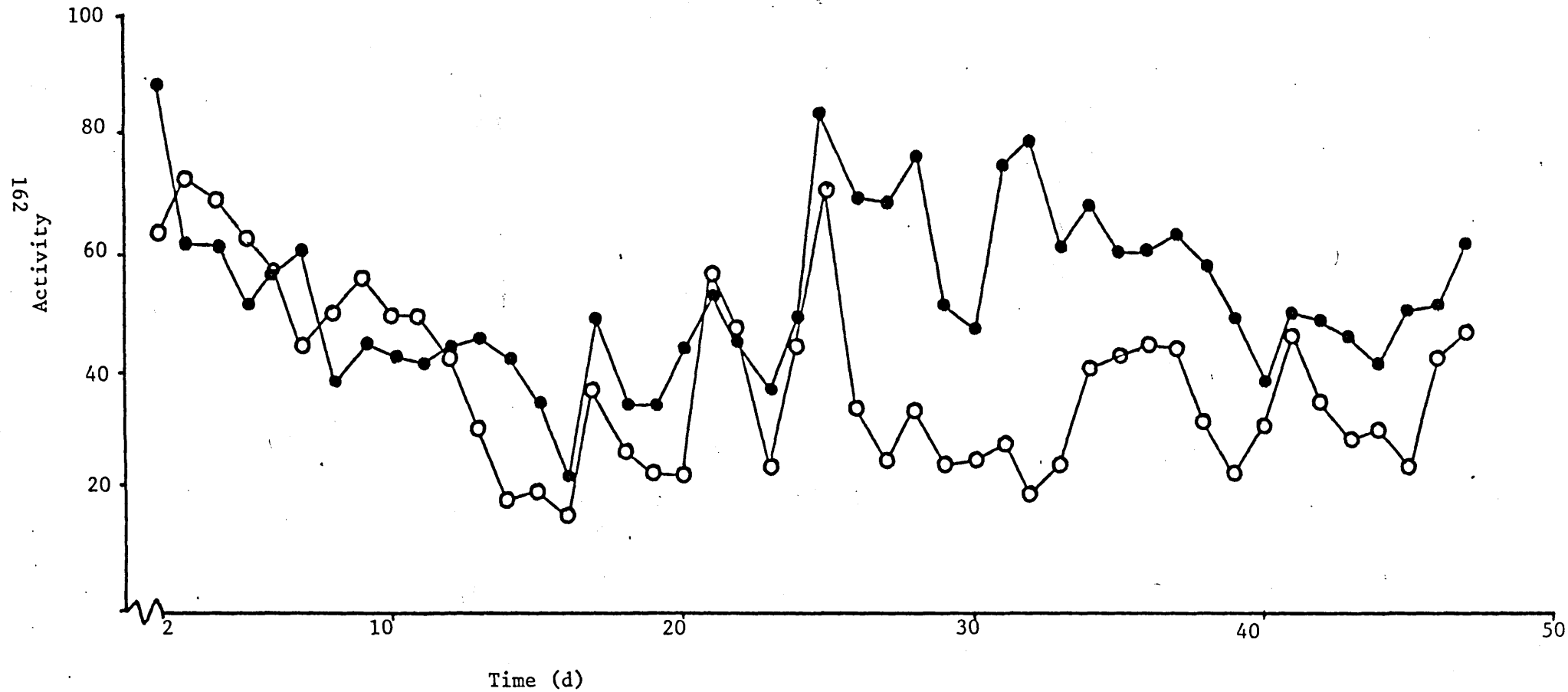

100
80
60
40
20
Activity
2
10
20
30
40
50
Time (d)

Figure 15 Juvenile activity during part of intermoult period in 12:12 LD, 250 lux, no shelter.

Open circles diurnal activity, closed circles nocturnal activity, (events.h^{-1}).

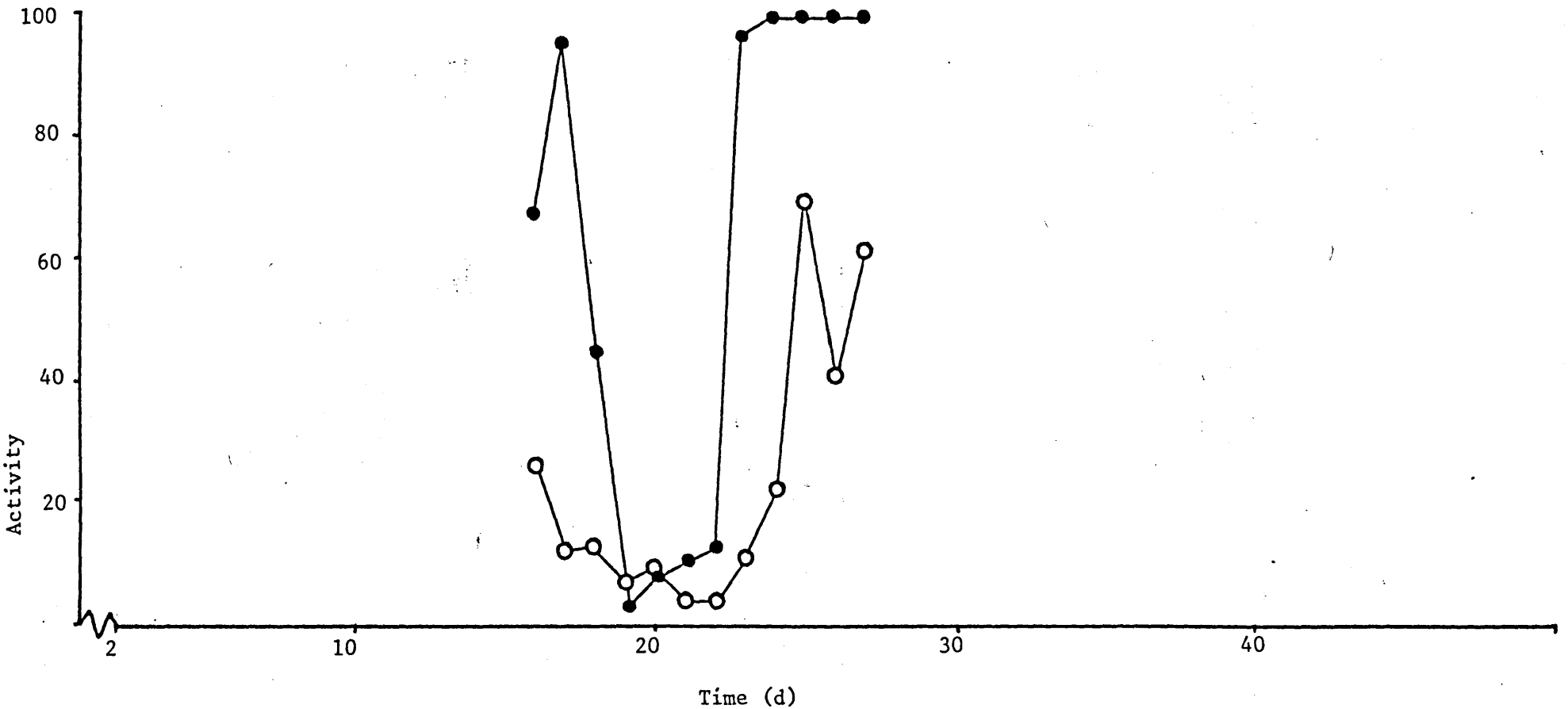
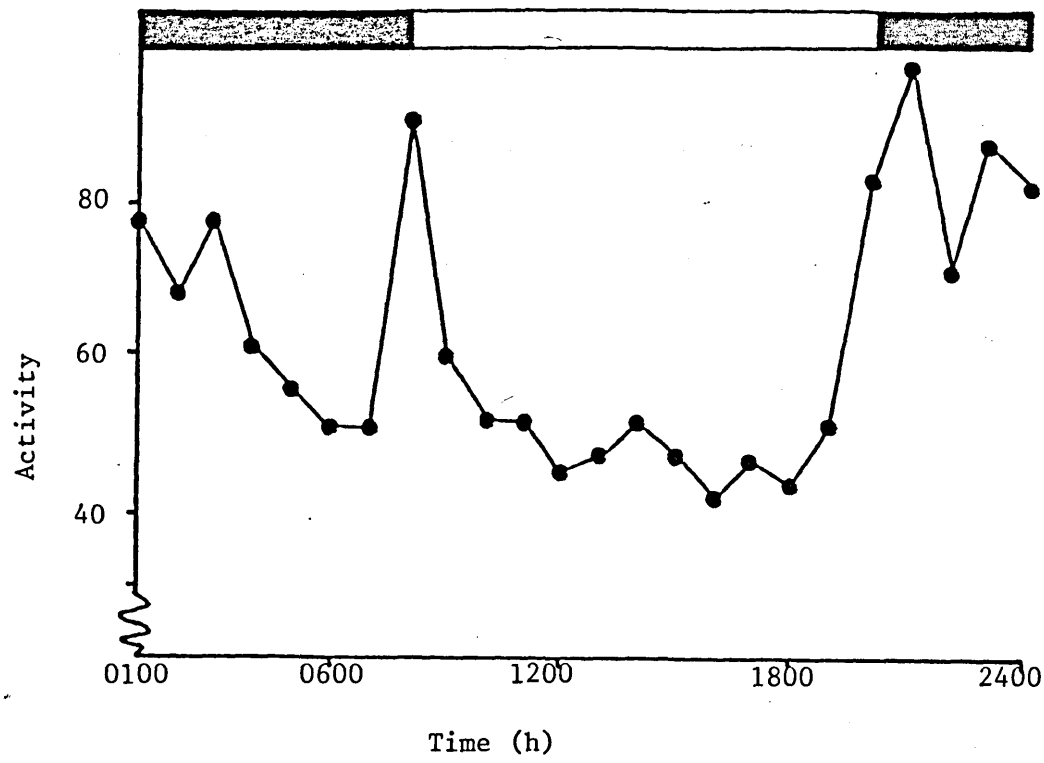

100
80
60
40
20
Activity
2
10
20
30
40
Time (d)

Figure 16a Locomotor activity of daily fed juvenile lobsters in 12:12 LD, 250 lux, no shelter.
24h form estimate (mean events.h^{-1})

Figure 16b Locomotor activity of starved juvenile lobsters in 12:12 LD, 250 lux, no shelter.
24h form estimate (mean events.h^{-1}).


80
60
40
Activity
0100
0600
1200
1800
2400
Time (h)

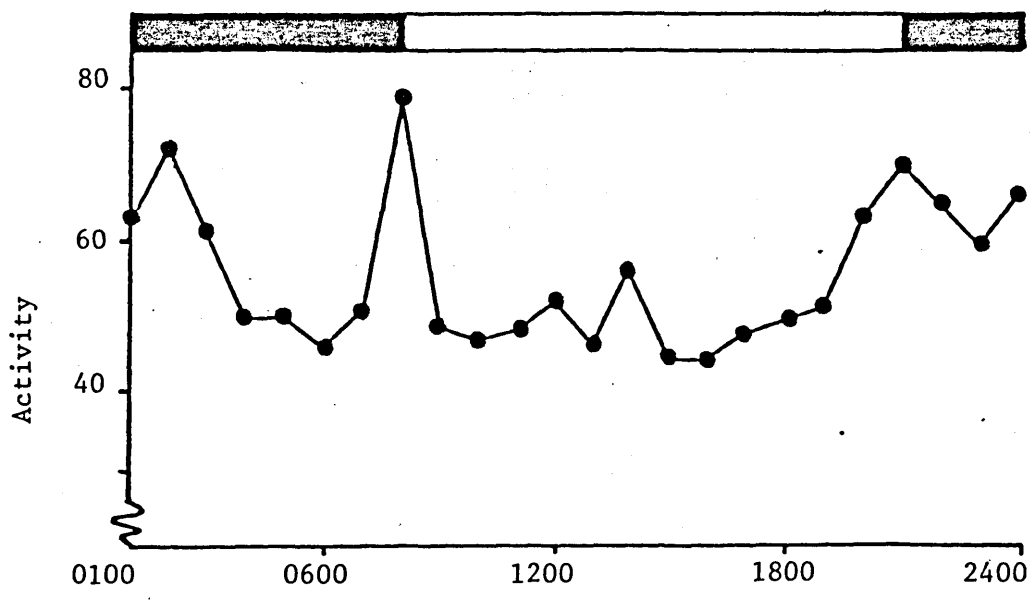
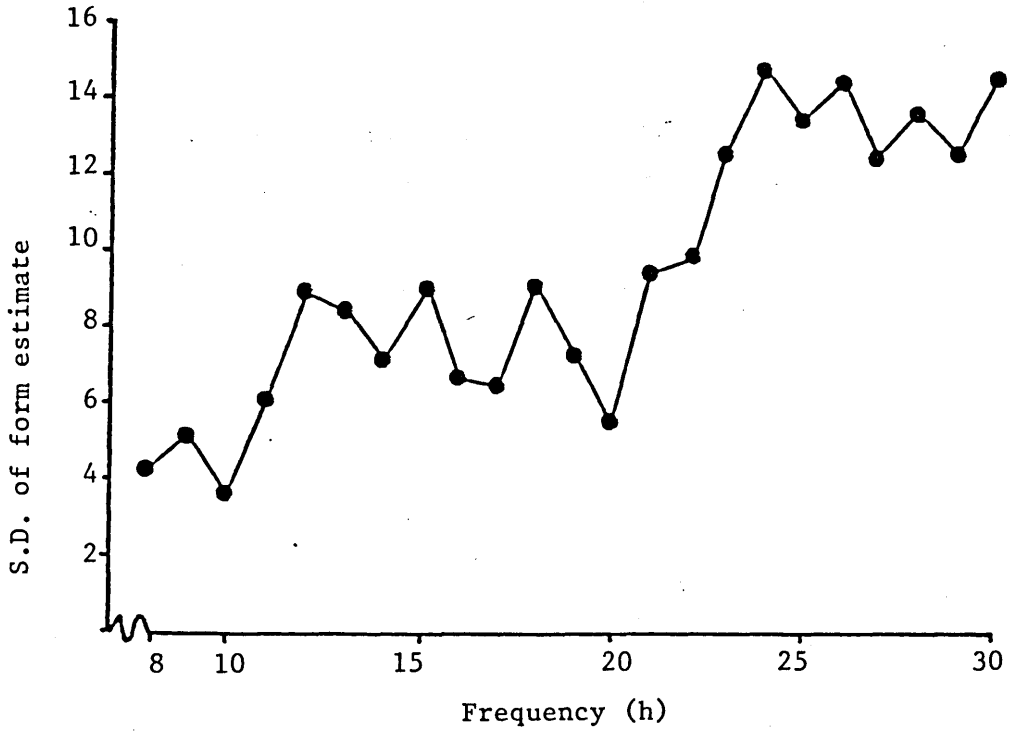

80
60
40
Activity
0100
0600
1200
1800
2400
Time (h)

Figure 16c Locomotor activity of starved juvenile lobsters in 12:12 LD, 250 lux, no shelter.

Periodogram of mean hourly activity values for frequencies of 8-30 h.

Figure 16d Locomotor activity of daily fed juvenile lobsters in 12:12 LD, 250 lux, no shelter.

Periodogram of mean hourly activity for frequencies of 8-30 h.


S.D. of form estimate
16
14
12
10
8
6
4
2
8
10
15
20
25
30
Frequency (h)

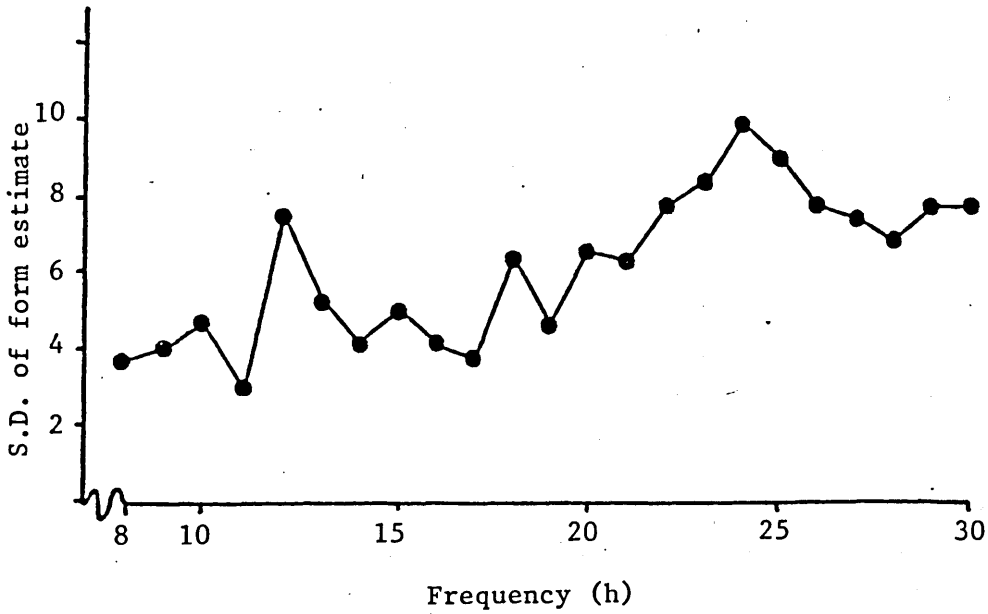

S.D. of form estimate
10
8
6
4
2
8
10
15
20
25
30
Frequency (h)

Figure 17 Feeding activity of a juvenile lobster in 12:12 LD, 200 lux, with shelter.

Open circles diurnal activity, closed circles nocturnal activity (events.h^{-1}).

Arrow indicates ecdysis.

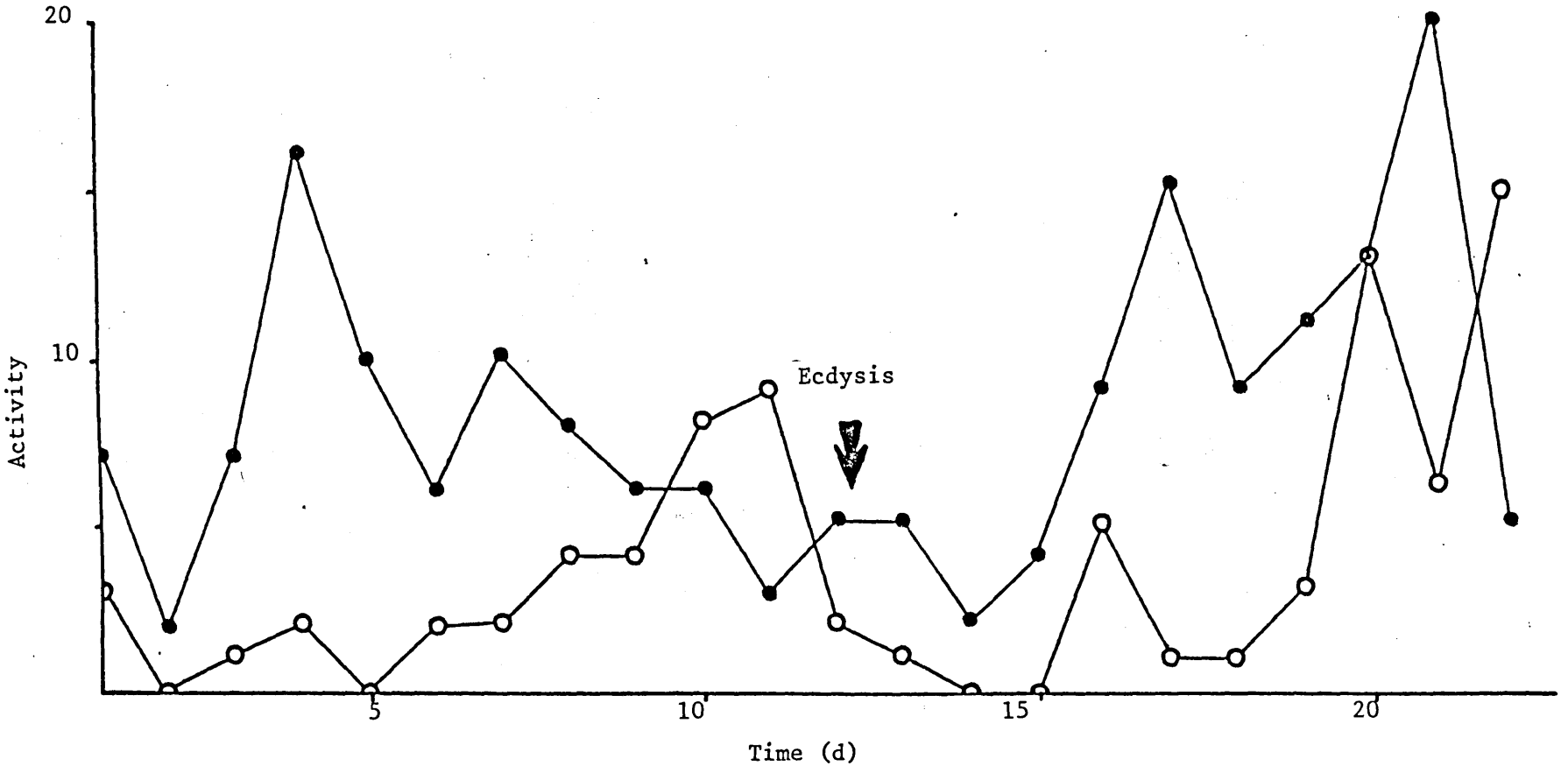
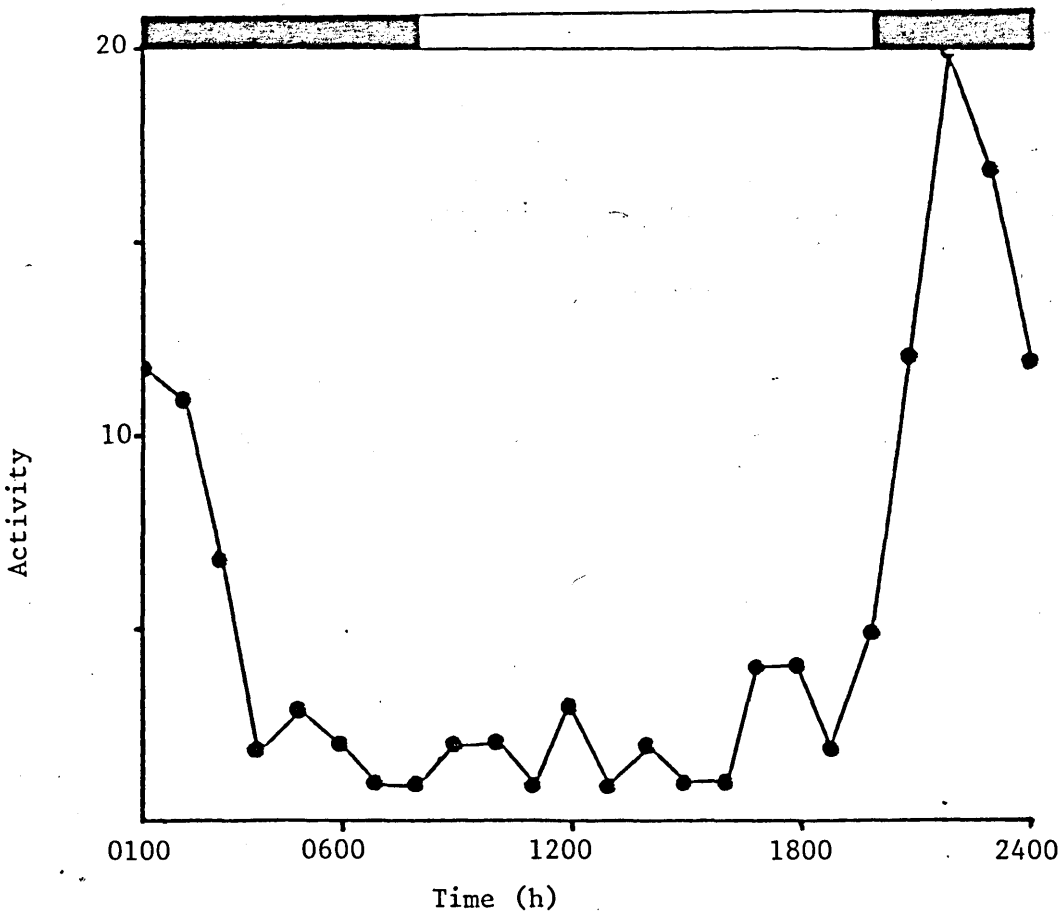

20
10
Activity
Ecdysis
5
10
15
20
Time (d)

Figure 18a Feeding activity during the period 11-5 days before ecdysis - 24h form estimate. (Mean events.h^{-1})

Figure 18b Feeding activity during the period 4-1 day before ecdysis - 24h form estimate. (Mean events.h^{-1})


20
10
Activity
0100
0600
1200
1800
2400
Time (h)

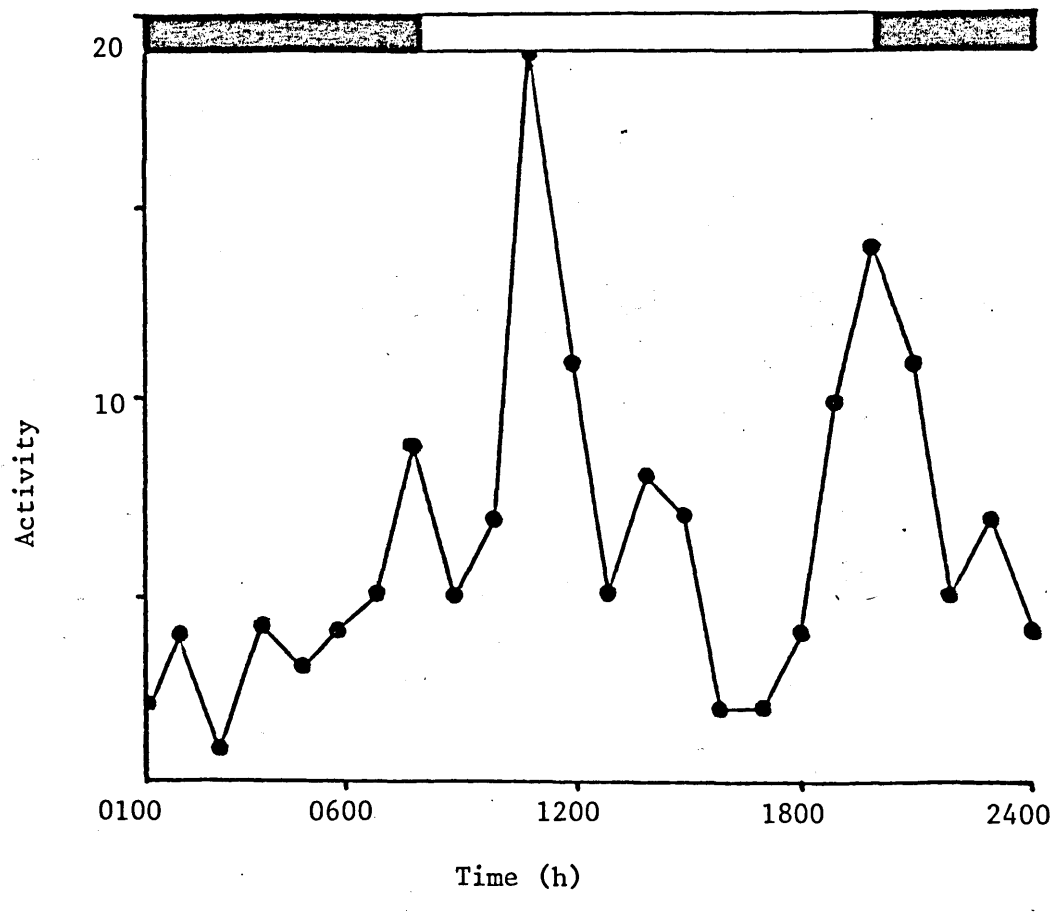
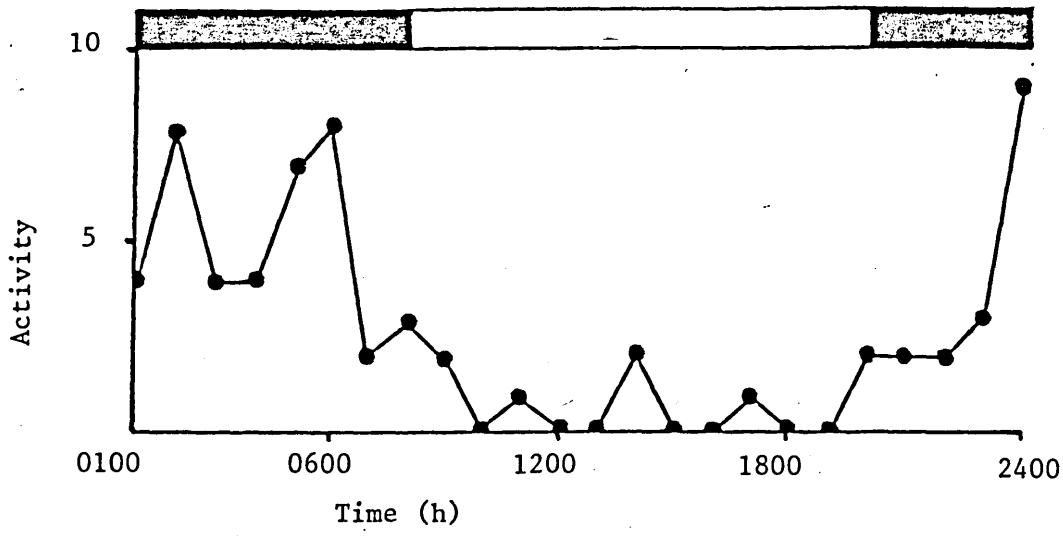

20
10
Activity
0100
0600
1200
1800
2400
Time (h)

Figure 18c Feeding activity during the period 1-4 days after ecdysis. 24h form estimate.
(Mean events.h^{-1}).

Figure 18d Feeding activity during the period 5-10 days after ecdysis. 24h form estimate.
(Mean events.h^{-1}).


10
5
Activity
0100
0600
1200
1800
2400
Time (h)

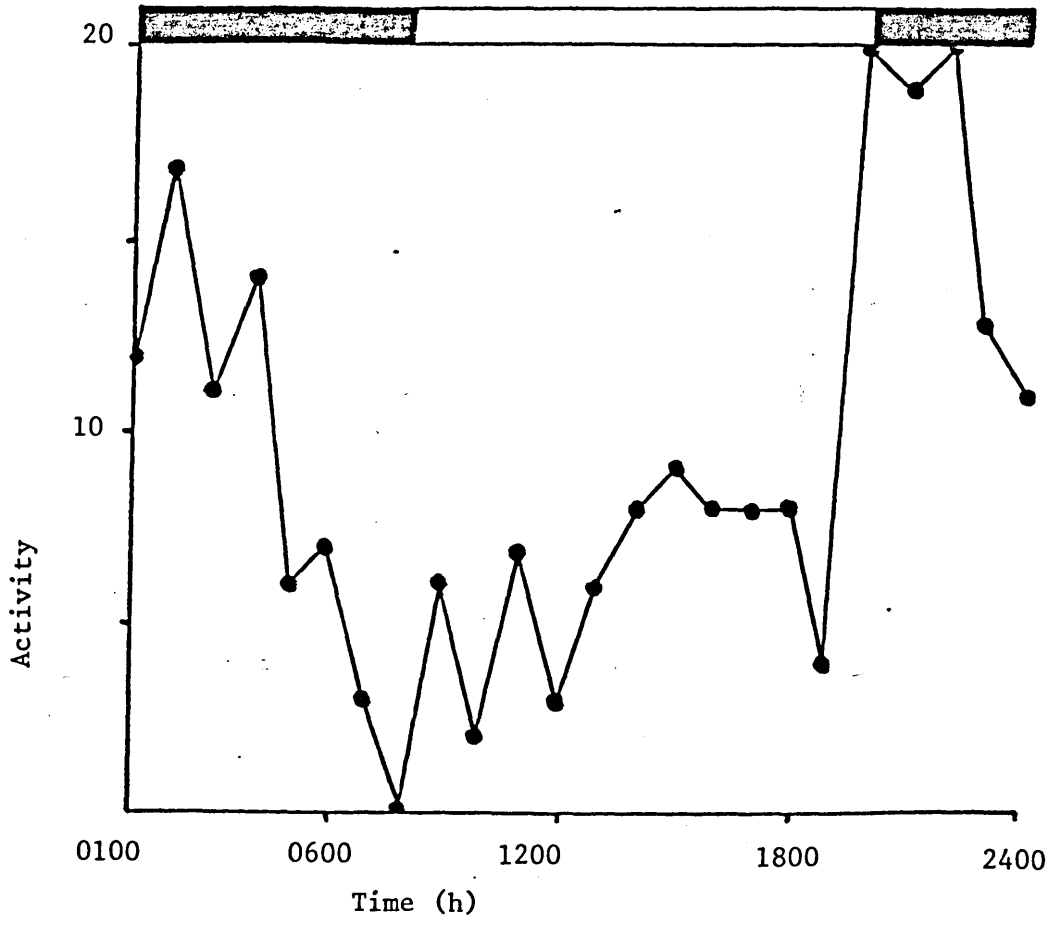

20
10
Activity
0100
0600
1200
1800
2400
Time (h)

Figure 19a Feeding activity of a juvenile lobster in DD, with shelter.
(events.h^{-1})

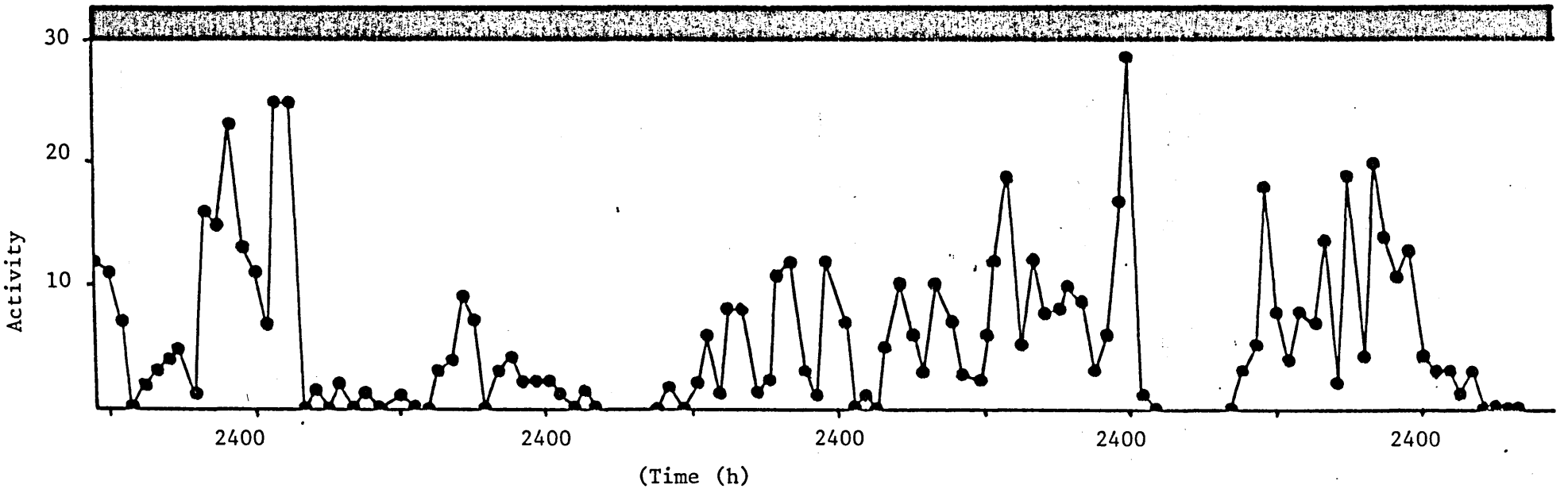
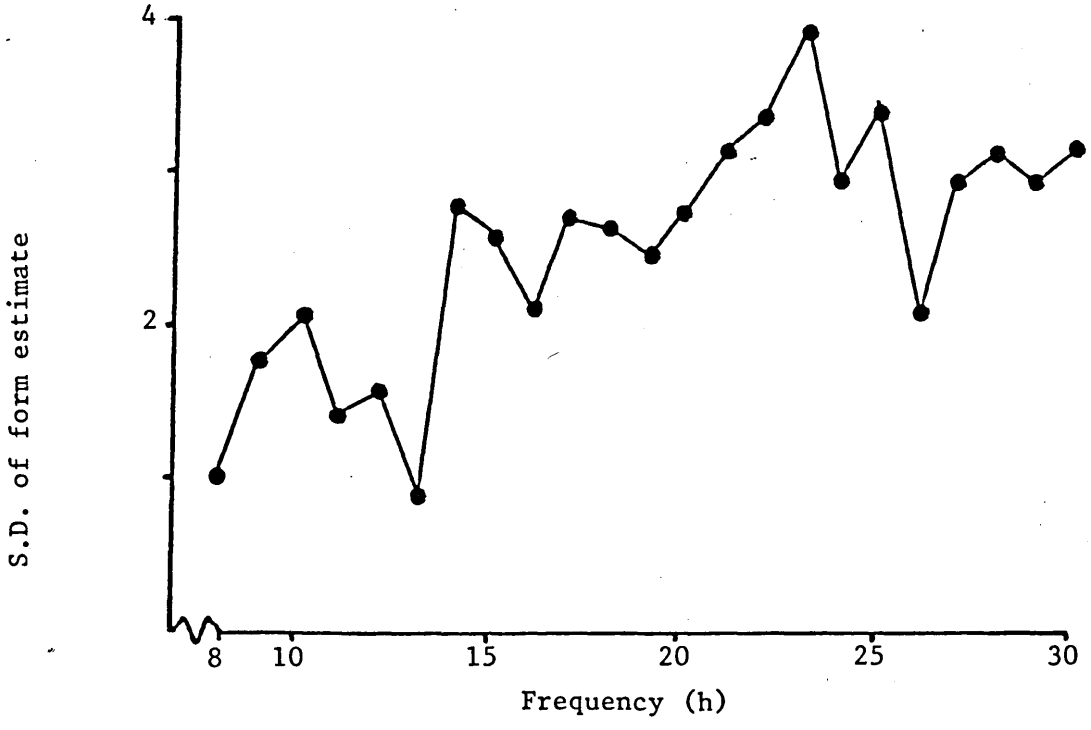

30
20
10
Activity
2400
2400
2400
2400
2400
(Time (h)

Figure 19b Feeding activity in DD, with shelter.

Periodogram of mean hourly activity values for frequencies of 8-30h.

Figure 19c 24h form estimate (Mean events.h^{-1}).


S.D. of form estimate
4
2
8
10
15
20
25
30
Frequency (h)

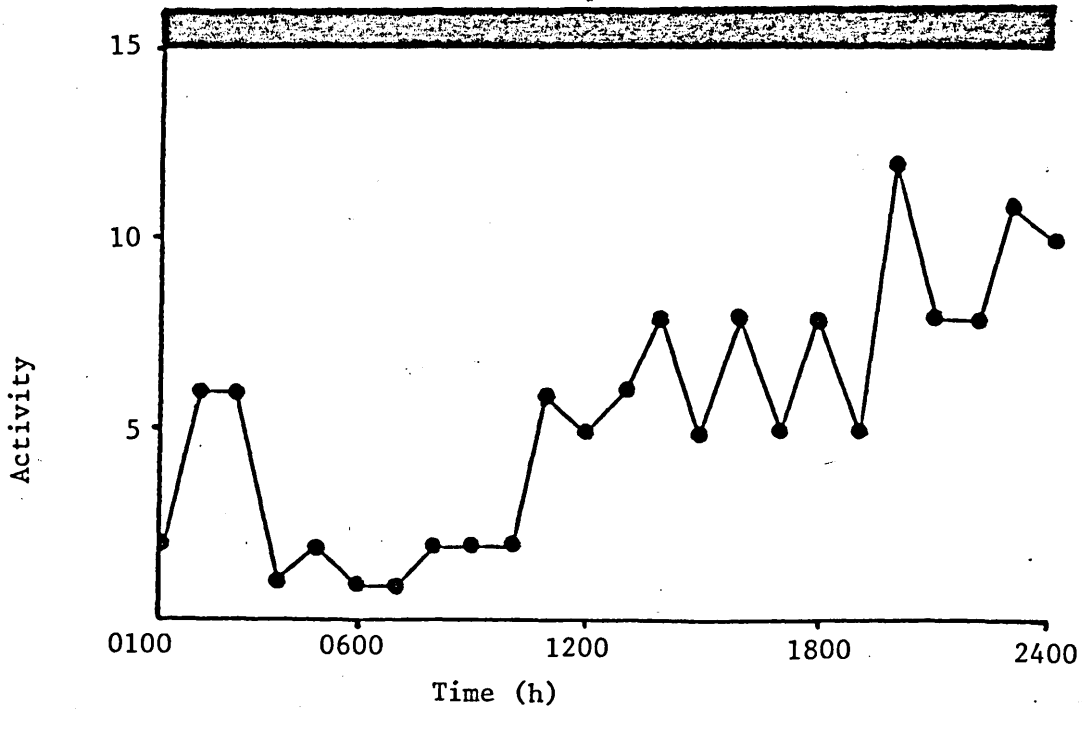

Activity
15
10
5
0100
0600
1200
1800
2400
Time (h)

Figure 20a Feeding activity of a juvenile lobster in LL, 200 lux, with shelter. (Events.h^{-1}).

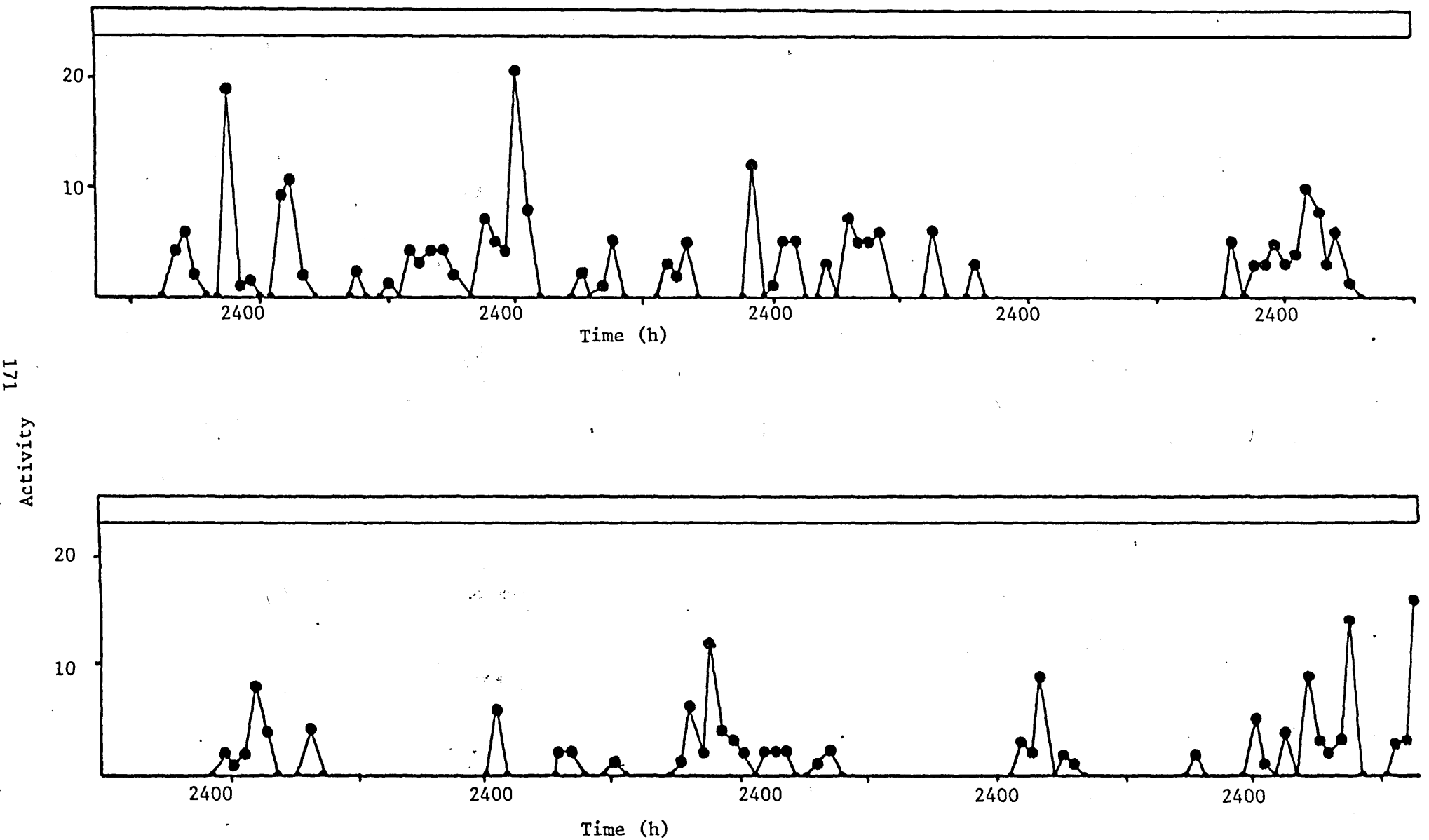
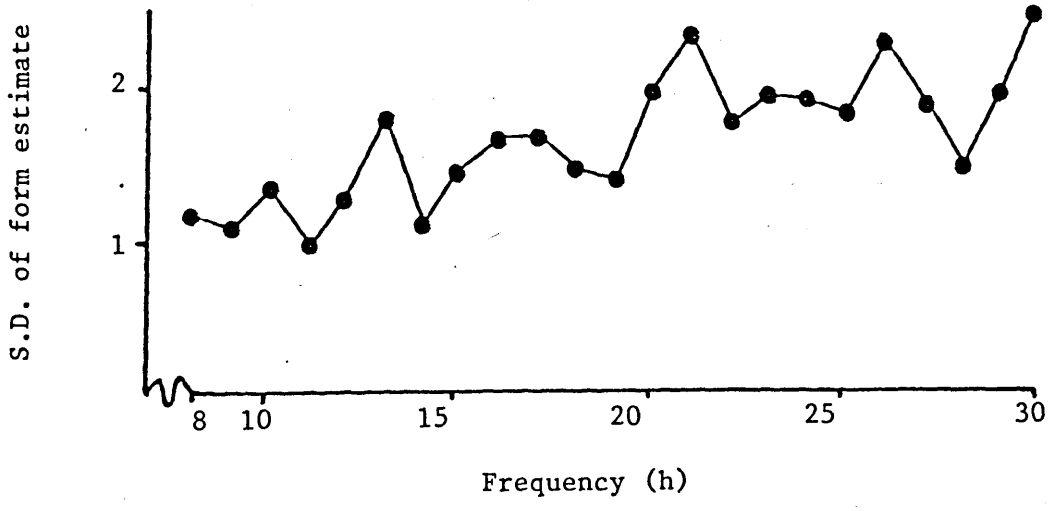

Activity
20
10
2400
2400
2400
2400
2400
Time (h)
20
10
2400
2400
2400
2400
2400
Time (h)

Figure 20b Feeding activity in LL, 200 lux, with shelter.

Periodogram of hourly activity values for frequencies of 8-30h.

Figure 20c 24h form estimate (mean events.h^{-1}).


S.D. of form estimate
2
1
8
10
15
20
25
30
Frequency (h)

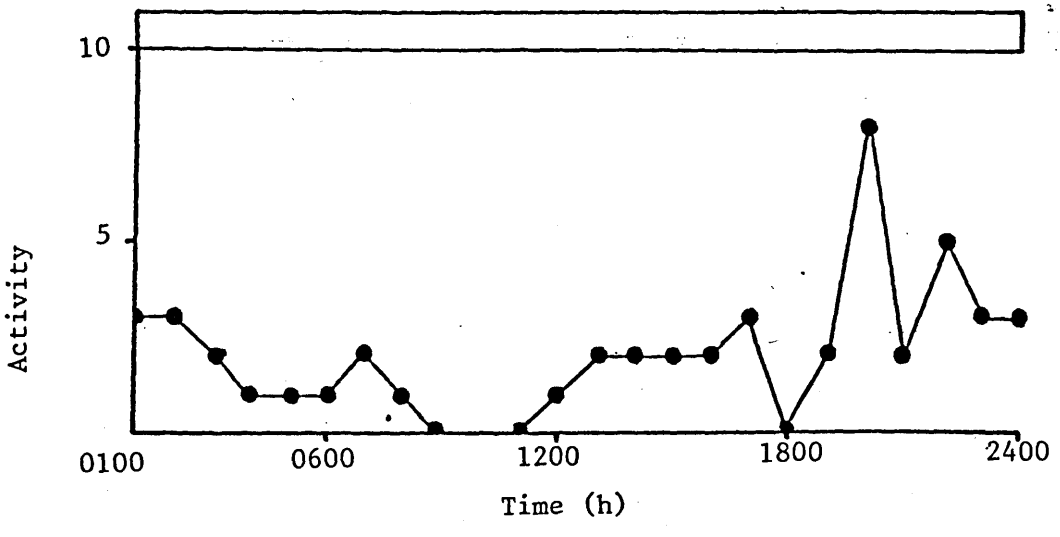
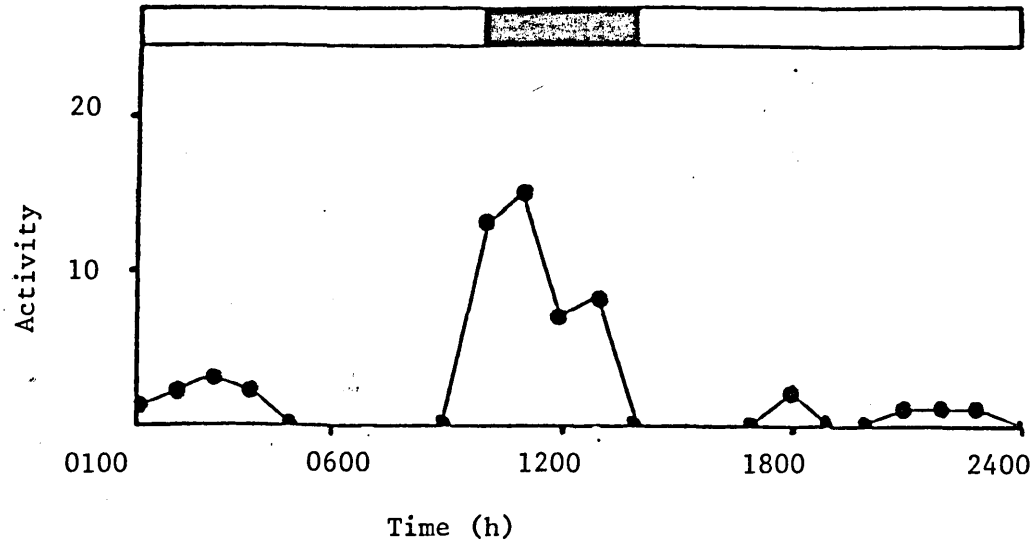

10
5
Activity
0100
0600
1200
1800
2400
Time (h)

Figure 21a Feeding activity of a juvenile lobster in 20:4 LD, 200 lux, with shelter, photoperiod 1400-1000h. 24h form estimate.

(Mean events.h^{-1}).

Figure 21b Feeding activity of a juvenile lobster in 20:4 LD, 200 lux, with shelter, photoperiod 2400-2000h. 24h form estimate. (Mean events. h^{-1}).


20
10
Activity
0100
0600
1200
1800
2400
Time (h)

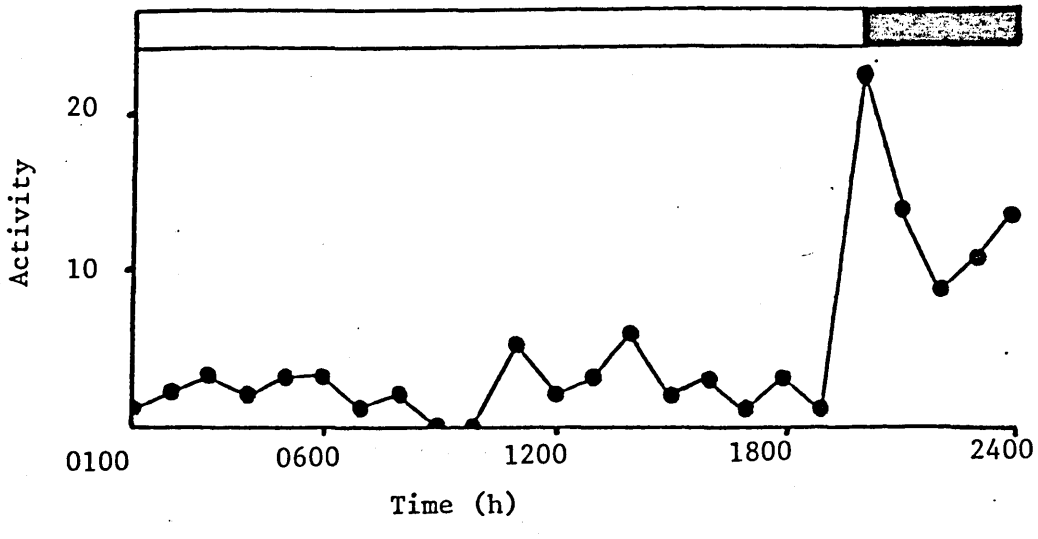
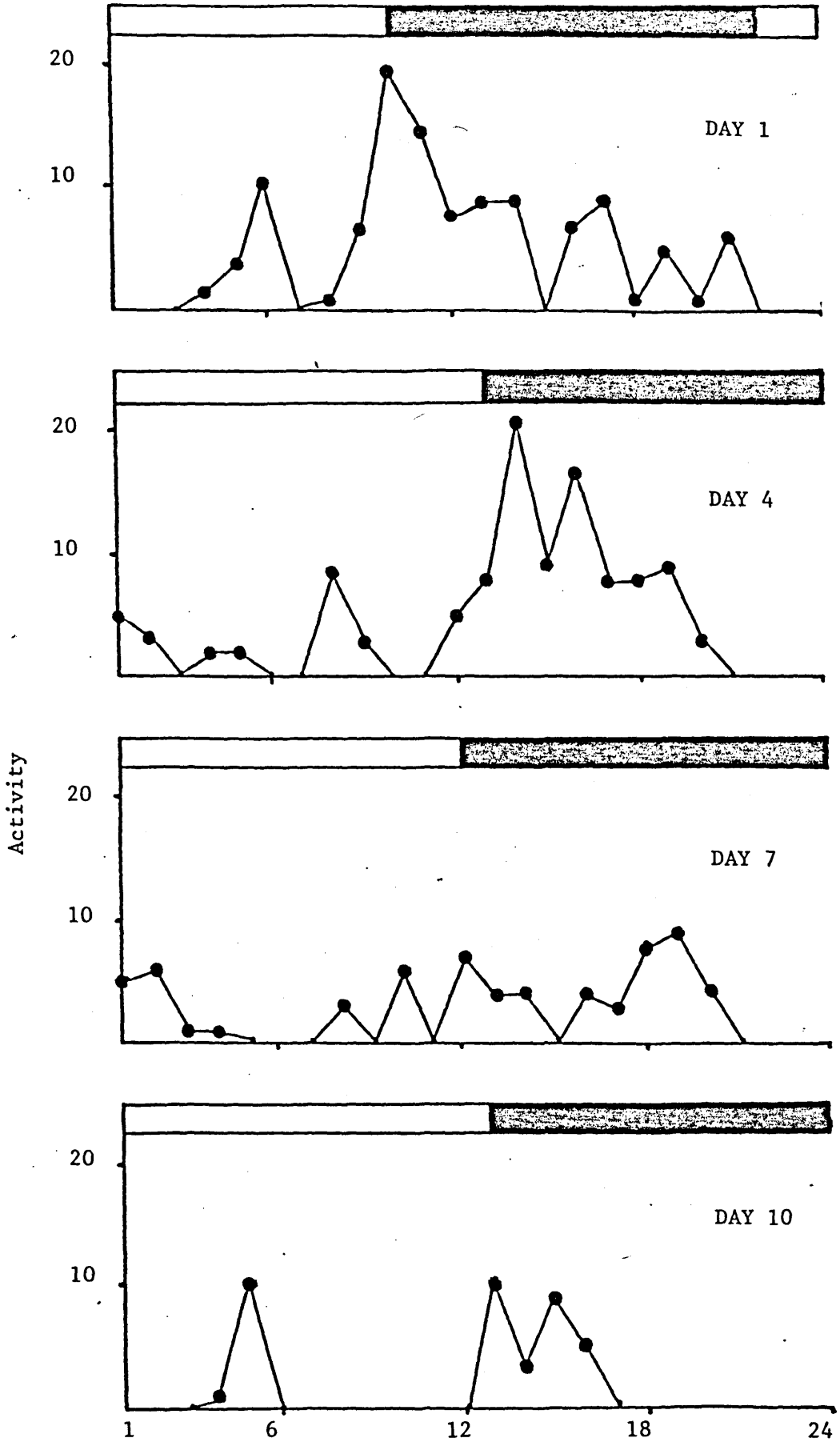

20
10
Activity
0100
0600
1200
1800
2400
Time (h)

Figure 22 Feeding activity of a juvenile lobster at reduced rations in 12:12 LD, 200 lux, with shelter.

24h form estimate (mean events. h^{-1}) on feeding days.


20
10
DAY 1
20
10
DAY 4
Activity
20
10
DAY 7
20
10
DAY 10
1
6
12
18
24
Time (h) from feeding

Discussion.

In contrast to the responses of many other decapods, the locomotor activity of juvenile H.gammarus is not markedly influenced by either photoperiod or shelter availability. Laboratory reared H. americanus show a clear nocturnal activity pattern, especially when shelters are provided, and in bare tanks more activity occurs during light periods (Zeitlin-Hale and Sastry, 1978). Wild caught adults are also nocturnal, exhibit little activity during light periods (Cobb, 1969) and show a clear relationship between burrow occupancy and light intensity (Weiss, 1970). Young juvenile H. gammarus (Stage 7) actively seek shelter under constant illumination and subsequently remain hidden (Howard and Bennett, 1979) but the amount of nocturnal activity in the adult varies throughout the year. Lowest levels (50%) are found between May and July and highest levels (100%) during March (Branford, 1979).

Activity responses are partly determined by the light intensity but there is no clear consensus of opinion on critical light levels for the lobster. H. gammarus can be observed actively foraging on the sea bed at 137 lux (Howard, pers. comm.) and marked inhibition of light period activity was recorded at 525-600 lux by Zeitlin-Hale and Sastry (1978) and at 840 lux, equivalent to the intensity found locally at 10 m depth, by Scrivener (1971). The intensities used in this study may therefore have been insufficient to stimulate shelter occupancy and reduce activity or the juveniles may have become acclimated to a higher light intensity for 200 lux is sufficient to stimulate shelter seeking in younger juveniles (Howard and Bennett, 1979).

The activity peaks associated with the beginning and end of light

phases do not appear to be a sign of the dawn and dusk emergence pattern found in some populations of Nephrops and apparently related to an optimum light intensity for activity (Arechiga and Atkinson, 1975) as well as other environmental influences (Möller and Naylor, 1980). H. americanus reacts the same way to light changes as H. gammarus and this was attributed by Cobb (1969) to a startle reaction, for the activity peaks were transient and decreased within 30 minutes. There is no sign of dawn feeding activity in H.gammarus.

Reynolds and Casterlin (1979) reported that under a natural photoperiod the activity of H. americanus gradually increased during dusk and began to decrease before dawn, while adult lobsters in the wild begin to emerge from shelter 15-25 minutes after sunset and generally return some 12 minutes before sunrise (Weiss, 1970). Juveniles exhibit a consistently high level of activity throughout the dark period (Zeitlin-Hale and Sastry, 1978).

Endogenous rhythmicity is poorly defined in the locomotor activity of H. gammarus. In some crustacea, rhythms have been initiated or rephased by chilling for a number of hours, but this technique has no effect on juvenile lobsters. The time of chilling might be critical as in Bathyporea (Fincham, 1970), but further investigation was not considered worthwhile because the temperature shock to the juveniles usually caused death. A weak endogenous rhythm has been demonstrated in adult H. americanus from inshore populations but this is not apparent in lobsters from offshore populations and may reflect the smaller diurnal fluctuations in light intensity experienced at the depths inhabited by offshore populations. Offshore lobsters also exhibit a greater reaction to light changes in the laboratory (Cobb, 1969). Scrivener (1971) concluded that there was no physiologically controlled rhythm after

observations of activity under a reversed light dark regime. Under conditions of 'dim' and 'bright' light, activity only occurred under the dim period of expected day and indicated that inhibition of activity by light was a stronger influence than any circadian activity pattern.

Endogenous rhythmicity is well defined in the release of larvae. Successful hatching depends on parental assistance and the same pattern of larval release is found under constant darkness as under a natural light-dark regime (Ennis, 1973a). The female releases larvae by pleopod beating for around one minute every night over a period of six weeks, and this feature probably aids larval survival by dispersal over a long period, especially when the environmental conditions at the place of release may be much different to those experienced during subsequent larval drift. The absence of any stereotyped activity pattern in the juvenile would be an advantage for an active and opportunist existence, and individual variation would further help the success of the species. In contrast, a more defined and therefore economical pattern of adult activity is made possible by a much reduced number of potential predators.

The failure to demonstrate a clear nocturnal activity pattern in the juvenile may be the result of a specific response to culture conditions which evoked activity patterns different to those occurring in the natural environment. Unnatural conditions seem to account for the random behaviour of Penaeus monodon when no substrate is available (Möller, 1974), while high and irregular activity in the absence of a suitable shelter has also been reported in Crangon (Hagerman, 1970b) and Praunus (Wallesby, 1973). The expression of endogenous rhythmicity may also be affected by

unsuitable environmental conditions (Atkinson and Naylor, 1973).

Some factors that may have influenced the response of juveniles are the high culture temperature, laboratory rearing and restricted tank size. High temperatures generally increase the activity level but do not appear to affect the pattern of activity - at least within the normal temperature range. The activity rhythm of Carcinus is the same at temperatures from 10-25°C (Naylor, 1963) and in H. americanus there is no difference in activity level between 10 and 20°C (McLeese and Wilder, 1958). Comparatively little work has been carried out on laboratory reared stock but in most cases the typical activity patterns are still present. Williams and Naylor (1967) showed that laboratory reared Carcinus are nocturnally active but the normal semi-diurnal tidal rhythm could be induced by chilling. Laboratory reared P. monodon also exhibit a clear nocturnal rhythm which persists for up to three days under constant conditions (Möller, 1974) and there is no reduction in the nocturnal activity of laboratory bred juvenile H. americanus (Zeitlin-Hale and Sastry, 1978), while laboratory bred H. gammarus show no hesitation in seeking shelter (Howard and Bennett, 1979). It is however possible that the limited exposure to shelter of the juveniles used in this study may have contributed towards a reduced shelter requirement. Juveniles were generally observed inside shelter, but observations were always kept to a minimum, and shelter occupancy may have been a temporary reaction to disturbance.

Container size is known to affect lobster growth (Aiken and Waddy, 1978; Shleser, 1974) but effects on decapod behaviour have been rarely noted. Weinberg (1975) has observed that Crangon is less active in small containers and in many vertebrate species restricted

conditions typically lead to abnormal behaviour patterns (Wynne-Edwards, 1962). The size of the tanks used in this study were as large as the calculated optimum size for lobster growth but larger containers would probably have been more favourable (see Section 2.2).

Apart from the possibility that unnatural conditions may have evoked atypical responses, moult stage and food availability also exert a significant influence over activity and there is considerable individual variation. Such variation has been clearly demonstrated in Uca, where 50% of a population exhibited an endogenous nocturnal activity pattern and the remainder were either diurnally active or random (Honnegger, 1973). Nocturnal activity in juvenile H. gammarus is more defined when food is available and at certain stages of the moult cycle, and these two factors may exert the major influence over activity in the natural environment although it was not possible to investigate the effect of shelter and light regime under all food and moult conditions.

A certain amount of locomotor activity must be associated with feeding and this partly accounts for the more pronounced nocturnal activity of fed lobsters, while lower activity during the day may reflect a reduced activity drive of food search. Reduced locomotor and feeding activity after starvation may indicate a compensatory response to restricted food supplies and this could be a factor in the improved food utilisation found in lobsters grown under the periodic starvation regimes described in Section 2.5. Respiration rates are generally lower in starved animals and the rate seems to be proportional to the nutritional state in Carcinus and Cancer (Aldrich, 1975). The usual circadian pattern of oxygen consumption in Cancer is also suppressed by starvation, but a single meal can rephase the rhythm

(Ansell, 1973). Activity in Crangon may be increased (Hagerman, 1970b) or decreased (Weinberg, 1975) by starvation, but the activity of P. monodon is unaffected by feeding (Möller, 1974). In juvenile Panaeus merguiensis feeding suppresses the short term activity cycles (period 2-3 h) that are superimposed on the normal circadian rhythm and which are thought to result from food searching activities (Hindley, 1975), while food availability modifies the nocturnal activity pattern characteristic of laboratory studies of Nephrops (Möller and Naylor, 1980).

Variations in activity during the intermoult period presumably reflect changing food and shelter requirements. Studies at the Conwy laboratory have shown that the food consumption of cultured lobsters varies from day to day, but generally decreases from a maximum level reached soon after ecdysis, and this is also found in Panulirus (Chittleborough, 1975) and Carcinus (Ropes, 1969). Minimum consumption occurs a little after halfway through the intermoult period and subsequently increases up to the next moult (Munford, pers. comm.). A similar pattern is evident in locomotor activity although the point of minimum activity does not quite coincide with the point of minimum food consumption. Just before and after ecdysis nocturnal activity is more pronounced and this would be expected during this critical period.

If the relative proportions of each moult stage are the same at elevated temperatures as at ambient temperatures, the period of declining activity encompasses stages A1-C2 (based on Drach, 1939; with further characterisation by Yamoaka and Scheer, 1970), and the point of minimum activity corresponds to the attainment of the hard-shelled condition. In the wild, postmoult activity while the shell is soft would not be expected to be high and the activity levels found in this study may be a result of stress at this

vulnerable stage. Any such stress would decrease as the shell becomes harder and unrestricted activity would follow complete calcification. Changes in aggression during the moult cycle lend support to this theory for Tamm and Cobb (1978) have reported that H. americanus in mid proecdysis dominate all other stages while lobsters in postecdysis are always subordinate.

The postecdysial decline in activity is also associated with a decrease in food consumption but it is not clear whether this reflects the normal pattern of food consumption in the wild or an increased energy demand from the high activity under culture conditions. The high and irregular activity that predominates for most of the remainder of the intermoult period is the type of activity found in the first series of experiments and seems to represent the typical juvenile response.

Feeding activity has a more pronounced circadian pattern than locomotor activity and is usually confined to darkness except during periods of high food demand as in Jasus (Fielder, 1965). Most feeding takes place during the first few hours of darkness and a unimodal peak is also evident under constant conditions. There are few records of feeding activity in other decapods - activity is presumably nocturnal in the majority of dark active species, but the pattern of activity within darkness is often not known. Dawn and dusk peaks have been recorded in Crangon septemspinosa (Wilcox and Jeffries, 1974) and an endogenous component is evident in Jasus (Fielder, 1965).

Despite the endogenous component to feeding in H. gammarus the light regime seem to have a greater influence. Feeding can be initiated outside the time of expected night by manipulation of

the light regime, although starved animals will wait for darkness before feeding. As with locomotor activity, a flexible feeding strategy would be an advantage to the juvenile and allow acquisition of food when lighting conditions were suitable. Feeding activity in the adult may be more rigid for a 12h cycle of digestive enzyme secretion in response to a meal has been demonstrated by Barker and Gibson (1977). There is however no evidence of a persistent cycle of secretion as found in Palaemon serratus (Van Wormhoudt and Ceccaldi, 1975), with maximum secretion occurring at 0900 and 2100 h. These peaks may reflect dawn and dusk feeding, but P. serratus normally exhibits a semi-diurnal tidal rhythm of locomotor activity (Rodriquez and Naylor, 1972) and it is more likely that the prawns were responding to an existing tidal rhythm.

It is not possible to determine to what extent these results are a fair reflection of juvenile activity in the wild, but juveniles do seem to exhibit most of the characteristic behaviour of the adult. One of the aims of this investigation was however to help define intensive culture conditions, and several useful facts have emerged:

Juvenile lobsters do not exhibit a clear circadian activity pattern in response to artificial light regimes and this indicates that light-dark cycles are not necessary. Suitable lighting conditions are therefore likely to be those that induce the least stress, and constant darkness or low level illumination have been found most beneficial in growth trials (Section 2.3). High light intensities may suppress activity but an increase in stress will probably outweigh any energy savings.

In this study, shelter availability was not critical for laboratory reared stock, and while shelter is apparently a general lobster

requirement, shelters are probably not necessary in a culture system. Provided that the lighting conditions are favourable, only the thigmotactic responses need to be considered in container design. Nevertheless, growth studies have shown that juveniles benefit from shelter provision under a natural photoperiod (Section 2.4).

Nocturnal feeding is well defined in the juvenile, so the animals should be fed at the end of the day to prevent unnecessary deterioration of food. The variation in juvenile activity through the intermoult period results in considerable differences in daily food consumption, and without complex record keeping, it will be impossible to provide the correct daily ration and achieve efficient food utilisation. If the ration size is sufficient for individuals at a maximum feeding level, food will be wasted by other juveniles, while if a smaller ration is provided, the growth rate may be adversely affected. This is a major husbandry problem but studies described in Section 2.5 indicate that periodic starvation may be a practical method of improving food utilisation, for there appears to be an interaction between activity and food availability.

Summary

1. Under artificial light regimes, the locomotor activity of mid-moult juveniles was irregular, with no defined fixed activity pattern. High activity occurred at the beginning and end of each light phase and appeared to be a startle reaction. Light intensities of 400 lux inhibited activity more than intensities of 250 lux but a clear nocturnal habit was not generally evident.

2. The provision of shelter did not greatly modify the response to light regimes, apart from causing a slight decrease in the general level of activity and less variation in mean hourly activity.

3. Evidence of an endogenous activity rhythm was found under constant conditions, but this feature was not pronounced.

4. A more pronounced circadian pattern of activity was found in daily fed animals and the general level of activity was greater than in starved animals.

5. The level of daily activity varied through the moult cycle. Activity decreased after ecdysis to a minimum one third of the way through the intermoult period. Activity subsequently increased and became irregular, with fluctuations in total daily activity and proportion of nocturnal and diurnal activity. Nocturnal activity predominated just before and after ecdysis.

6. Feeding activity was generally confined to darkness and under constant conditions an endogenous rhythm was evident, although feeding could be initiated outside the normal period by manipulation of the light regime.

7. Periodic starvation caused a decrease in the intensity and duration of feeding activity.

8. It is not clear whether these results truly reflect the activity of juveniles in the wild, or whether they represent a specific response to culture conditions. Most of the characteristic behaviour of the adult is present to some degree in the juvenile, and it is concluded that the responses observed in this study signify a flexibility of behaviour which would be advantageous to juvenile existence.

9. The implication of these results to intensive culture conditions is discussed.

SECTION 4

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