THE INFLUENCE OF THERMAL POLLUTION
ON VARIOUS ASPECTS
OF THE BIOLOGY OF THREE SPECIES OF CRAB

by

Lesley Beviss-Challinor

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Department of Zoology

UNIVERSITY OF CAPE TOWN

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The long thrust of life, over the millenia, is inevitably towards any new energy source that will succour it. The next move into nuclear energy is inevitable. Life now expresses itself, through ourselves, consciously. We should not use our fears to try to turn the clock back but instead use our intelligence in order to enjoy the benefits of nuclear power safely.

\- Sir Alan Cottrell, F.R.S.

ABSTRACT

The construction of a nuclear power station on the west coast of South Africa will result in a large volume of heated effluent being discharged into the ocean, thus raising the temperature of the surrounding sea by a few degrees. The physiological effect that this hot water will have on three species of crab common along the west coast, is presented in this paper. Parameters of the energy equation $C = P_g + R + U_{ex} + F + U_e$ have been measured for adult *Plagusia chabrus*, *Hymenosoma orbiculare* and *Cyclograpsus punctatus*. It appears that rate-temperature responses increase with increase in temperature for all three species. Favourable water temperatures were found to be between 16°C and 21°C for the three species, with temperatures of 26°C being detrimental, especially during moulting in *P. chabrus* and *H. orbiculare*. The energy budget and energetic efficiencies are calculated for all the species and it appears that the increased temperatures around Koeberg Power Station will be beneficial to the adult crab species.

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1. INTRODUCTION

All biological activities depend upon chemical reactionswithin cells and this constitutes the metabolism of the organism. These reactions are influenced by a number of external factors, one of the most important of which is temperature. Living organisms vary greatly in their ability to withstand exposure to temperatures beyond normal ranges of activity, and this aspect of biology has been studied extensively by scientists.

Animals have an upper and lower limit of thermal tolerance to which they have adapted in their particular niche (Kinne 1970, Vernberg & Vernberg 1972; Precht et al. 1973; Newell & Branch 1980). Taylor (1982) states that these maximum and minimum tolerance levels are genetically defined for a given physical or chemical factor, but the tolerance range of one factor may be greatly affected by variation of other factors. This statement is exemplified by Mangum and Towle (1977), de Fur and Mangum (1978) and McMahon et al. (1978) who showed that responses of isolated systems of animals cannot be assessed alone, but as a small change in a complex integrated change of many variables. Bayne (1973) in work on Mytilus edulis found that organisms that are unable to compensate physiologically for temperature changes often exhibit a reduced growth potential and are usually more vulnerable to other environmental changes. The 'zone of tolerance' can be modified by long-term changes in environmental temperature (acclimation), and the lethal limits altered until the 'ultimate' lethal limits are reached (Spoor 1955; McLeese 1956; Newell 1969; Newell et al. 1971; Precht et al. 1973; Diwan et al. 1976; Newell & Branch 1980).

It has been suggested (Precht et al. 1973) that one factor accounting for this metabolic compensation is the freewater to bound water ratio in animal tissues. Precht et al. (1973) found a direct relationship between animal tissue water and acclimation temperature, and concludes that the increase of water might lead to a reduction in metabolic rate through a reduction in the proportion of respiring tissue. At ultimate temperature limits, damages incurred by the organism are irreversible and death occurs.

The most common physical property of a large volume of water is the capacity to buffer physical effects and to absorb, break down or recycle introduced materials. If this capacity is exceeded, additional forms of energy, such as that released by power stations, may become pollutants.

The construction of nuclear power stations is a comparitively recent development in time and may involve the use of seawater in the cooling system. This has resulted in gross localized sudden increases in water temperatures along various shores around the world. How this will affect the populations of various marine invertebrates is still under study, although work done by Naylor (1965a, b), Leffler (1972), Cook (1977), Taylor (1982) and Cook and Achituv (in press) show that definite changes are likely to occur, especially in the duration of life cycles and breeding cycles of animals. However, much of this work has only been done on individual species and on the short-term effects of raised temperatures. Population dynamics as a whole may change dramatically and also larval forms which usually require a narrow range of temperature for development (Taljaard 1975; Taylor 1982) could succumb to a slight increase in temperature and species could be completely eliminated from that area.

Short-term experiments may prove that a species is resistant to a temperature rise of a few degrees. However, the organism may be in its 'incipient lethal level' in which it can no longer live for an indefinite period of time - i.e. the animal has not yet reached the zone of resistance, but will nevertheless eventually die (Fry 1947; Taylor 1982). This factor is very difficult to determine and it could take many months of continuous monitoring to measure the absolute effect of a temperature rise on any one species. (See also Adams (1969) for work done on species found in the United States.)

Basson (1976) postulates that a reduction in the numbers and types of species may occur due to the decrease in available oxygen and probable increase in bacteria, as well as rate increases of chemical and biochemical reactions. Taylor (1982) also found that crabs cannibalized each other to a significantly greater extent during increased temperature. An increase in temperature causes supernormal activity and then sub-normal activity as upper limits are approached, therefore making the animals more susceptible to predation.

The first nuclear power station in South Africa is due to be opened by about the end of 1983. The station is situated 28 km north of Cape Town and may eventually accommodate several reactors. When the first two reactors are in full use, about 80 m^3 of seawater per second will be used for cooling, and this will be returned to the sea about 10°C above the original temperature. Sea temperatures at Koeberg vary between 8°C and 14°C and the shore temperatures average 12°C for most of the year. If a 10°C rise in temperature is experienced at the outlet and along the shore, then the maximum temperature that could be obtained when the power station is in use, would be 24°C. However, once dispersion of the warm water occurs, and provided that this warmer water is not recirculated, a conservative estimate of the rise in temperature due to this discharge into a body of seawater, say two metres deep, 600 m wide and flowing at 0,5 m s^{-1} is only 1°C (Straszacker 1972). If this is the case, it appears that the most that the heated water will do to the surrounding area, is to heat it up to temperatures corresponding to those found in False Bay, and subsequently marine life similar to that of False Bay could become common in the area (Mallory & Cook 1974).

The purpose of this paper is to examine the effect of heated water on three species of crab found in the vicinity of the power station - *Plagusia chabrus*, *Hymenosoma orbiculare* and *Cyclograpsus punctatus*.

Adult animals were used in this study and parameters of the equation

$$C = F + U_E + U_{EX} + P_G + R$$

(where C is energy consumed; P_G and R is the energy used in production and metabolism; and F, U_E and U_{EX} is the energy lost in faeces, excretion and exuvia) were measured. The species were chosen on the basis of availability and ease of capture, and were hardy and adapted well to laboratory conditions. They are also fairly common on the shores of Koeberg and therefore likely to come under the influence of the heated effluent.

Plagusia chabrus (Family Grapsidae) or familiarly called the Cape rock crab, occurs subtidally and is a common scavenger in low tide pools and on rocky shores (Plate 1). Its range extends from Luderitz to Port Shepstone. _P. chabrus_ is an active swimmer, with fringes on its legs to assist swimming. The species is typified by the red-brown colour and smooth velvety dorsum. The sides of the carapace have three post-orbital teeth (Day 1974).

Hymenosoma orbiculare (Family Hymenosomatidae) is found mainly in estuaries, but small specimens are dredged on sand banks in the sea (Plate 2). They are omnivorous and the colouring is usually grey-green often with dark markings. They are found between Luderitz and Inhambane (Day 1974).

Cyclograpsus punctatus (Family Grapsidae) is one of the commonest species of crabs found around South Africa, extending from Port Nolloth to Kosi Bay (Plate 3). It can also extend into estuaries and can live for up to a week out of water. C. punctatus is also a scavenger (Day 1974).

Plate 1 Plagusia chabrus

Plate 2 Hymenosoma orbiculare

Plate 3 Cyclograpsus punctatus

2. MATERIALS AND METHODS

2.1 Collection of Material

P. chabrus were collected using SCUBA from Oudekraal on the West Coast in March 1982. Thereafter the numbers were maintained by collections made from Hout Bay Harbour in April, June and July. It was noticed that, on average, the crabs taken from Hout Bay Harbour were smaller and therefore more suitable for growth and moulting experiments. The size range of the crabs varied from 14 mm to 48 mm. The carapace width was measured between the points of the third pair of lateral teeth to an accuracy of ± 0,1 mm with vernier calipers. The crabs were dried with tissue paper, weighed on a Mettler balance (to within 0,01 g) and measured individually. Each crab was labelled with a numbered disc which was glued onto the back of the carapace with cyanoacrilate glue.

The initial collection of Hymenosoma was taken from Hout Bay Harbour in October 1982. However, only large specimens were obtained - the width varying from 12,3 mm to 27,6 mm (width taken at the widest part of the carapace) and most of the crabs were found to have a parasitic nematode living in the thoracic cavity. The nematode in some cases, accounted for up to 15% of the dry weight of the crab. The infected crabs were discarded. Further collections of crabs were taken in November and December 1982 from Langebaan Lagoon, where the size ranged from 8 mm to 17,5 mm. These crabs were not infected with the parasite. The crabs were again weighed and labelled using numbered discs cut from a surgical glove and glued onto the carapace (Richard 1978).

Cyclograpsus were captured in February 1983 on the rocky shore at Green Point. A further collection was made in March. The animals were found high up on the shore in the Littorina zone. The size range varied from 12,6 mm carapace width (at the widest point) to 27,4 mm. The crabs were labelled with numbered rubber discs.

The crabs were territorial and cannibalized each other, particularly after moulting, and therefore were kept in separate chambers or in 54 ℓ tanks stocked with plenty of rocks where they could escape predation.

All crabs were fed ad lib. on whole mussel Choromytilus meridionalis, throughout the duration of the experiments. For the feeding experiments only the mantle and foot tissue of the mussel was used (Section 2.4.1.).

2.2 Growth and Moulting

Plagusia and Cyclograpsus were housed in 14 cm diameter, 7 cm high, plastic tubes tied onto 3 mm thick rectangular pieces of plastic gauze.

Six cubicles fitted onto one piece of gauze and two of these structures fitted into a 54 ℓ aquarium tank, one on top of the other, thereby housing 12 crabs per aquarium. Enough space was left on one side of the tank for heaters, air hoses and a water hose. Smaller 7 cm diameter cubicles were made for Hymenosoma, but again only 12 were put into each tank. The plastic cubicles were painted three-quarters of the way around with marine high gloss enamel paint. This prevented visual contact between crabs but also allowed light to enter from the one side. This prevented the possibility that visual contact with other crabs may have inhibited the size increment at moulting (Klein-Breteler 1975a).

Temperatures were kept constant at one of the three experimental temperatures 16°, 21° and 26°C, by means of thermostatically controlled heaters. The laboratory in which the tanks were kept was maintained at 11°C so the 11°C aquaria required no other temperature regulation.

Lighting conditions (12 h light and 12 h dark) and salinity (35‰) were identical in all experiments and the water flow into each tank was adjusted so that the temperatures could be maintained within 1°C of the experimental temperatures.

Two experiments were run concurrently for each of the three species for a period of 80 days. Crabs that died were replaced by others that had previously been housed in 54 ℓ tanks with other crabs. At the end of the 80 day period, the same crabs were used for the next two temperature experiments. This was done in order to assess the approximate length of the intermoult period, even though this may not have been obtained at the one temperature. In a few cases, the crabs did not moult at all in the laboratory - a period of over 160 days.

When necessary, especially at the higher temperatures, the tanks were thoroughly cleaned in order to prevent excessive growth of algae and build-up of faeces.

2.3 Respiration/Metabolism

Oxygen consumption was determined by means of a YSI oxygen electrode connected to a digital acid-base analyser (PHM 72 MK2). The analyser was in turn connected to a Philips PM 8000 chart recorder so that oxygen consumption rate could be determined from the resultant slope.

P. chabrus were placed in one litre bottles containing previously aerated filtered (0,45 µm) seawater at the designated temperature. The bottles were completely sealed by a lid through which the oxygen probe had been placed.

Cyclograpsus and large Hymenosoma were put into 500 mℓ jars while the oxygen consumption of small Hymenosoma was recorded from 134 mℓ jars.

The crabs were transferred from the original aquarium to the respiratory jar in the minimum possible time to avoid disturbing the animal. The duration of the experiment was 30 min. No stirrer was used as it was thought that this would disturb the crab. Movement of the crab appeared sufficient to stir the water.

Cyclograpsus is found in the Littorina zone and therefore spends much of its time out of water. Respiration in air was therefore also measured. This was done using a Gilson differential respirometer. The crabs were placed in 50 mℓ washed and dried flasks with a side arm containing concentrated potassium hydroxide solution. The animals were left for 20 min in air at a temperature equivalent to the water temperature in which they had been acclimated. The whole system was then closed and the experiment run for 30 min with readings being taken at 5 min intervals.

2.4 Food Consumption, Faecal Production and Dissolved Organic Carbon Analysis (DOC)

2.4.1 Food consumption

Consumption experiments were carried out in separate 2 ℓ beakers. Each *P. chabrus* was placed in a beaker containing 1800 mℓ of 0,45 µm filtered seawater. *Hymenosoma* and *Cyclograpsus* were placed in 1 ℓ of seawater. An air hose led into each beaker and the beakers were covered with kaylite to prevent the crabs from escaping and water evaporating at the higher temperatures.

A weighed amount of *Choromytilus meridionalis* mantle edge or foot muscle was given to each crab. Only these portions of the mussel were used as other parts of the mussel tended to disintegrate with time. After 24 h the unconsumed food was collected, freeze-dried and weighed. The wet weight was not taken, as a great deal of water was imbibed into the tissues during the 24 h. Equivalent samples of *C. meridionalis* food and mantle edge were freeze-dried to obtain the wet:dry ratio, thereby allowing all measurements to be converted to dry weight.

It soon became apparent that *P. chabrus* was under stress in this situation and this may have affected the feeding. The base of the beaker was not covered with mesh, in order to prevent the break-up of faeces, so the crabs could not grip onto anything. The majority of time was spent hanging upside down from the air stones. In order to rectify this, 14 ℓ tanks were used instead of the beakers, and 3,6 ℓ of filtered seawater was placed in them. Smooth rocks that had previously been scrubbed clean of dirt and algae were placed in the tanks and either one, two or three crabs of similar size were placed in the tanks.

In the experiments with *Hymenosoma* and *Cyclograpsus* previously scrubbed rocks were placed in the 2 ℓ beakers.

The experiments on each crab ran for five days and control beakers with samples of food were left for the same period of time at the different temperatures, so that natural disintegration of food could be monitored.

2.4.2 Faecal production

The top 250 mℓ of water from each experiment were poured into a jar for measurement of suspended material. All but the last 250 mℓ of water in the beaker were discarded. The last 250 mℓ which contained the unbroken faeces were filtered through prewashed, preashed and preweighed G.F.C. filters. The filters were then dried, weighed, ashed and reweighed to obtain the faecal production of each crab. The same was done to the 250 mℓ suspension samples, the results of which were then multiplied by

$$\frac{\text{total volume} - 250\ \text{m}\ell\ \text{(faeces)}}{250\ \text{m}\ell}$$

to give the total suspension of disintegrated faeces (after correction using the control for suspended food particles). This result was added to the faecal result.

The filters and faeces were washed with 3,5% ammonium formate to remove the salt. Numerous control readings were taken to assess changes in weight due to the loss or gain by the filter papers themselves.

2.4.3 Dissolved organic carbon analysis

After each 24 h feeding experiment a small sample of water was taken for DOC analysis. This was carried out on a Technikon Autoanalyser II and the results were added to those obtained from faecal production. Values were subtracted originally from the control readings to eliminate that portion of DOC due to the disintegration of C. meridionalis.

2.5 Excretion

It is normally assumed that the amount of energy lost through urine/ammonia excretion is negligible and can be calculated as the difference between the amount consumed and energy lost in faeces, growth and reproduction, and metabolism. However Achituv (pers. comm.) in work on Palaemon pacificus, found that this energy loss was significantly large enough to play an important role in determining energy expenditure. Furthermore Achituv found that the amount of ammonia produced increases with an increase in temperature, although other workers (discussed in Section 3.4) have found excretion to be temperature independent. Experiments were therefore carried out to determine the effect of temperature on excretion of P. chabrus, H. orbiculare and C. punctatus.

The method of measurement was that employed by Solórzano (1969). This involves the addition of a phenol-alcohol solution, sodium nitroprusside and an oxidizing reagent to a sample of seawater in which the crabs had been placed. All glassware used had been previously washed in Contrad, dilute HCl and double distilled water and dried in an oven. H. orbiculare and C. punctatus were left in 250 mℓ and P. chabrus in 500 mℓ of filtered, autoclaved seawater for 1 h at the lower temperatures and 30 min at 21° and 26°C. Controls were included with each experiment. The water was not aerated during the experiment and the beakers were covered with aluminium foil to prevent escape of ammonia. Temperatures were kept constant by means of a water-bath.

After addition of the reagents the blue colouration was allowed to develop for 2 h at room temperature and the concentration determined on a Beckman Model 25 Spectrophotometer. A calibration graph was constructed using $(NH_4)_2SO_4$. Concentration was converted to atoms $N\text{-}NH_3\ \ell^{-1}$ by means of the linear regression equation

$$Y = 19{,}4327X - 0{,}0438 \ (r = 0{,}99).$$

This figure was converted to protein ($\mu g\ \ell^{-1}$) on the assumption that nitrogen makes up 16% of total protein. A calorific value was calculated by multiplying by 23,657 ($kJ\ g^{-1}$) (Crisp 1971).

2.6 Reproduction

Reproduction was not studied in detail in this project. However, in order to obtain some information on the energy used in reproduction, females in berry were collected. P. chabrus females were collected from Hottentots Huisie in August and September. H. orbiculare were collected in November and December from Hout Bay and Langebaan Lagoon, and C. punctatus were collected from Green Point in February. The eggs were scraped from the females and either counted directly then weighed, or, if the eggs could not be separated, were dried and weighed in whole batches. The calorific value of the eggs was established so that an approximate measure of the amount of energy used in reproduction could be calculated.

The female crabs that had been scraped of their eggs, moulted within a few days of treatment in most cases. Others produced another batch of eggs, despite the absence of males, but these were shed immediately. Sperm is stored in the spermathecae of the female and remains viable for long periods, even through moults (Warner 1977) so the second batch of eggs may well have been fertile, but shed due to unnatural laboratory conditions.

2.7 Statistical Methods

All data obtained were fitted to a least-squares linear regression model and the resulting fitted lines were tested for significant differences between the temperatures using the F-test for comparing two or more slopes - Analysis of Covariance (ANOCOVA) after assumptions of least-squares curve fitting had been met (Zar 1974). If the slopes were found to be equal the F-test comparing two or more elevations was considered (Zar 1974).

The student's t-test (Zar 1974) was employed when testing the difference between two means.

The r and t values of the regression lines are also given to test the correlation between the X and Y values.

Although in most cases, the r value was greater in the simple linear regression, most authors use logarithmic transformations especially in respiration work, so logarithmic results have been included in the appendix for direct comparisons.

Analysis of variance (ANOVA) was used to establish the equality of several means after variances were proved to be homoscedastic and normality was tested using the method employed by Shapiro and Wilk (Zar 1974).

3. RESULTS AND DISCUSSION

3.1 Moulting and Growth

Crustacean growth can only proceed in a series of steps by means of successive moults or ecdyses. The increase of body size occurs during this short period of ecdysis. The moult cycle involves several stages and a brief description of the main physiological changes within each stage is given for later reference.

Stage A: Newly moulted

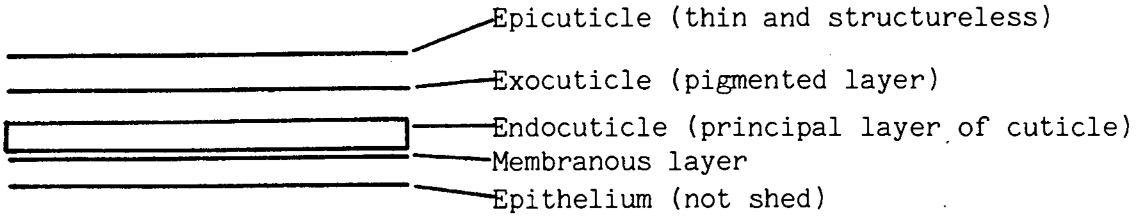
The animal emerges with a soft cuticle which has been secreted by the epithelium. Organic reserves and sometimes inorganic salts that were reabsorbed into the body from the old cuticle are now transferred to the new cuticle and mineralization begins.

Stage B: The exoskeleton becomes more rigid.

Stage C: The exoskeleton becomes completely rigid and a new membranous layer is formed. The animal is feeding normally and metabolic reserves begin to accumulate. This is the main period of tissue growth, and under favourable conditions this is the longest phase of the moult cycle.

Stage D0: There is an accumulation of glycogen reserves in the epithelium and sub-epithelial connective tissue, and calcium levels in the blood rise. If limbs were missing and a bud has formed, rapid growth of these buds will occur at this stage. In unfavourable conditions the Do phase of proecdysis can be stopped and in some cases reversed - the only phase in which this can happen.

Stage D1: The beginning of the formation of a new exoskeleton, secreted by the epithelium



Stage D2: Secretion by the epithelium, and protein turnover reach their peak. New muscle attachments are formed to the new skeleton and the old attachments break down.

Stage D3: The mineral and organic matter is removed from the endocuticle and in some cases, but more commonly in freshwater crustaceans, the exocuticle may be decalcified. Specific resorption occurs along the epimural sutures.

Stage D4: Continued resorption along the epimural sutures, followed by a rise in the osmotic pressure of the blood.

Stage E: Due to the rise in blood osmotic pressure, there is a rapid uptake of water - mainly through the digestive tract. The animal remains immobile (passive phase). Expansion of the animal causes a split in the epimural sutures. Oxygen uptake increases and the active phase is entered into, in which the animal rapidly withdraws from the old skeleton. During this time respiration is interrupted and after emergence the animal becomes quiescent, but pumps at the maximum rate allowing rapid water flow over the gills. The haemoglobic concentration in the blood also rises.

More detailed descriptions of the moult cycle are given by Passano (1960) and Warner (1977).

The time taken for a crab to reach full growth depends upon the size increment at moulting and the moult frequency. Factors that alter either of these two parameters will ultimately affect the growth rate of the crab to a greater or lesser extent. Furthermore, it has been found that, in general, the period between moults lengthens as the crab gets older (Adelung 1971; Klein-Breteler 1975a; Warner 1977) and the growth increment decreases (Warner 1977). A rise in temperature usually results in an increased growth rate (Roberts 1957a; Passano 1960; Zein-Eldin & Griffith 1966; Leffler 1972; Klein-Breteler 1975a; Young & Hazlett 1978; Bursey 1978; Johns 1981a, 1982).

Tables 1 - 3 show the growth rates and intermoult periods of the three species of crabs studied. The crabs selected for these experiments were large and it appears that most of them had reached maturity.

TABLE 1 The effect of temperature on the growth rate (dry mass in g) of the three crab species

a) Plagusia

Days	11°C	16°C	21°C	26°C *
0	9,94 ± 4,01	7,09 ± 4,25	7,87 ± 3,78	7,96 ± 3,86
20	10,00 ± 3,95	7,18 ± 4,22	8,48 ± 3,62	7,96 ± 3,86
40	10,01 ± 3,96	7,56 ± 4,41	8,86 ± 3,44	7,96 ± 3,86
60	10,01 ± 3,96	7,77 ± 4,33	9,58 ± 3,60	8,80 ± 4,18
80	10,01 ± 3,96		9,93 ± 3,44	9,40 ± 3,44
Total increase	0,07	0,68	2,06	1,44
% increase	7,0	9,6	26,2	18,1

b) Hymenosoma

Days	11°C	16°C	21°C	26°C
0	0,18 ± 0,05	0,70 ± 0,28	0,20 ± 0,22	0,24 ± 0,12
20	0,18 ± 0,05	0,78 ± 0,46	0,32 ± 0,24	0,39 ± 0,23
40	0,18 ± 0,05	0,93 ± 0,60	0,41 ± 0,24	0,40 ± 0,23
60	0,26 ± 0,11	1,02 ± 0,53	0,41 ± 0,24	High mortality
80	0,26 ± 0,11	1,05 ± 0,51	0,52 ± 0,43	High mortality
Total increase	0,08	0,35	0,32	0,16
% increase	44,4	50,0	160,0	66,7

c) Cyclograpsus

Days	11°C	16°C	21°C	26°C
0	1,05 ± 0,45	0,69 ± 0,59	0,68 ± 0,32	0,81 ± 0,46
20	1,05 ± 0,45	0,82 ± 0,67	0,75 ± 0,50	0,88 ± 0,49
40	1,13 ± 0,56	0,47 ± 0,11	0,82 ± 0,52	1,01 ± 0,45
60	1,13 ± 0,56	0,51 ± 0,06	0,85 ± 0,49	1,14 ± 0,63
80	1,13 ± 0,56	High mortality	0,85 ± 0,49	1,14 ± 0,63
Total increase	0,07		0,17	0,33
% increase	6,7		25,0	40,7

* These values were obtained from the six Plagusia that survived ecdysis at 26°C

TABLE 2 The effect of temperature on the growth rate (width in mm) of the three crab species

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a) *Plagusia*

Days	11°C	16°C	21°C	26°C*
0	38,98 ± 4,68	33,55 ± 6,91	35,74 ± 5,70	36,40 ± 6,44
20	39,10 ± 4,56	33,85 ± 6,75	36,94 ± 5,18	36,40 ± 6,44
40	39,25 ± 4,71	34,75 ± 7,31	37,26 ± 4,91	36,40 ± 6,44
60	39,35 ± 4,79	35,26 ± 6,86	38,08 ± 4,92	37,28 ± 6,35
80	39,35 ± 4,79		38,56 ± 4,55	37,90 ± 5,93
Total increase	0,37	1,71	2,82	1,50
% increase	9,5	5,1	7,9	4,1

b) *Hymenosoma*

Days	11°C	16°C	21°C	26°C
0	12,18 ± 1,32	20,12 ± 2,93	11,95 ± 4,29	13,34 ± 2,19
20	12,18 ± 1,32	20,68 ± 3,94	14,44 ± 4,23	16,07 ± 3,18
40	12,18 ± 1,32	21,62 ± 4,82	16,29 ± 3,72	16,30 ± 2,90
60	13,95 ± 2,33	22,78 ± 3,89	16,29 ± 3,72	High mortality
80	13,95 ± 2,33	23,09 ± 3,67	17,16 ± 4,74	High mortality
Total increase	1,77	2,97	5,21	2,96
% increase	14,5	14,8	43,6	22,2

c) *Cyclograpsus*

Days	11°C	16°C	21°C	26°C
0	17,60 ± 2,69	15,10 ± 3,74	15,82 ± 2,34	15,47 ± 2,93
20	17,60 ± 2,69	16,50 ± 4,25	16,28 ± 3,33	16,51 ± 3,52
40	18,10 ± 3,34	16,50 ± 4,25	16,70 ± 3,60	17,33 ± 3,21
60	18,10 ± 3,34	16,89 ± 3,95	17,15 ± 3,22	17,89 ± 3,59
80	18,10 ± 3,34	High mortality	17,15 ± 3,22	17,89 ± 3,59
Total increase	0,5	1,79	1,33	2,42
% increase	2,8	11,9	8,4	15,6

* These values were obtained from the six *Plagusia* that survived ecdysis at 26°C

TABLE 3 The effect of temperature on the intermoult period (days) of the three crab species. A two-sample t-test for the one tailed hypothesis - mean intermoult period is longer at the lower temperatures - was applied, for results from <u>P. chabrus</u> ($p > 0,05$).

Temperature	n	Mean	s.d.	s.e.	Result of t-tests
a) <u>Plagusia</u>					
11°C	11	No Moult			
11 - 21°C	11	76,64	± 8,27	2,49	μ_1 (11-21) > μ_2 (21)
16°C	12	Only one moult over 60 days			
16 - 26°C	8	65,75	±13,87	4,90	μ_1 (11-21) > μ_2 (16-26)
21°C	11	47,73	± 5,92	1,78	
26°C	6	44,83	± 9,54	3,89	μ_2 (21) = μ_2 (26)
b) <u>Hymenosoma</u>					
11°C	6	58,83	±13,78	5,62	
16°C	13	66,80	±18,90	5,31	
21°C	9	Intermoult period was found to be a linear regression of dry weight. Y=12,078+58,990X(±11,850) r = +0,73			
26°C	9	All died 26,1 ± 12,3 days after first moult			
c) <u>Cyclograpsus</u>					
No intermoult period obtained at any temperature.					

TABLE 4 Parameters of the linear regressions of initial width against percentage growth increment for Hymenosoma

Temp	n	a	b	syx	r	P value
11°C	4	1,90	2,23	2,82	0,77	Not Sig.
16°C	8	1,34	0,78	1,75	0,81	0,02
21°C	14	36,85	-0,97	5,07	-0,64	0,01
26°C	6	-44,12	5,41	8,64	0,68	0,1

Unfortunately there is little in the literature to determine when Plagusia chabrus reaches maturity. However Hill and Forbes (1979) in work on Hymenosoma orbiculare recorded 8% of the females measuring 5 mm in width to be carrying eggs. All H. orbiculare caught for these experiments measured over 8 mm and the majority of females were ovigerous. Broekhuysen (1941) states that Cyclograpsus punctatus males are fully grown at 20 mm width. The size range used in this study was between 12,6 and 27,4 mm. Results for intermoult periods for H. orbiculare and C. punctatus were not obtained as most of the crabs had reached maturity.

The experiments in which no moulting occurred will be discussed first.

P. chabrus experiments at 16°C were started 15 days after the other experiments, due to failure of the air pump killing the initial crabs. This experiment was therefore only run for 60 days as opposed to the 80 days duration of the others. However, not withstanding the shorter period, all but one crab underwent one moult at this temperature. It is interesting to note that the crab that did not moult was one of the smallest measuring 24,6 mm in width, and hence should have a shorter intermoult duration. This inhibition to moult may be due to a number of reasons.

Experiments conducted by Cobb and Tamm (1974, 1975) and Cobb et al. (1982) on communally reared lobsters show that neither visual nor chemical communication is sufficient to significantly cause the decrease in moult rate of smaller or subordinate animals. By removal of claws from the dominant lobsters, however, Cobb *et al*. (1982) concluded that only tactile communication can cause the decrease in moult rate, resulting in the subordinate not obtaining enough food and thus altering the moulting period.

Other experiments conducted by Bliss and Boyer (1964) on the land crab, Stewart and Squires (1968) on adult lobsters and Rossi (1971) on the hermit crab, appear to demonstrate that a delay in moulting is caused by communal situations.

Nelson *et al*. (1980) allowed only chemical communication between juvenile lobsters and found a significant lowering of the growth rate. He postulated the presence of a short-lived chemical. Cobb *et al*. (1982) do not deny that this could be the cause, but say that the chemical may have been too short-lived and did not have time to cross their experimental borders.

In this study, tactile and visual communication were prohibited, so only chemical communication could have altered the moulting rate of the particular *P. chabrus* at 16°C. The flow-through system employed in this experiment would have enabled a chemical to reach other crabs in a very short space of time. With 12 crabs in the aquarium, the presence of a chemical may be significant.

Other reasons that may have inhibited the *P. chabrus* from moulting at 16°C could be that the crab had moulted just prior to capture or it may have been starved before capture and this is known to be a limiting factor (Roberts 1957; Passano 1960).

The preceding discussion may also explain the moult inhibition of *Cyclograpsus* at all temperature. The average width of the captured crabs was 16,01 ± 2,87 mm so the crabs would not have been fully grown at that stage (Broekhuysen 1941). It must be remembered, however, that *C. punctatus* is an intertidal crab and spends more than 12 h a day out of water. During the course of this study, the crabs were kept submerged in order to regulate the temperature. This is an unnatural condition and may cause stress. Indeed Broekhuysen (1941) in his extensive research on *C. punctatus* found that it is essential for the normal hardening of the crab after moulting, to be exposed to both air and water for certain periods of time. This would explain the incidence of deaths that occurred a few days after moulting in many crabs especially at 16°C and 26°C. Broekhuysen also found that temperature did not seem to play an important role in the hardening process and had little influence on the length of the intermoult period in the laboratory. He found the interval between moults at 16°C for 12 mm crabs was 87 - 98 days and for 20 mm crabs, about 184 days. At 21°C the intermoult period was 58 and 79 days for 12 mm and 20 mm crabs respectively. Larger crabs had even longer periods between moults - 221 - 244 days at 18°C for 25 mm width.

Respiration of *C. punctatus* is greater in water than in air (see Section 3.2) and with continuous submergence, the metabolic cost may have increased to such an extent as to inhibit growth. Johns (1982) states that the net response of the integration of biochemical and physiological mechanisms can be measured at the whole organism level by comparing the partitioning of growth and maintenance requirements against the environmental factors. C. punctatus appears to be using the energy for metabolic maintenance to the detriment of its growth. Crabs that died for no apparent reason may not have been able to compensate physiologically for environmental change and were therefore more vulnerable to other changes, such as a rise in temperature, which lowered resistance and led to death (Brett 1958; Bayne 1973).

Dame and Vernberg (1982) in work with the mud crab Panopeus herbistii found that crabs acclimated to cyclic thermal environments utilize energy more efficiently than crabs held at constant temperature. As C. punctatus is intertidal, it experiences cyclic thermal conditions. The unnatural constant thermal conditions experienced in the laboratory may have contributed to an abnormal partitioning of energy away from growth.

At 11°C moulting was inhibited in all but three of P. chabrus. These three moults may have resulted from failure of the thermostats in the laboratory which resulted in a sudden rise in temperature to 17°C for two days. The crabs could enter the D1 phase of proecdysis having halted in the Do phase at the beginning of the experiment. However, it appears from the results that the low temperature does have a significant effect on the length of the intermoult period (Table 3). This difference in intermoult periods is also significantly shorter at 26°C than at 16°C. However, at 26°C, 62,5% (10 out of 16) of the animals which moulted died soon afterwards. The crab either managed to free itself from the exuvia but died shortly afterwards or it died trapped in the exuvia. Unsuccessful moulting at high temperatures has also been noted by Leffler (1972) in his work on juvenile blue crabs. The oxygen content of water at 26°C is low and the effort required to free the crab from the exuvia and make up the oxygen debt it incurs during ecdysis is too great and death results (Roberts 1957; Passano 1960).

A linear regression equation for initial carapace width versus percentage growth increment was found to be

$$Y = -0{,}28X + 15{,}51 \quad (n = 31; \quad r = -0{,}57)$$

The r value is significant $(p > 0{,}05)$ so it can be concluded that P. chabrus experience a lower percentage increase in width as they get older. This is supported by Broekhuysen (1941) for C. punctatus, Klein-Breteler (1975a) for C. maenas, and Warner (1977) in his general review of crab growth. However, both Broekhuysen and Klein-Breteler found that this was not true under natural conditions, probably because of the fluctuating temperatures and lack of food in certain seasons. Hartnoll (in Warner 1977) found that the growth increment varied from 3 - 44%. In this study the growth increment of P. chabrus did not exceed 14,3%.

H. orbiculare seems to be less sensitive than P. chabrus to temperatures of 11°C. Fifty percent (3 out of 6) of the crabs moulted at this temperature and one crab moulted twice, with an intermoult period of 60 days. All crabs at 16°C moulted once, but no second moult was observed within the 80 day period. It is unfortunate that the crabs used in the 16°C experiment were mainly from the initial batch of crabs caught at Hout Bay and were significantly larger $(p > 0{,}05)$

than the crabs used at the other three temperatures. The regression coefficient of dry weight versus intermoult period of H. orbiculare held at 21°C shows that the intermoult period does increase with size of crab.

$$Y = 12{,}078 + 58{,}990\,X \pm 11{,}850$$

$$(n = 9; \quad r = +0{,}73)$$

This makes the comparison of the intermoult period at 16°C with those of the other temperatures difficult. It can be reasonably concluded, however, that the intermoult period is significantly longer at 11°C than 16°C as only 50% of the crabs at 11°C moulted compared to the 100% moult rate at 16°C despite the significantly larger crabs at 16°C.

All crabs at 21°C underwent two moults, with the average period between moults being 26,2 ± 16,2 days for animals measuring between 8,1 and 21,6 mm width.

In every case, H. orbiculare held at 26°C moulted once and then died 26,1 ± 12,3 days after moulting.

Analyses of variance on the width and weight increments at the four different temperatures show no significant difference in these parameters. Regression equations of the percentage increase in width against initial width were calculated and are shown in Table 4. There seems to be little correlation between the two parameters.

Only at 21°C is there a negative correlation showing a definite decrease in percentage width increase as size increases. 16°C shows a positive correlation. The poor correlations may be due to the small size range of the crabs used within each group and the small numbers of observations. If the mean percentage increase in each group is considered, only the increase between 11°C and 16°C ($11° > 16°$) and 16°C and 26°C ($26° > 16°$) differs significantly ($p > 0{,}05$ and 0,1 respectively) and may be due to initial size discrepancy between 16°C and the other two temperatures. The largest percentage width increase was 43,8% at 26°C followed by a 32,2% increase at 11°C.

Figures 1 - 5a, b and c show the graphs and parameters of growth and moulting that were calculated from this study. Figures 3a, b and c show that 19% of the dry mass of P. chabrus, 53% of H. orbiculare and as much as 65% of the dry mass of C. punctatus is shed at moulting. The calorific values of the moults are 2,44 kJ g^{-1} dry mass (P. chabrus), 4,36 kJ g^{-1} dry mass (H. orbiculare) and 0,79 kJ g^{-1} dry mass (C. punctatus) after correction for endothermy (Paine 1966). The calorific values of the average sized animals used were 12,79 kJ g^{-1} dry mass (P. chabrus), 8,88 kJ g^{-1} dry mass (H. orbiculare) and 9,88 kJ g^{-1} dry mass (C. punctatus).

P. chabrus therefore loses 19% of its calorific content, H. orbiculare 49% and C. punctatus, only 8% at each moult. If crabs at higher temperatures moult more frequently than those at lower temperatures then in order to compensate for the energy lost either the feeding rate would have to be increased or energy would have to be transferred

$Y = 0{,}799 + 0{,}286\,X \pm 0{,}241$

$r = 0{,}98 \quad (t = 13{,}585)$

$n = 11$

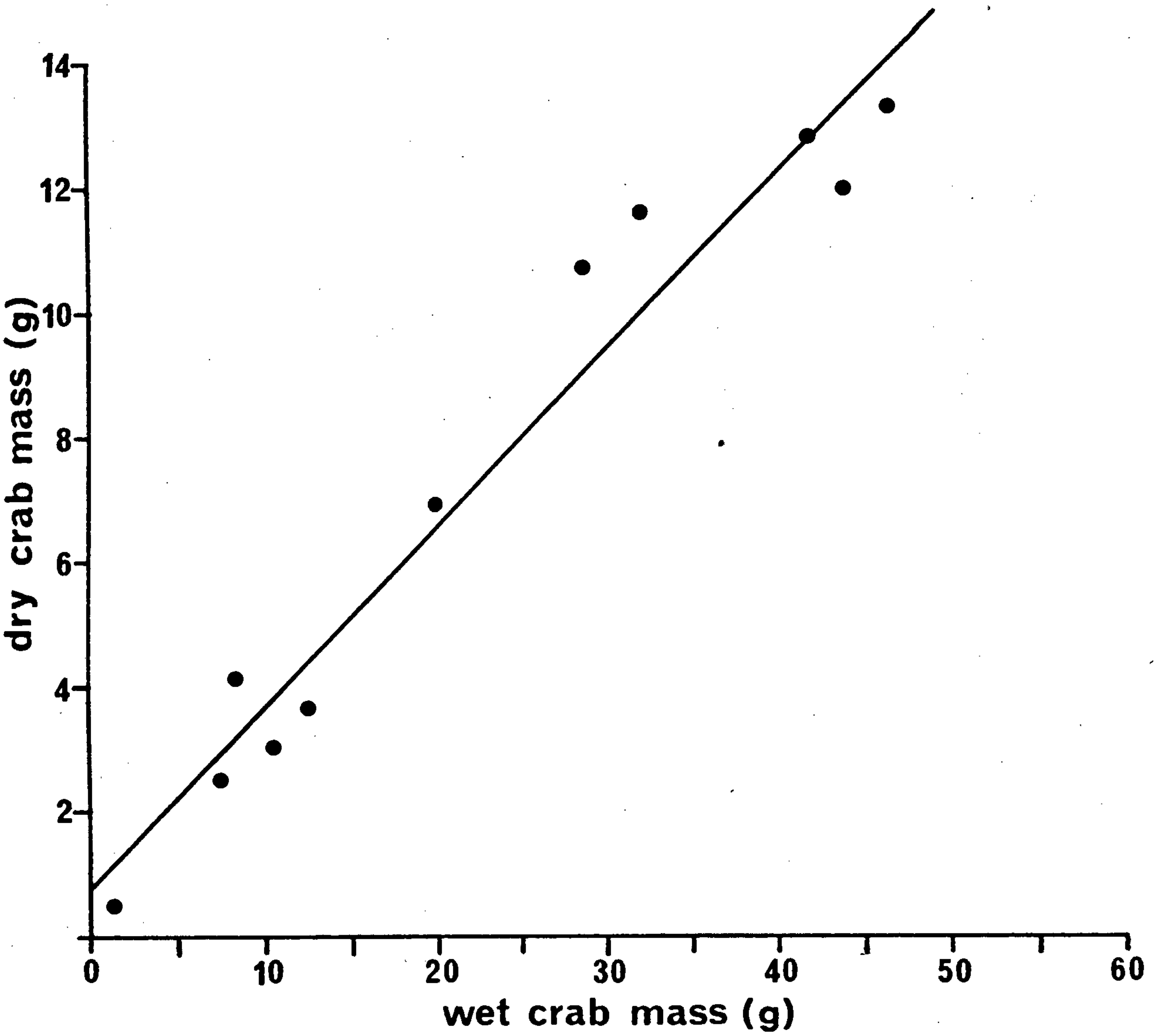


Fig. 1a Linear relationship between wet crab mass and dry crab mass of Plagusia.

$Y = 0{,}006 + 0{,}243\,X \pm 0{,}114$

$r = 0{,}94 \quad (t = 17{,}132)$

$n = 40$

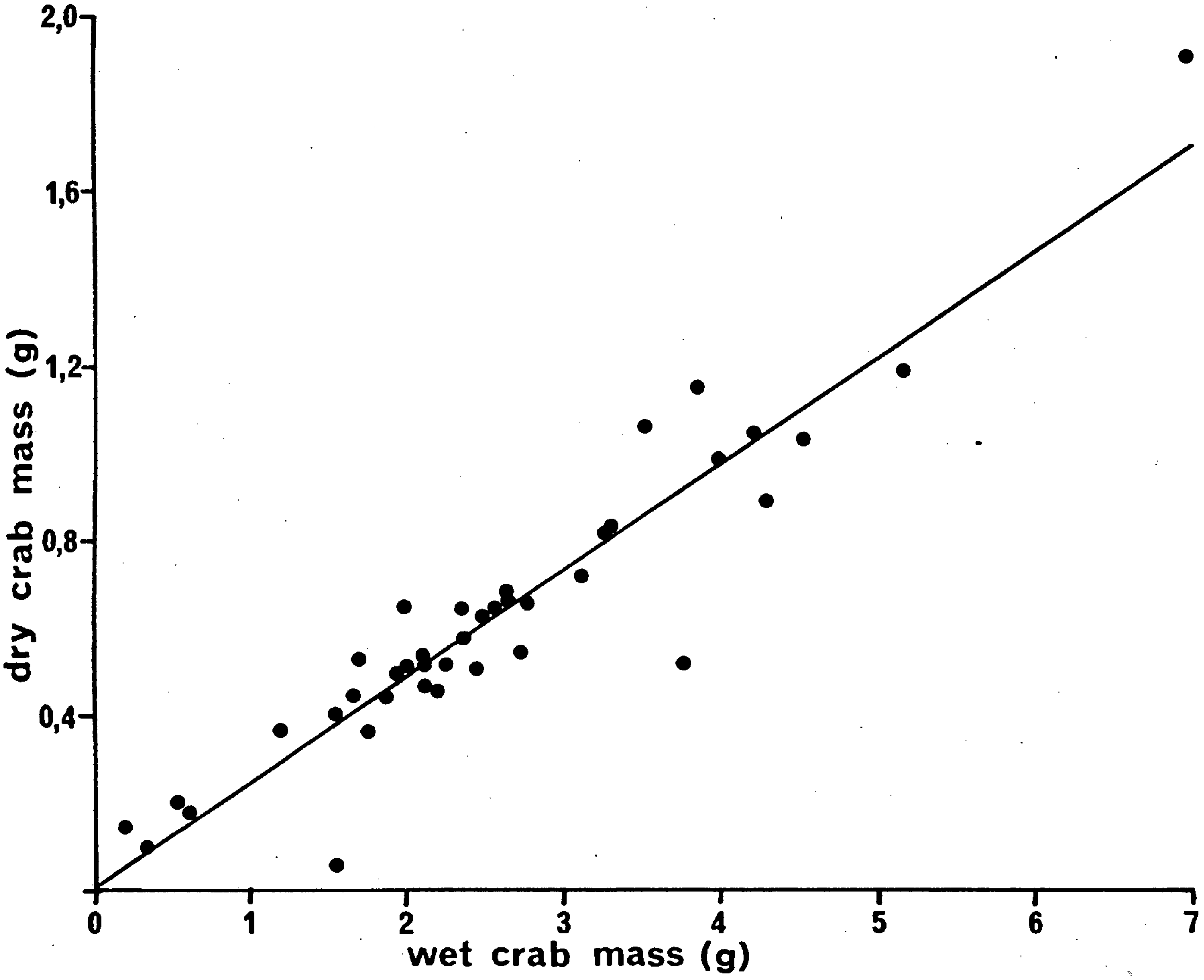


Fig. 1b Linear relationship between wet crab mass and dry crab mass of Hymenosoma.

$Y = 0{,}005 + 0{,}374\,X \pm 0{,}138$

$r = 0{,}96 \quad (t = 13{,}476)$

$n = 25$

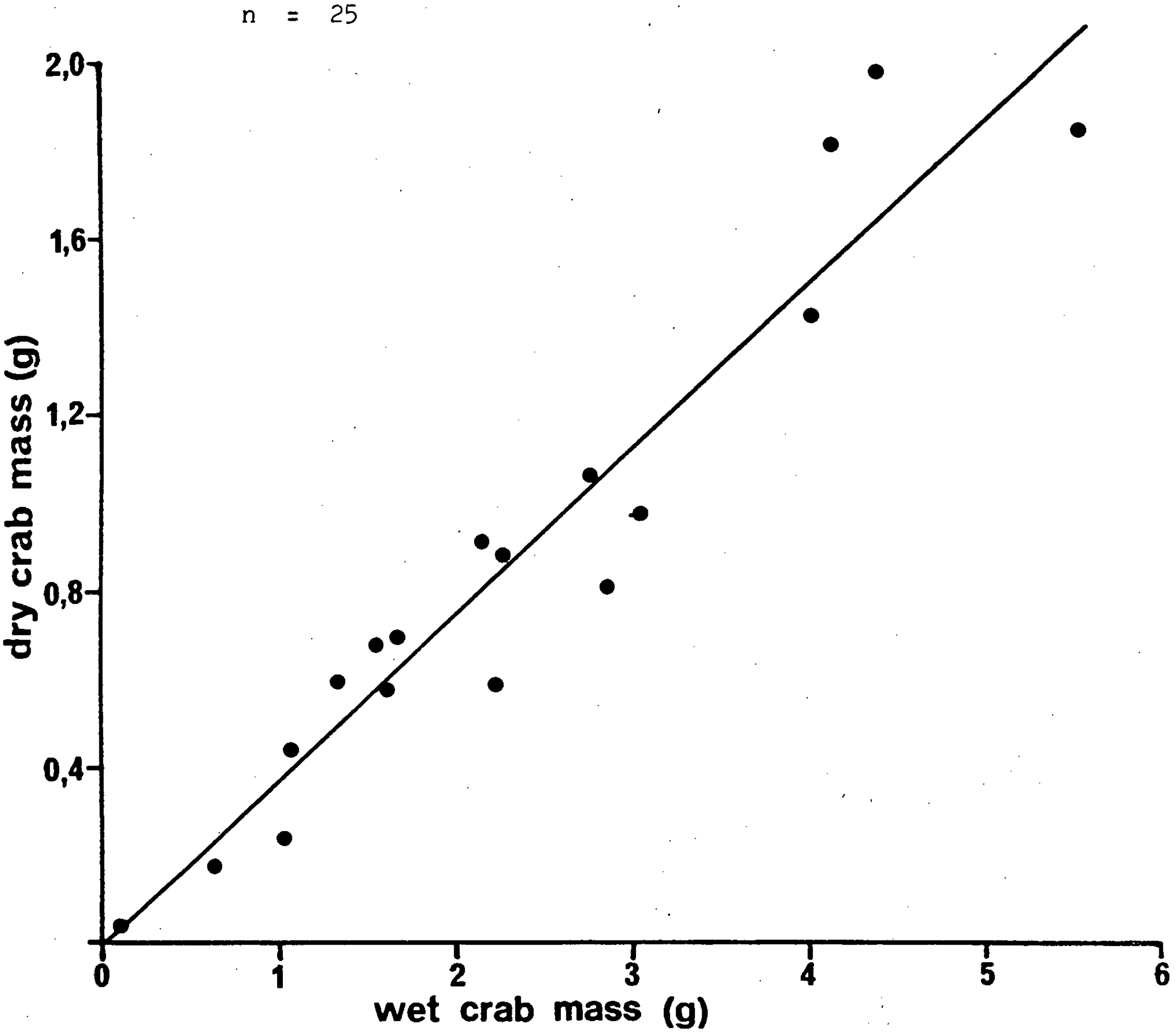
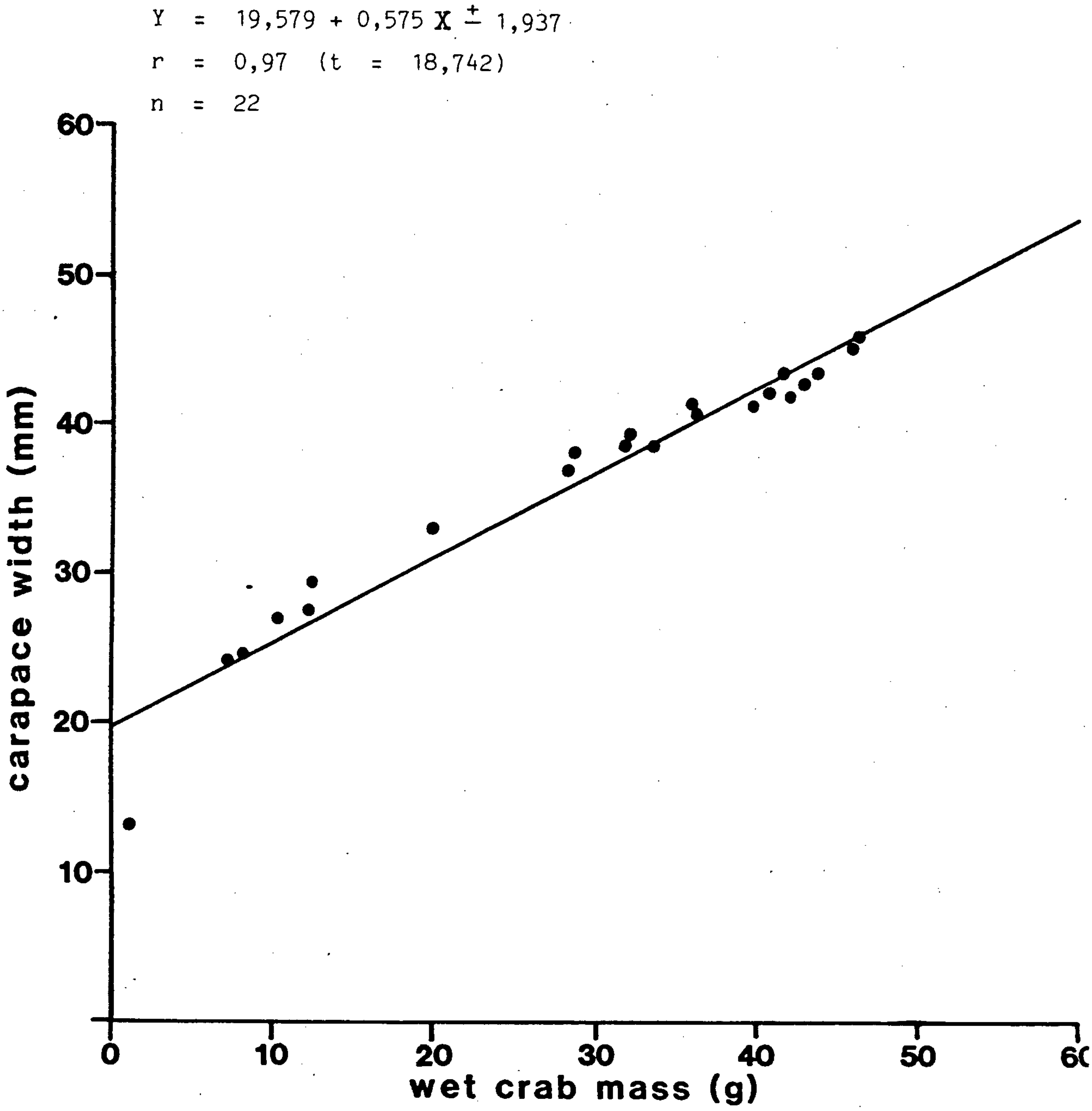


Fig. 1c Linear relationship between wet crab mass and dry crab mass of *Cyclograpsus*.



$Y = 19{,}579 + 0{,}575\,X \pm 1{,}937$

$r = 0{,}97 \quad (t = 18{,}742)$

$n = 22$

Fig. 2a · Linear relationship between wet crab mass and carapace width of Plagusia.

Y = 11,652 + 2,862X ± 1,422

r = 0,93 (t = 16,759)

n = 44

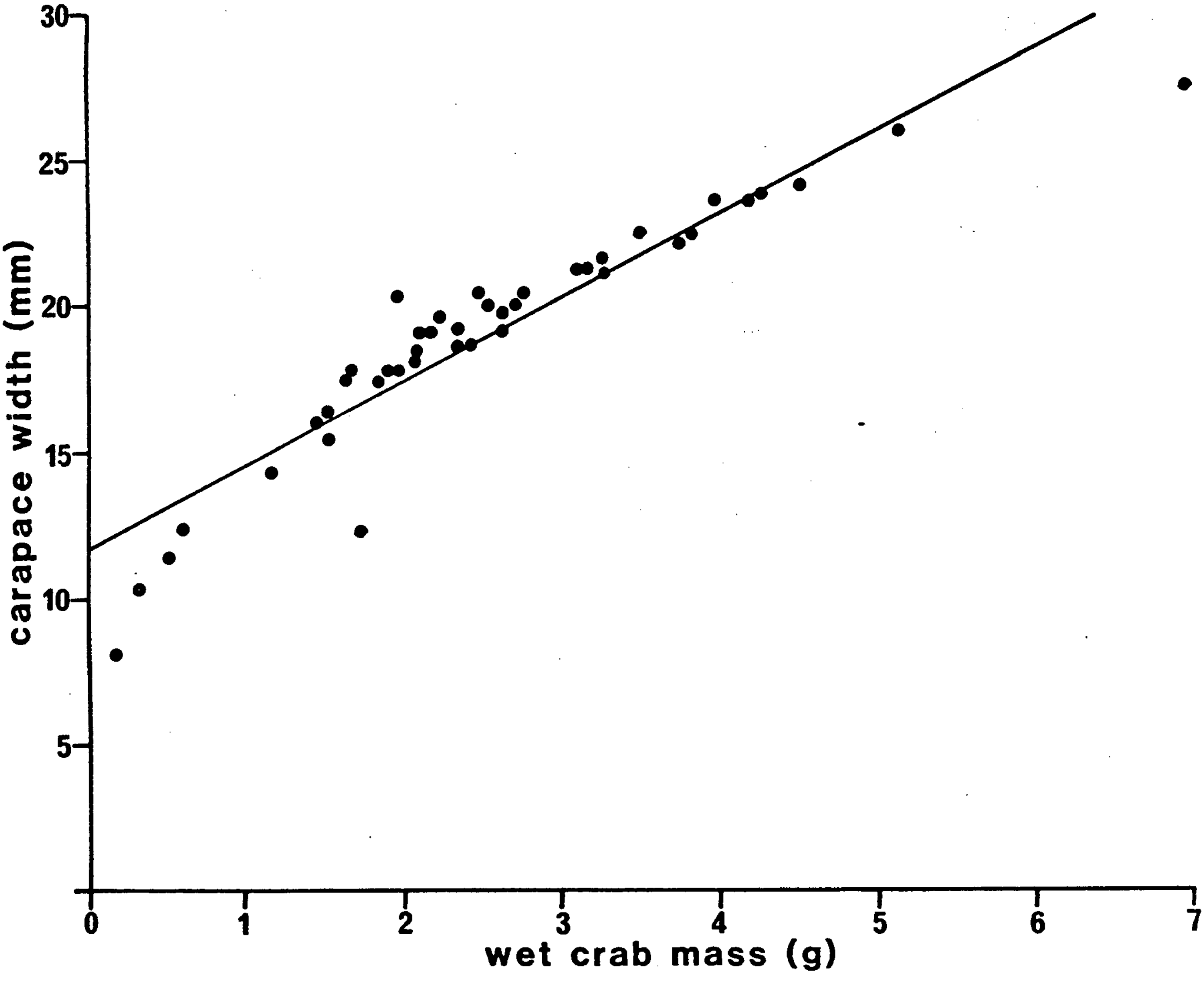


Fig. 2b Linear relationship between wet crab mass and carapace width of Hymenosoma.

Y = 10,517 + 2,628 X ± 1,385

r = 0,93 (t = 12,221)

n = 25

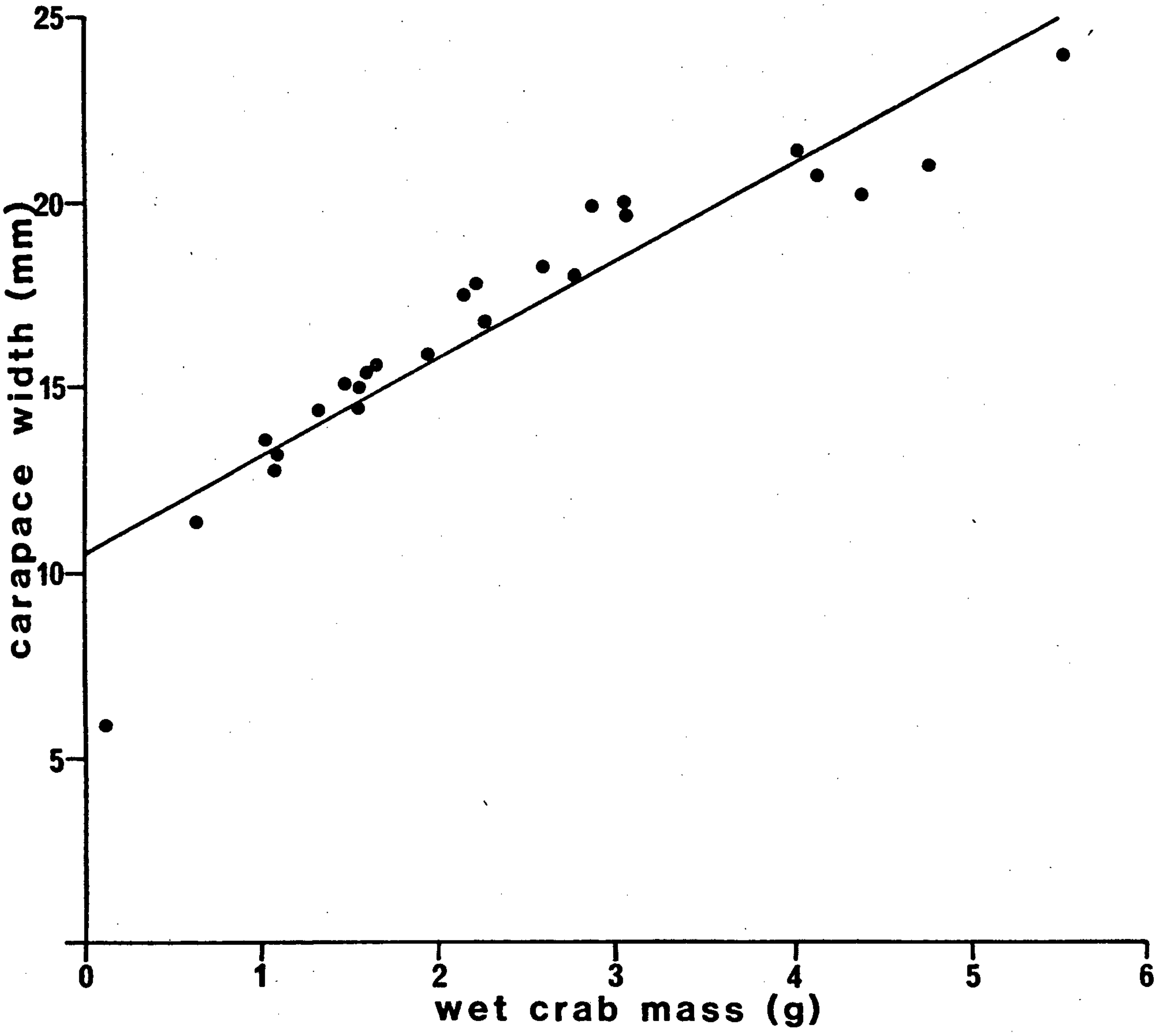


Fig. 2c Linear relationship between wet crab mass and carapace width of Cyclograpsus.

$Y = 12{,}077 + 5{,}493\,X \pm 2{,}295$

$r = 0{,}80 \quad (t = 6{,}304)$

$n = 25$

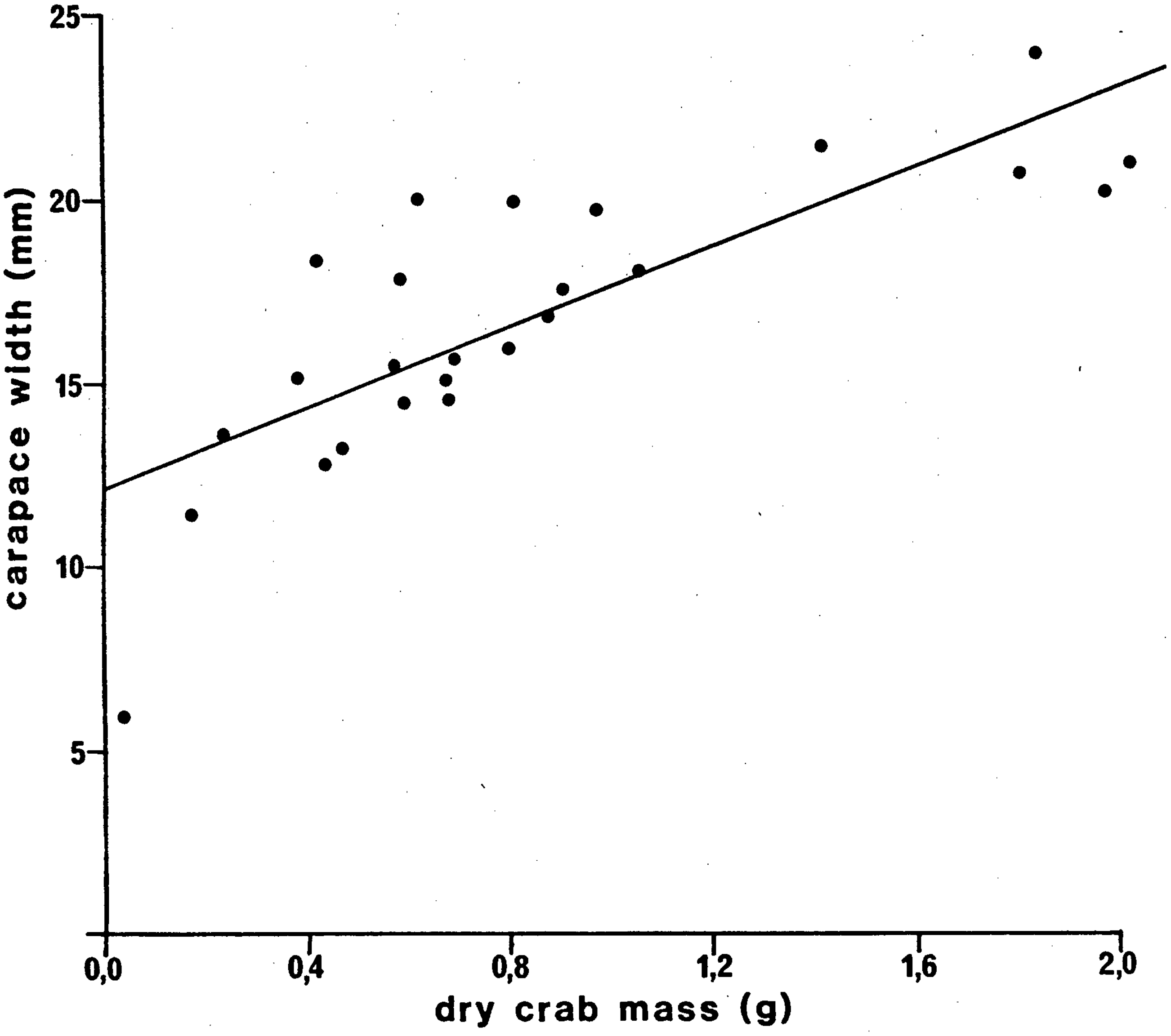


Fig. 2d Linear relationship between dry crab mass and carapace width of Cyclograpsus.

$Y = -0{,}391 + 0{,}577X \pm 0{,}369$

$r = 0{,}98 \quad (t = 21{,}914)$

$n = 20$

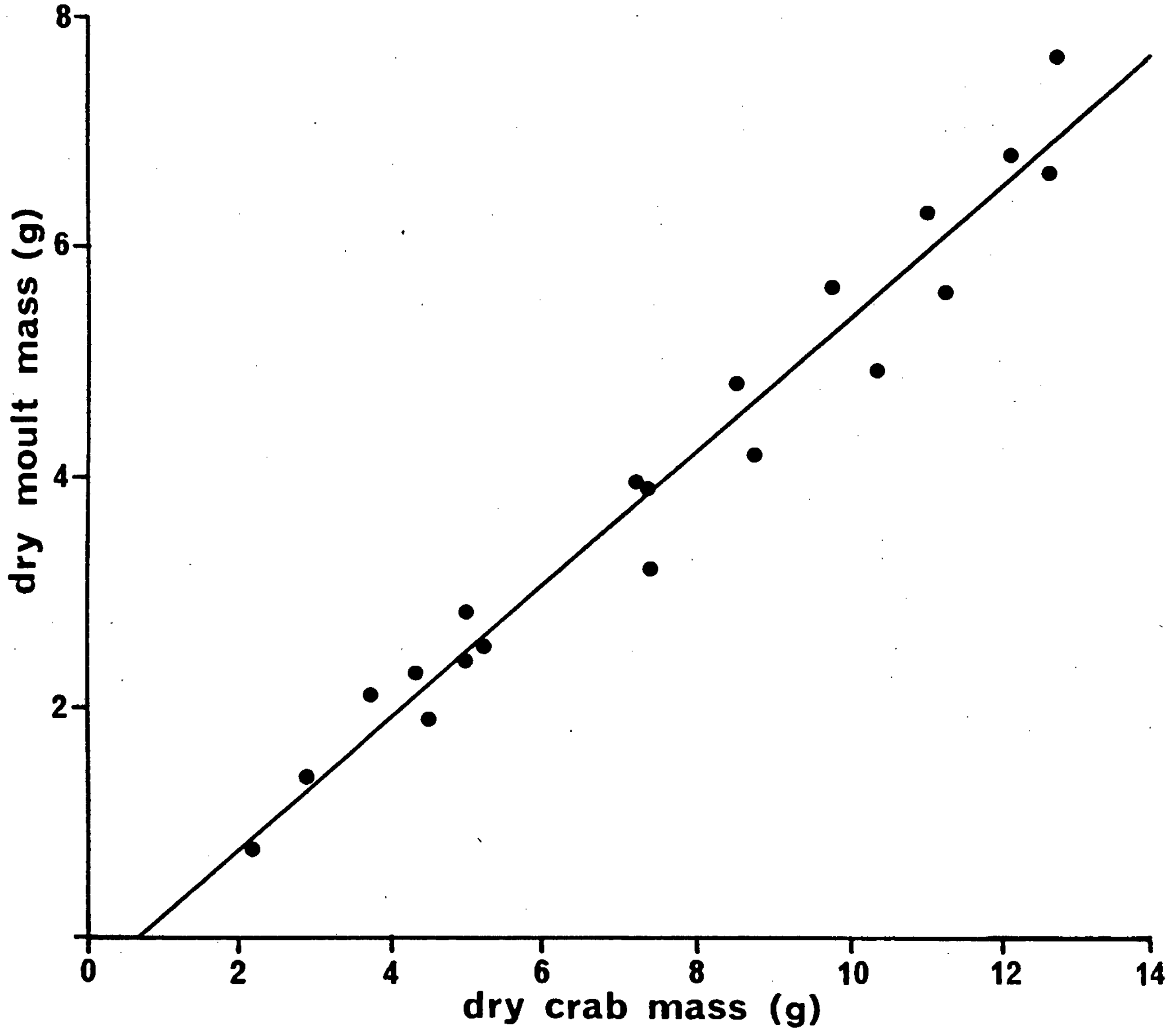


Fig. 3a Linear relationship between dry crab mass and dry moult mass of Plagusia.

$Y = 0{,}009 + 0{,}525\ X \pm 0{,}026$

$r = 0{,}98 \quad (t = 29{,}550)$

$n = 29$

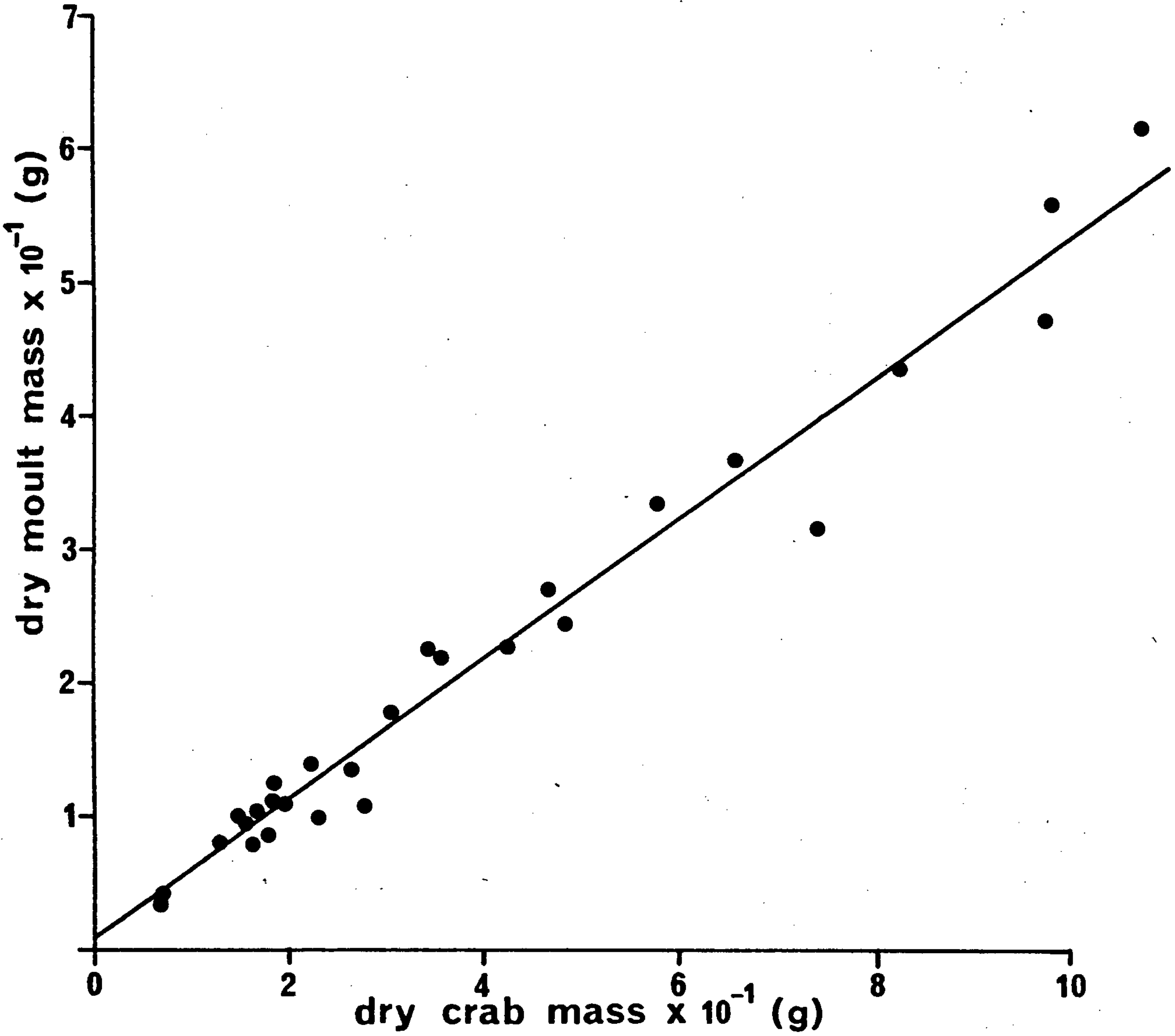


Fig. 3b Linear relationship between dry crab mass and dry moult mass of Hymenosoma.

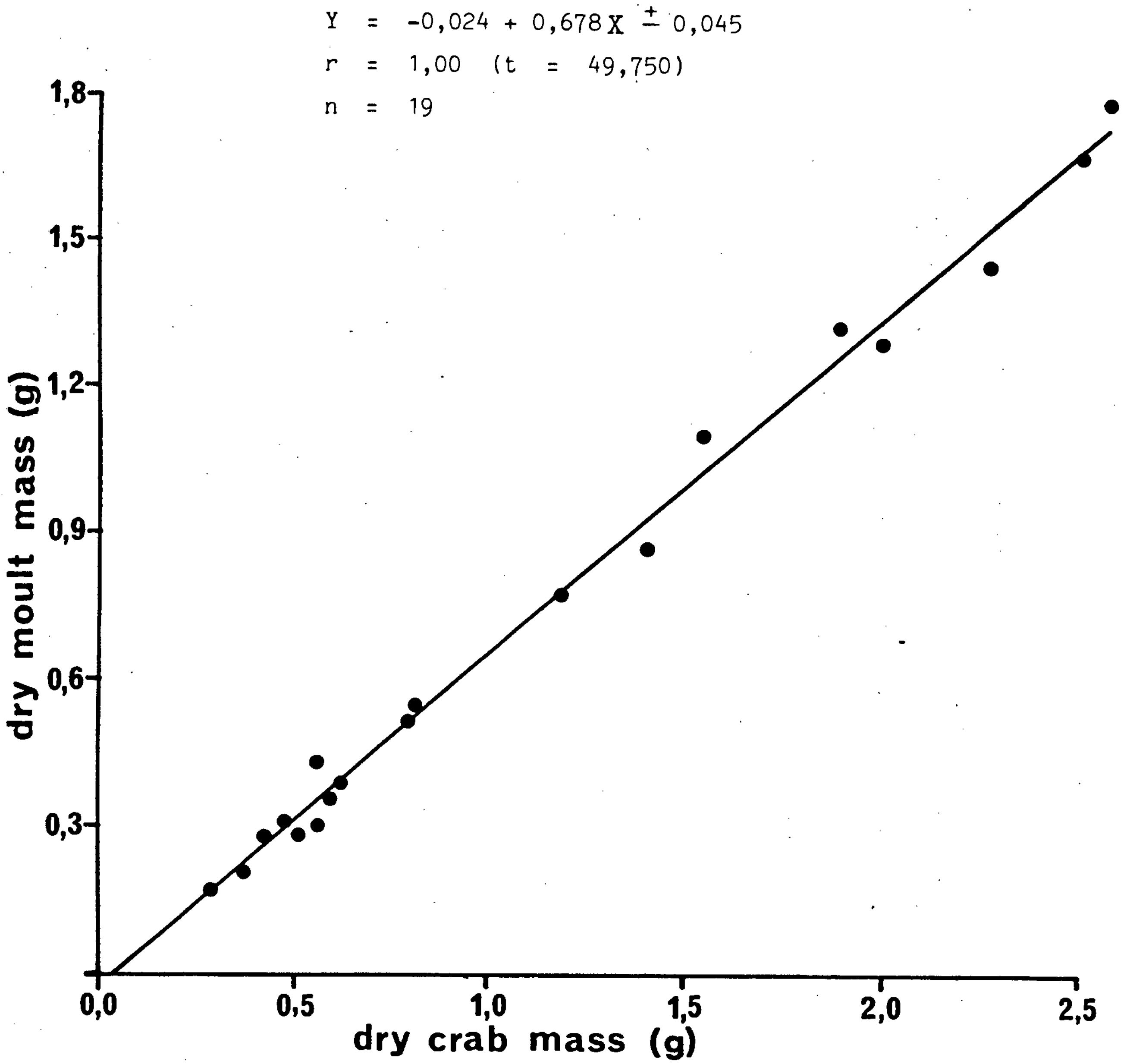
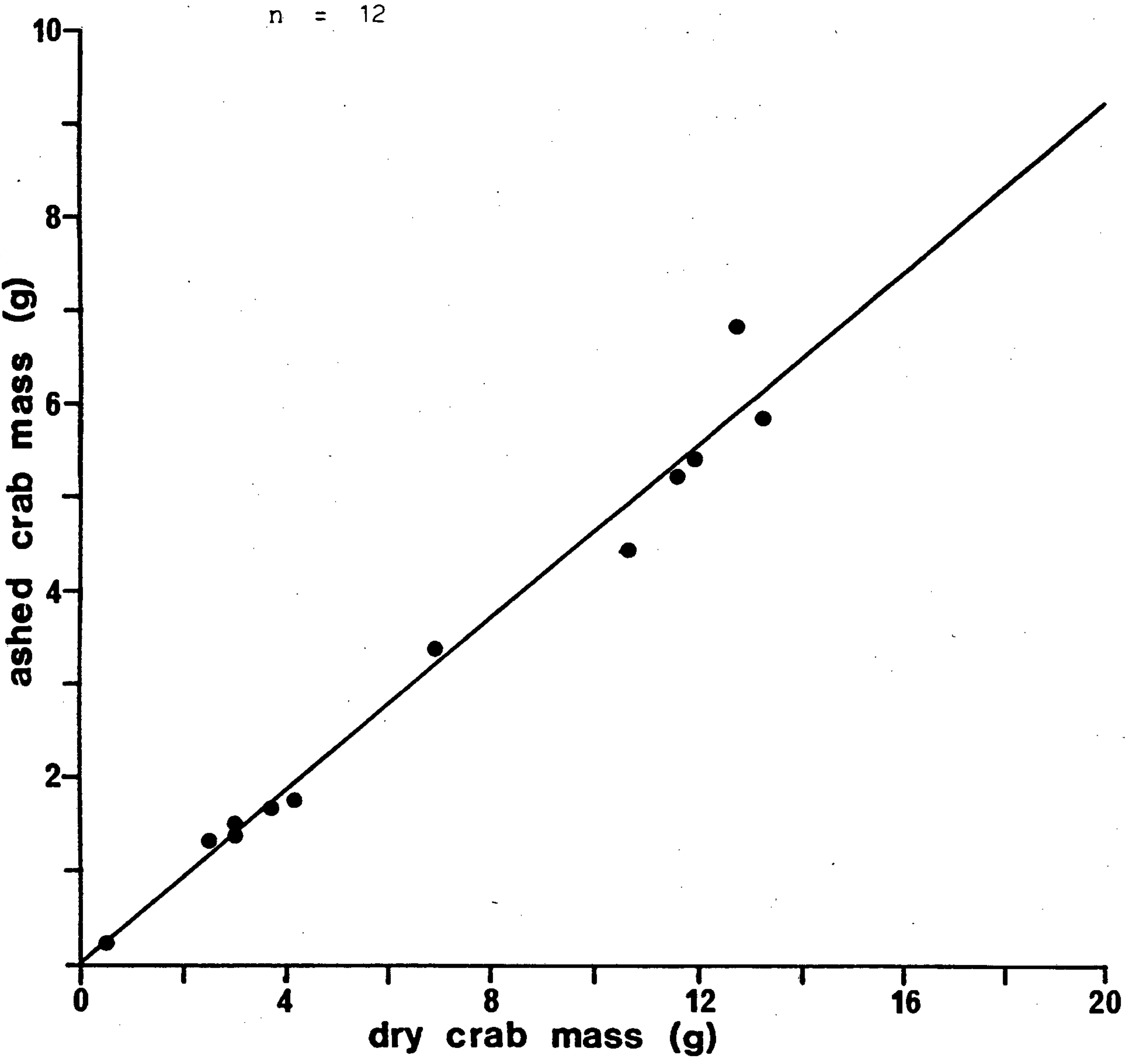


Fig 3c Linear relationship between dry crab mass and dry moult mass of Cyclograpsus.



$Y = 0{,}027 + 0{,}461X \pm 0{,}330$

$r = 0{,}99$ $(t = 19{,}993)$

$n = 12$

Fig. 4a Linear relationship between dry crab mass and ashed crab mass of whole *Plagusia*.

Y = -0,015 + 0,502 X ± 0,032

r = 0,98 (t = 29,049)

n = 40

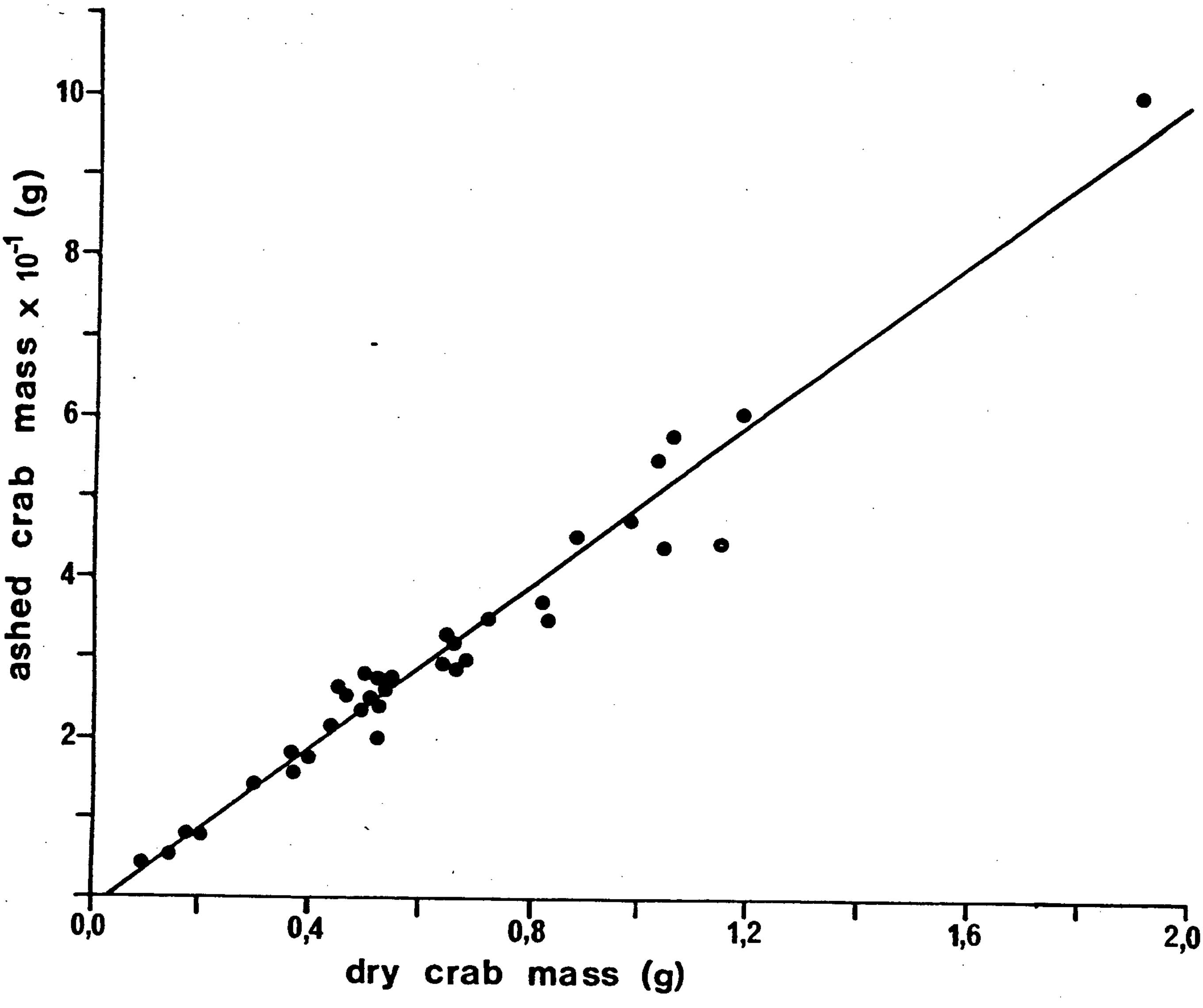


Fig. 4b Linear relationship between dry crab mass and ashed crab mass of whole <u>Hymenosoma</u>.

$Y = -0{,}012 + 0{,}522X \pm 0{,}024$

$r = 1{,}00 \quad (t = 57{,}437)$

$n = 25$

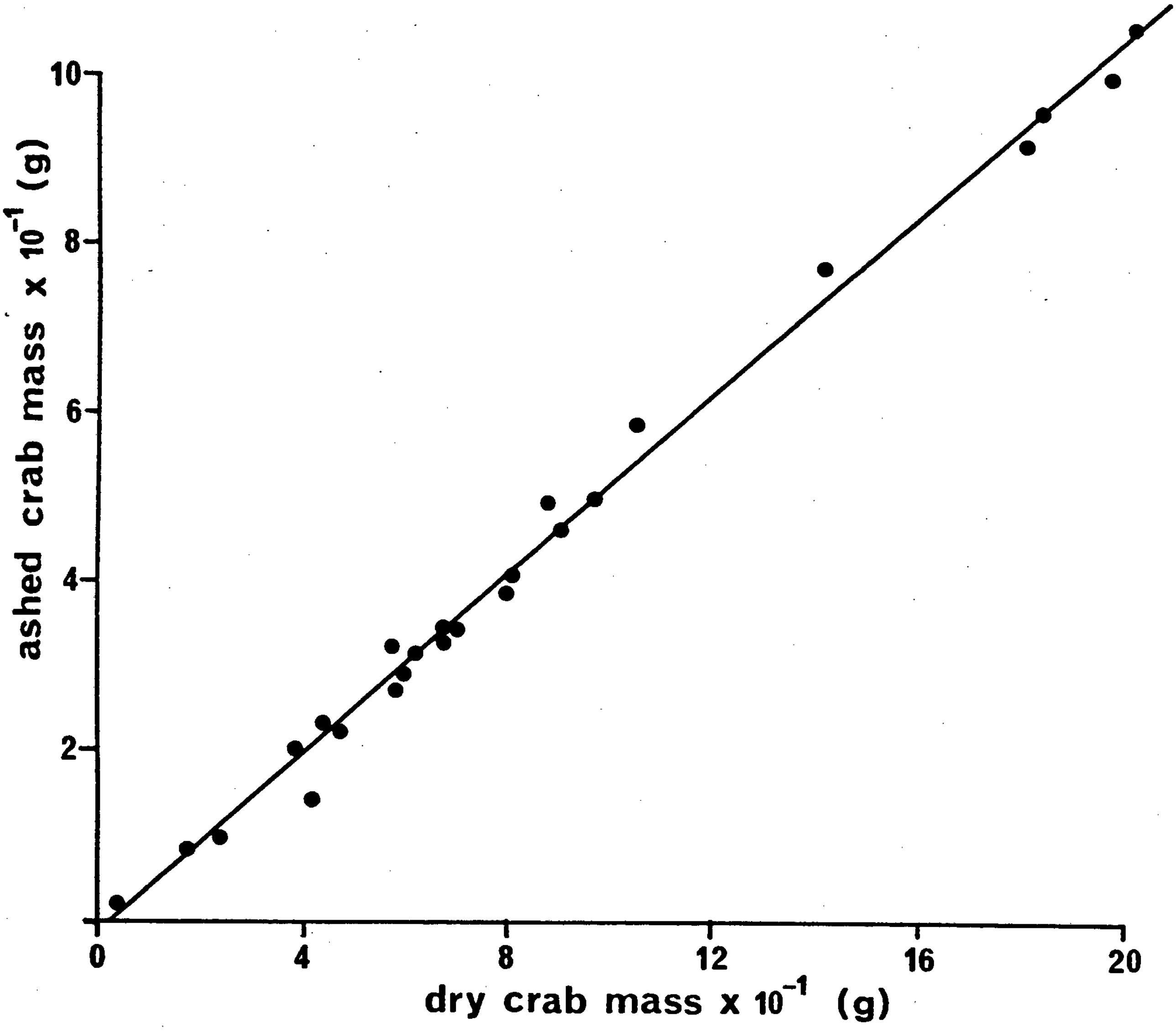


Fig. 4c Linear relationship between dry crab mass and ashed crab mass of whole <u>Cyclograpsus</u>.

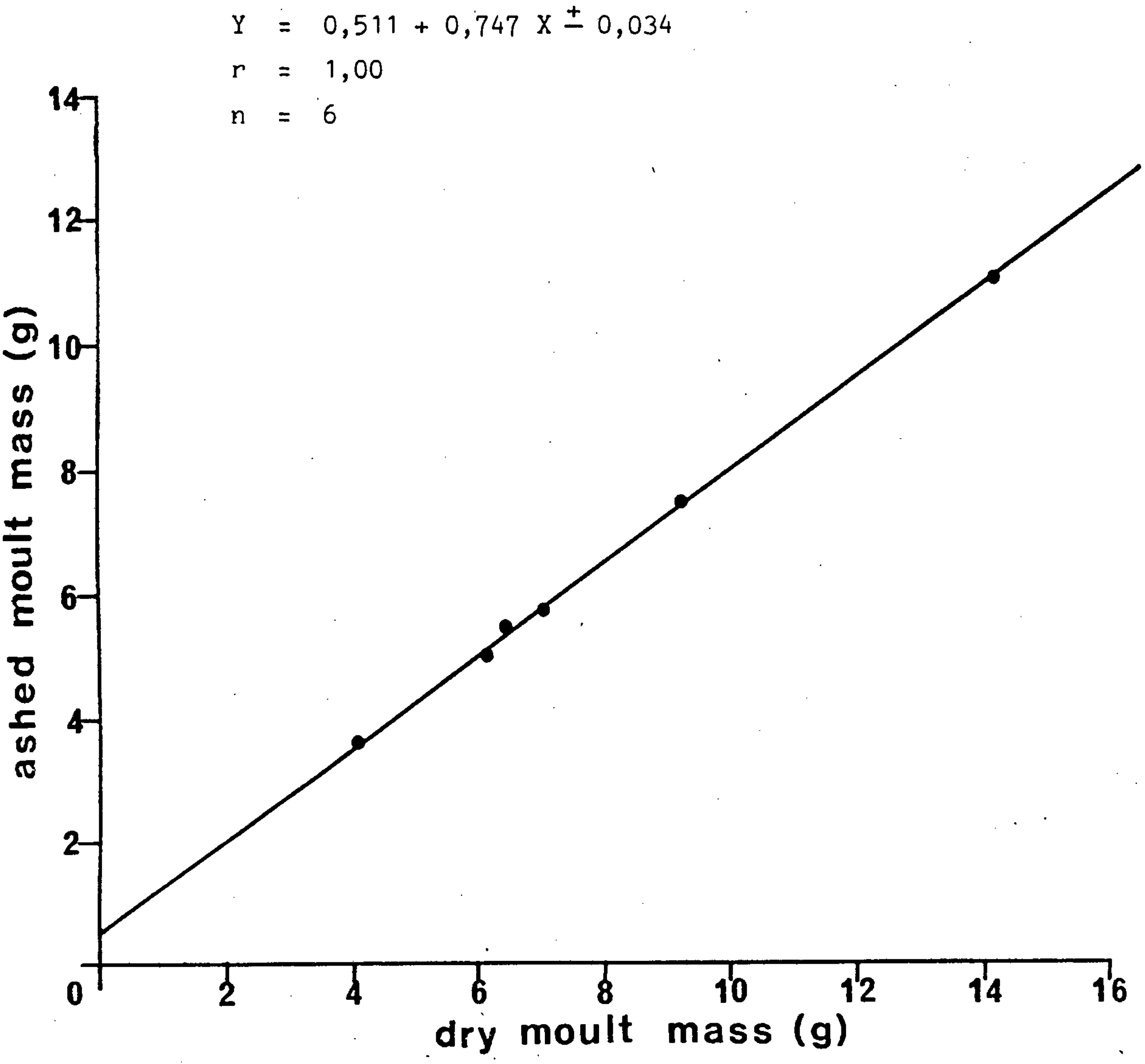


Fig. 5a Linear relationship between dry mass and ashed mass of Plagusia exuvia.

$Y = 0{,}000 + 0{,}699X \pm 0{,}003$

$r = 1{,}00 \quad (t = 166{,}728)$

$n = 43$

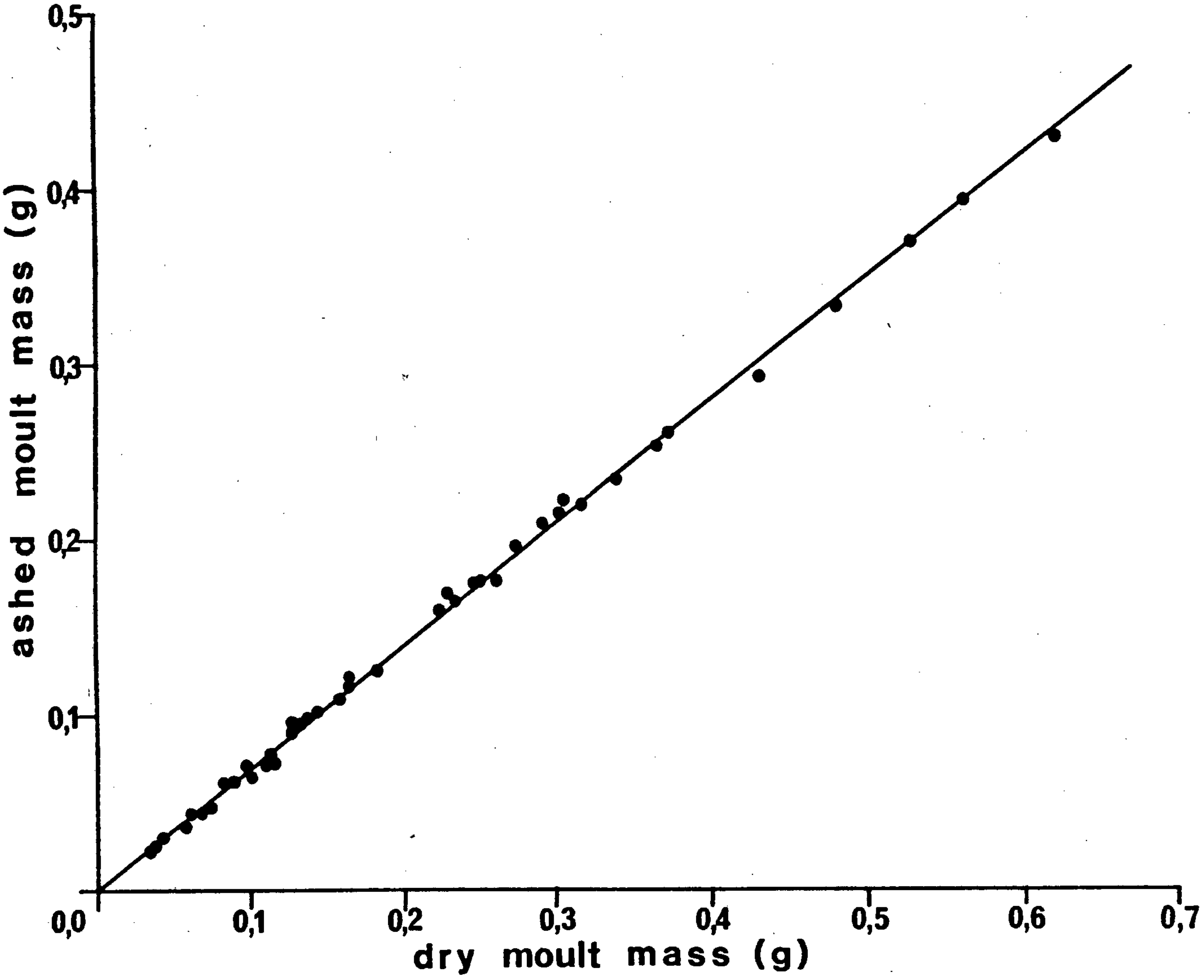


Fig. 5b Linear relationship between dry mass and ashed mass of Hymenesoma exuvia.

Y = 0,006 + 0,833 X ± 0,009
r = 1,00 (t = 213,069)
n = 21

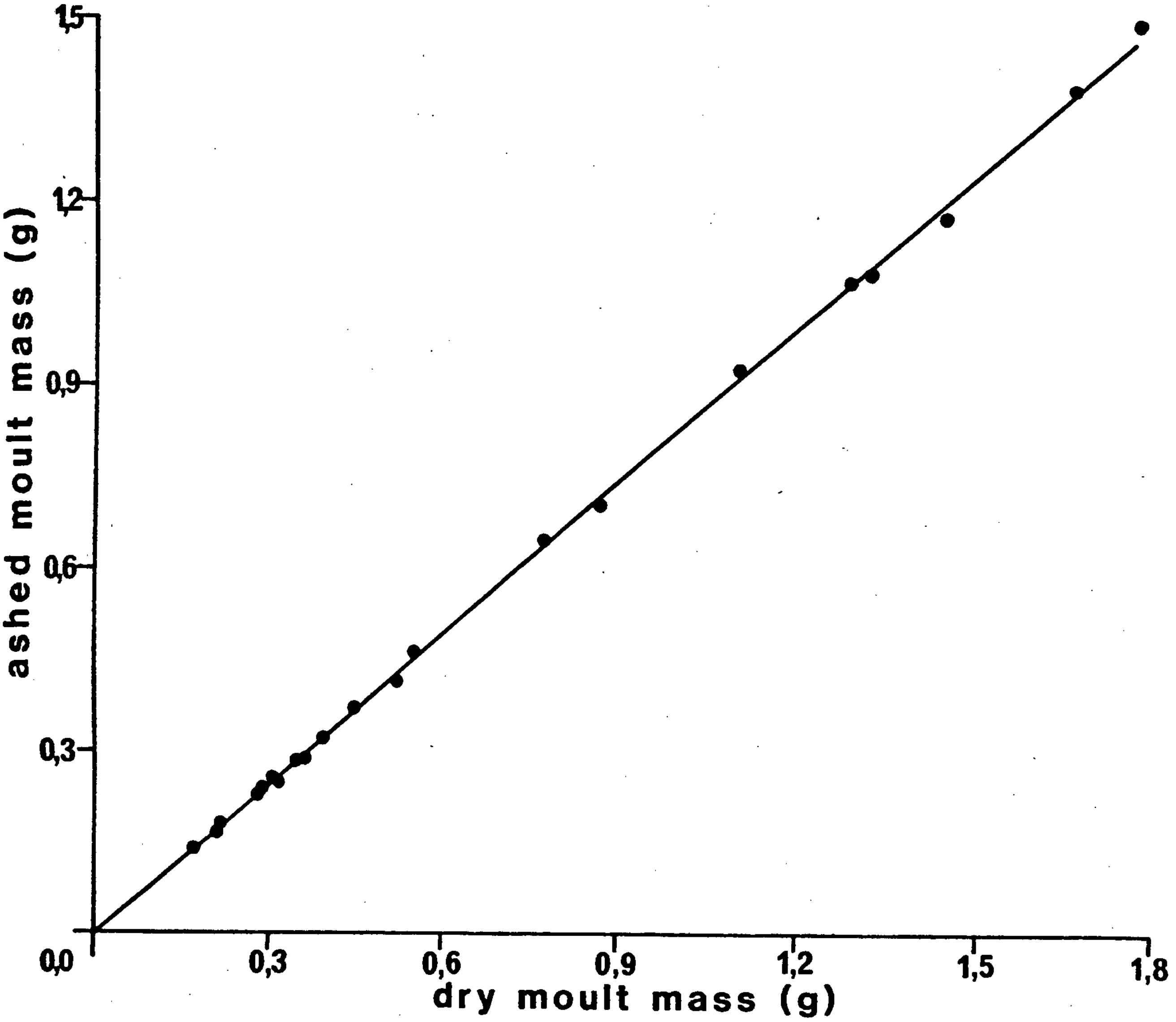


Fig. 5c Linear relationship between dry mass and ashed mass of Cyclograpsus exuvia.

from other sources. This could be achieved by an increased assimilation efficiency, but if this were not possible then energy which would normally have been channelled into reproduction may no longer be available for that purpose.

3.2 Respiration/Metabolism

Oxygen consumption has been extensively studied in many different crustaceans and under different conditions. See, for examples Thomas (1954) on Homarus, Roberts (1957b) on Pachygrapsus, Wolvekamp (1960), McFarland and Pickens (1965) on Palaemonetes, Wallace (1972) and Newell et al. (1972) on Carcinus and Newell (1979). These studies show great variations due to temperature, latitude, size and sex. The generally accepted formula for describing the rate of oxygen consumption (Q) of Crustacea is

$$Q = \alpha W^{\beta} \qquad \text{(Newell 1979) equation (1)}$$

where α is the level of metabolic expenditure and

β is the rate of change of metabolism with body weight, W.

The values for the coefficients α and β vary between 0,06 for Pagarus criniticornis larvae (Vernberg et al. 1981) and 0,668 for adult P. bernhardus (Shumway 1978), to 0,95 for small crustaceans up to 5 mg (Zeuthen 1953). However, most data published on the respiration of invertebrates is so scattered that significant differences in slopes under varying conditions is difficult to establish and often the mean common regression coefficient is used in the interpretation of data.

Sushchenya (1973) after studying all data published up to 1973 gives the value of β to be 0,75 and α to be 0,174 ($\log \alpha = -0{,}760$). If the calorific equivalent of oxygen is taken as 20,098 kJ ℓ^{-1} (Crisp 1971) the expenditure for respiration in energy units can be expressed as

$Q = 3{,}497\ W^{0,75}$ kJ animal^{-1} h^{-1} equation (2)

or $Q = 83{,}928\ W^{0,75}$ kJ animal^{-1} day^{-1} equation (3)

From equation (3)

$\log Q = 1{,}924 + 0{,}75 \log W$ is derived. equation (4)

In this study, the linear regression equations obtained, showed a better correlation than the logarithmic equations, so the linear data will be discussed in this section. Logarithmic data is presented in the appendix (Tables I and II and Graphs 1a, b, c and d) in the form of equation (4) for comparison with the literature. The better correlation in the linear form may be due to the small size range of the crabs under study, because the data represents a tangent to the logarithmic curve. This explanation also applies to the data for the food consumption and faecal production of the crabs in Section 3.3.

The values for metabolic rates obtained in these experiments should be considered as routine rates. The crabs had been fed ad lib. up until the time of the experiment and were left undisturbed in a dark bottle during the course of the experiment. The water was not stirred.

TABLE 5 Parameters of the linear regression equation obtained for crab dry mass (g) against respiration (kJ day^{-1}). Y = a + bX. Syx is the standard error of the estimate, r is the correlation coefficient; P is the significance level in a two-tailed t-test.

Temp	n	a	b	±Syx	t	P	r
a)				Plagusia			
11°C	7	-0,281	0,205	0,462	4,093	0,01	0,88
16°C	8	0,390	0,193	0,217	8,172	0,001	0,96
21°C	8	0,467	0,193	0,382	3,019	0,05	0,78
26°C	8	0,635	0,164	0,412	4,119	0,01	0,86
b)				Hymenosoma			
11°C	10	-0,023	0,585	0,125	2,591	0,05	0,68
16°C	12	-0,074	0,354	0,069	6,172	0,001	0,89
21°C	10	0,045	0,334	0,103	3,924	0,005	0,81
26°C	6	0,069	0,387	0,050	1,799	0,2	0,67
c)				Cyclograpsus (Water)			
11°C	9	0,055	0,004	0,037	0,197	N.S.	0,07
16°C	12	0,005	0,116	0,064	7,165	0,001	0,91
21°C	9	0,101	0,151	0,077	3,606	0,01	0,81
26°C	10	0,158	0,151	0,180	2,479	0,05	0,66
d)				Cyclograpsus (Air)			
11°C	10	0,0002	0,0010	0,0000	4,605	0,002	0,85
16°C	7	0,0011	0,0005	0,0000	0,996	N.S.	0,41
21°C	8	0,0008	0,0009	0,0000	3,564	0,02	0,82
26°C	12	0,0027	-0,0002	0,0000	-0,303	N.S.	0,10

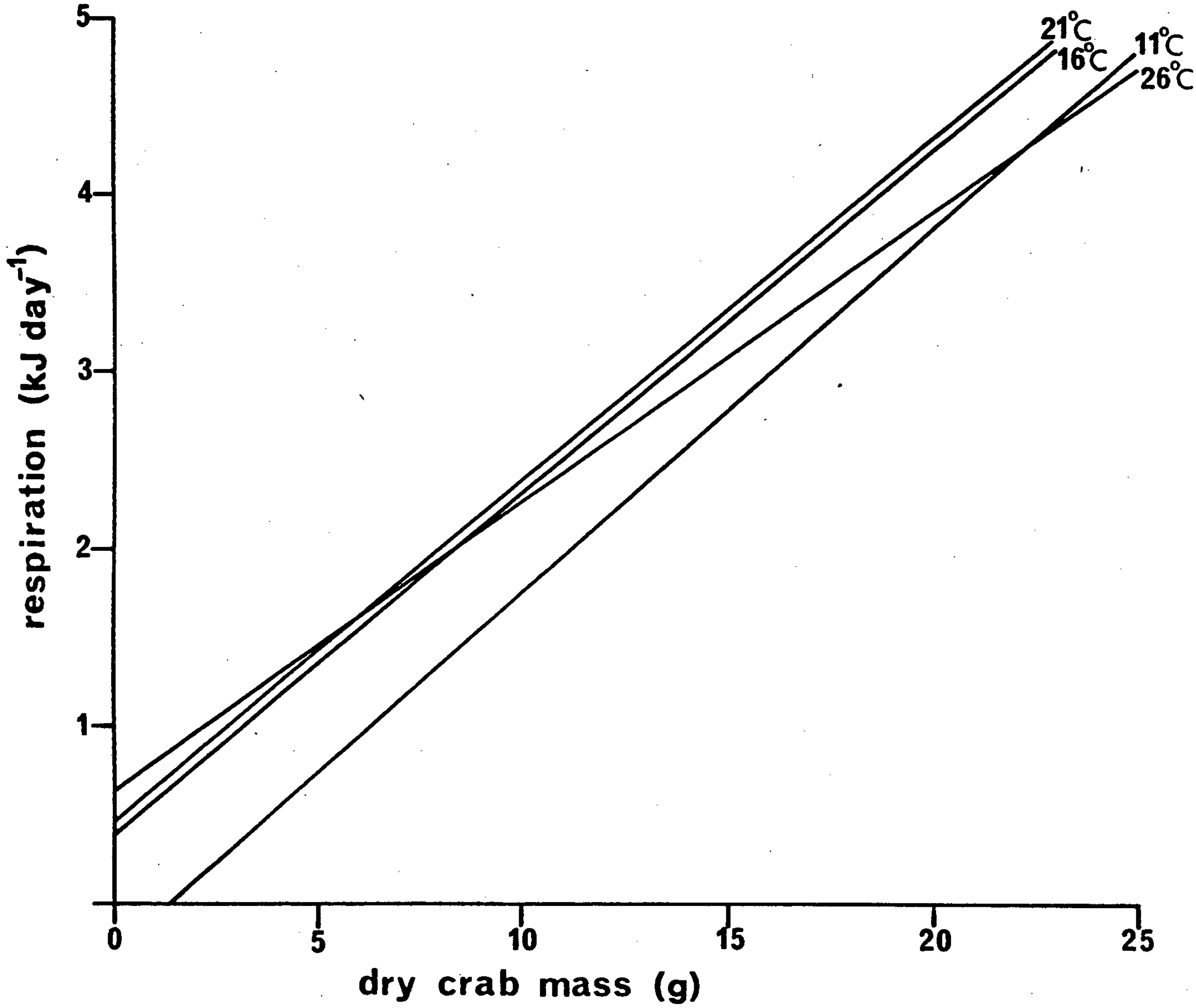


Fig. 6a The linear relationship between crab dry mass (g) and respiration (kJ day^{-1}) for Plagusia at the four temperatures.

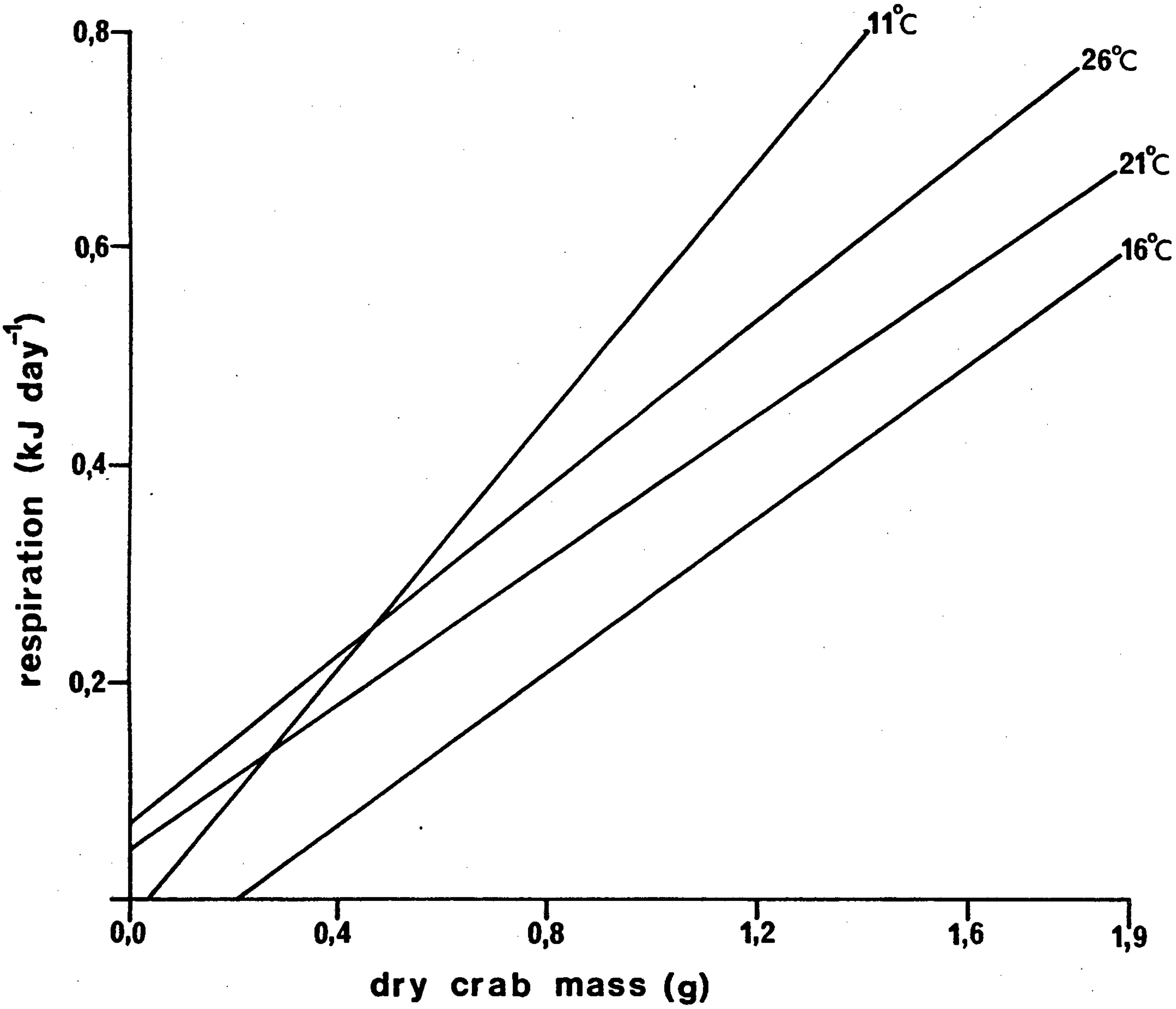


Fig. 6b The linear relationship between crab dry mass (g) and respiration (kJ day^{-1}) for <u>Hymenosoma</u> at the four temperatures.

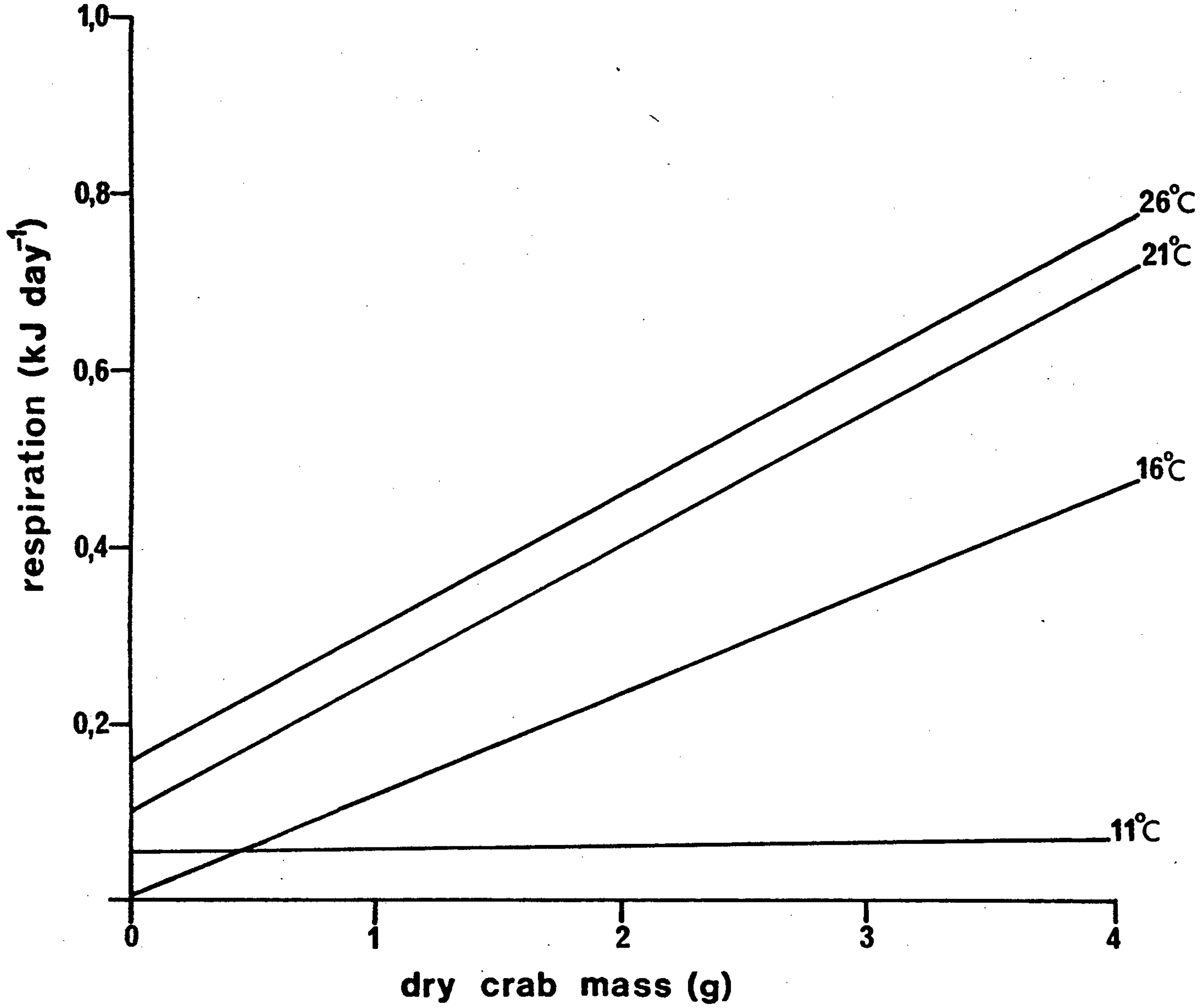


Fig. 6c The linear relationship between crab dry mass (g) and respiration (kJ day^{-1}) for Cyclograpsus at the four temperatures.

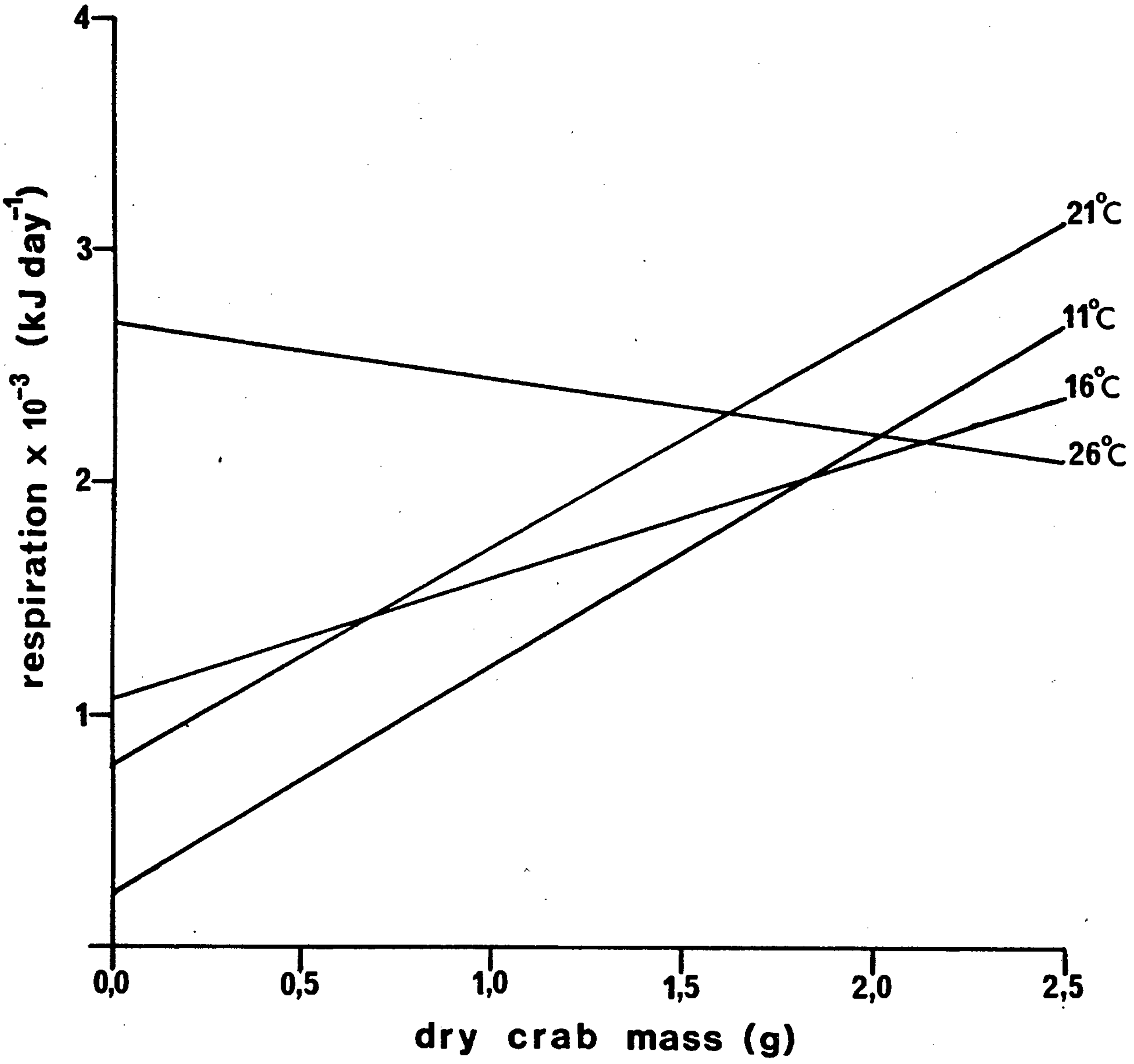


Fig. 6d The linear relationship between crab dry mass (g) and respiration in air (kJ day^{-1}) for Cyclograpsus at the four temperatures.

TABLE 6 Results of ANOCOVA tests between the linear regression slopes obtained for crab dry mass (g) against respiration (kJ day^{-1}) ($p > 0,05$) F_s - F-test between slopes; F_e - F-test between elevations.

	▨	11°	16°	21°	26°	
	11°	▨	F_e=4,787 ≤Sig	Not Sig	Not Sig	Hymenosoma
Plagusia	16°	F_e=7,201 Sig	▨	F_e=6,391 Sig	F_e=12,031 ≫ Sig	
	21°	F_e=6,660 Sig	Not Sig	▨	Sig	
	26°	Not Sig	Not Sig	Not Sig	▨	

Cyclograpsus (in Water and Air)

	▨	11°	16°	21°	26°	
	11°	▨	Not Sig	Not Sig	Not Sig	Air
Water	16°	F_s=10,421 ≫ Sig	▨	Not Sig	Not Sig	
	21°	F_s=9,051 Sig	F_e=18,924 ≫ Sig	▨	Not Sig	
	26°	F_e=15,742 ≫ Sig	F_e=12,544 ≫Sig	Not Sig	▨	

The t-values of the individual linear slopes for respiration rate in water against crab mass are all significant ($p>0,05$) except for the 26°C slope of H. orbiculare which is significant at $p>0,2$ and the 11°C slope of C. punctatus which shows that there is no correlation between respiration rate and size at this temperature (Table 5). Figures 6a, b and c show the results graphically. Table 6 gives the results of the analysis of covariance tests to determine if the difference between the slopes obtained at the four temperatures is significant for the three species. Where the slopes showed no significant difference an F-test between the elevations was performed.

The three species will be discussed separately.

Slopes and elevations of the linear graphs obtained for P. chabrus show a significant difference between the elevations of 11°C and 16°C and 11°C and 21°C (Table 6), but not between 11°C and 26°C. From Figure 6a, it appears that the respiration rate of small P. chabrus is significantly greater at 26C° than at 11°C as the Y-intercept at 26°C is above those of 16°C and 21°C. However, the larger crabs respire at a similar rate to those at 11°C, indicating that large individuals may adapt better to warmer water than small. The convergence between the lines at 11°C and 26°C may explain the apparent discrepancy in Table 6 in the significant difference between the lines.

Values obtained for the slopes (β) in the logarithmic graphs at 16°C, 21°C and 26°C (Table I) correspond well with that obtained from the literature - 0,75 (equation (4)). However, the value of log α is very low in comparison to the value in equation (4).

The standard sized *P. chabrus* in this study had a dry mass of 7,484 g. The Q_{10} value for a crab of this mass would be 1,53 between 11°C and 21°C and 1,01 between 16°C and 26°C, where Q_{10} is calculated as

$$Q = {\frac{R_1}{R_2}}^{\frac{10}{T_2 - T_1}}$$

R_1 and R_2 are the rates of respiration at temperatures T_1 and T_2 respectively. In the 11°C - 16°C range the Q_{10} value is 2,49 and between 21°C - 26°C it is 0,97. These values are in agreement with those found by Vernberg *et al*. (1981) working on *Pagurus criniticornis*, where Q_{10} values in the 15 - 20°C range were higher than those in the 20 - 25°C range. Similar results were also obtained by Bullock (1955), Roberts (1957b), Wallace (1972), Newell *et al*. (1972), Sastry and McCarthy (1973), Klein-Breteler (1975b), Moreira and Vernberg (1978), Prentice and Schneider (1979) and Moreira *et al*. (1980) on work on various crustaceans. It seems that the higher Q_{10} values are normally noted at temperatures below that of the habitat.

Values of the linear regression equations obtained for *H. orbiculare* (Table 6) show significant correlation coefficients for the slopes at 11°C, 16°C and 21°C ($p > 0,05$). The difference between the slopes of the lines at 11°C and 16°C is significant ($p > 0,1$) and elevations at 16°C and 21°C and 16°C and the best fitting line at 26°C also show a significant difference ($p > 0,05$). It is apparent from Fig. 6b that large H. orbiculare respire at a noticeably increased rate at 11°C and 26°C than at 16°C and 21°C. Newell (1979) reported similar results for Littorina. The slopes of the lines vary directly with temperature showing that the influence of temperature is more pronounced on large individuals and that exposure temperature beyond normal temperatures experienced naturally, results in a greater increase in metabolism at the extremes of the temperature range. For small individuals at 11°C, the oxygen consumption rate is equivalent to that of crabs at 16°C and 21°C, so metabolic rate is also equivalent. As no excess energy is partitioned into metabolism, growth can continue, as is verified by results obtained in Section 3.1.

Q_{10} values for an average size H. orbiculare of 0,337 g dry mass are 0,07 between 11°C and 16°C, 12,35 between 16°C and 21°C, 1,59 between 21°C and 26°C, 4,43 between 16°C and 26°C and 0,91 between 11°C and 21°C.

Linear results of respiration in water of C. punctatus (Figure 6c and Table 6) show a significantly large difference between slopes at 11°C and 16°C, and 11°C and 21°C, and between elevations at 11°C and 26°C, 16°C and 21°C and 16°C and 26°C. The X and Y values at 11°C, however, show little correlation, so the slope obtained, may not represent the true situation. The results indicate that at water temperatures of 26°C small C. punctatus respire at an increased rate, but the large crabs are able to adapt to the warmer temperatures and respire at a rate equivalent to or below the rates at the lower temperatures.

The Q_{10} values for a standard sized animal of 1,033 g dry mass is 4,40 between 11°C and 16°C, 4,28 between 16°C and 21°C, 1,49 between 21°C and 26°C, 4,34 between 11°C and 21°C and 6,38 between 16°C and 26°C.

C. punctatus respiration in air did not differ significantly at any of the temperatures on the linear graph (Table 6) and only between the elevations at 11°C and 26°C on the logarithmic graph (Table II). Direct comparison of the linear lines obtained for respiration at each temperature in air and water for C. punctatus showed that the lines differ significantly from each other ($p > 0,05$). Aerial respiration rate is 2,3% of the aquatic respiration rate obtained at 11°C, 1,2% at 16°C and 6,9% at 21°C and 26°C suggesting that C. punctatus lowers the metabolic rate on exposure to air. Newell (1979) reports that aerial oxygen consumption in other organisms such as Mytilus edulis is relatively unaffected by exposure temperature thus showing a pattern of energy conservation common in intertidal animals.

It is interesting to note that Taylor and Wheatly (1979) showed that there was no significant difference in oxygen consumption of Carcinus maenas in air and water at 15°C, 25°C and 30°C. However, if the humidity of the air was low then thermoregulation could be achieved by evaporative cooling, and this resulted in a significant lowering of the metabolic rate in air. Similar results were obtained by Ahsunullah and Newell (1977), also with Carcinus.

Rhythmical variations in oxygen consumption are common amongst Crustacea

(Wallace 1972; Aldrich 1979; Newell 1979; Dye and van der Veen 1980), and are usually determined by diurnal and lunar rhythms. Dye and van der Veen (1980) found that the peak respiration in grapsoid crabs was at low tide at night. Aldrich (1975) showed that oxygen consumption of Cancer and Maia is not only rhythmical, but the amplitude of the peaks also differ and are affected by factors such as handling and starvation. Rates recorded in this study were taken from animals kept submerged, well fed and which were accustomed to handling. This implies that starvation, tidal rhythms and excitement due to handling were unlikely to be influencing factors. Light and dark could have had the overriding effect on respiratory rates of the crabs (Aldrich 1979). All these experiments were conducted during light hours.

Klein-Breteler (1975b) measured oxygen consumption in Carcinus over a 24 hour period of 12 h light and 12 h dark and found periods of high and low levels of respiration. McMahon and Wilkens (1977) and McMahon et al. (1978) observed that during these 'low' periods there was a complete cessation of branchial and cardiac pumping for periods of over 20 minutes. This 'low' in metabolic activity will conserve a significant amount of the food resources, which is important at the low temperatures because of the decrease in food intake (see Section 3.3).

At 11°C, 16°C and possibly also 21°C the values obtained for the metabolic rate per day of the three species studied may well be lower than those stated in the above results due to long periods of unilateral pumping (only one scaphognathite pumping) or pausing in the beating of the scaphognathites. If this is so, the results obtained in Section 3.6 for energy expenditure are excessive. At 26°C the oxygen content of the water may be too low to allow for long periods of complete cessation of branchial pumping. Indeed Mangum and Towle (1977) and McMahon et al. (1978) showed that a 5°C rise in ambient temperature causes an increase in pumping of heart and scaphognathites which decreases after 12 - 24 hours. This decrease may be due to internal compensation or a decline in the avoidance response. Although the internal oxygen content decreased with the increase in temperature, the oxygen tension remain unchanged. This suggests that hyperventilation is sufficient to maintain oxygen tensions even with a lowered external oxygen concentration and a lowered binding property of haemocyanin (which causes the oxygen content decrease). No increase in lactate was observed therefore McMahon et al. suggest that no anaerobic respiration takes place. Carcinus emerges into air when stressed by higher temperatures (Taylor & Wheatly 1979) and it is possible that C. punctatus being a littoral zone crab, would do likewise, thereby conserving energy.

3.3 Food Consumption and Faecal Production

The quantity of food consumed by intertidal animals per unit time depends upon the nature and abundance of food, temperature, tidal levels, body size, age, physiological condition and the presence of feeding and digestive rhythms (Laudien 1973; Ivleva 1973; Newell

1979). There is insufficient data on crustacean feeding to draw a definite conclusion but consumption (C) appears to be related to body weight (W) according to the following equation:

$$C = \alpha' W^{\beta'} \qquad \text{(Sushchenya 1973)}$$

whence $\log C = \log \alpha' + \beta' \log W$

where β' is very similar or identical to β in the generally accepted equation relating respiration to body weight (Section 3.2). The Y-intercept $\log \alpha'$ is only constant at a particular concentration of food and increases with increase in food concentration (Richman, in Sushchenya 1973).

Parameters from the linear regression lines obtained for the food consumed and faeces produced for the three species are given in Tables 7 and 8 respectively. Figures 7 and 8a, b and c show these results graphically. As discussed in Section 3.2, the linear graphs are given as the t and r values show the correlation to be better in most cases, than the logarithmic graphs. The logarithmic values and graphs are given in the appendix for comparison with the literature - Tables III, IV and V and Graphs 2 and 3a, b and c. Table 9 in this section gives the mean values of the food consumed and faeces produced at each temperature for P. chabrus, because the correlation coefficients obtained were very low probably due to the small number of observations.

Wallace (1973) in work on the shore crab Carcinus maenas, also found wide scatter around the regression lines, but concluded that food intake for the large individuals is greater than that for the small crabs but weight specific consumption rate is greater for small crabs. Klein-Breteler (1975) in his work on C. maenas found values for the parameters log α' and β' of the logarithmic graphs to be -0,2152 and 0,7383 respectively. Sushchenya gives log α' to be between -1,4318 and -1,0458 and β' to be between 0,47 and 0,67 for various Crustacea.

Mean values of consumption obtained for P. chabrus at the four different temperatures (Table 9) show significant differences between feeding at 11°C and 21°C, 11°C and 26°C, 16°C and 26°C and 21°C and 26°C (Table 10) with the maximum feeding rate attained at the maximum temperature. Mean faecal production also increases to a maximum at 26°C with the production at 26°C being significantly higher than the production at 11°C and 16°C (Table 10). The faeces produced account for between 10% and 20% of the total mass of food consumed at 16°C and 21°C respectively with values of 13% and 16% being obtained at 11°C and 26°C. It appears by simply comparing the amount of food consumed and faeces produced that assimilation efficiency is greatest at 16°C followed by 11°C and lowest at 21°C. (Assimilation efficiency based on calorific values of food and faeces will be presented in Section 3.6.) For a standard sized P. chabrus of 7,484 g dry mass the increase in consumption is 2,1-fold between 11°C and 16°C, 1,1-fold between 16°C and 21°C, and 2,3-fold between 21°C and 26°C. Wallace (1973) found the increase in consumption for Carcinus to be 2,4-fold between 10°C and 24°C. The increase in this study between 11°C and 21°C is 2,3.

The linear regressions obtained for H. orbiculare and C. punctatus

TABLE 7 Parameters of the linear regression equations for crab dry mass (g) against food consumption (mg day^{-1}). Y=a+bX, syx = std. error of the estimate; r = correlation coefficient. P = significance level in a two-tailed hypothesis.

Temp C°	n	a	b	±syx	t	P	r
a)				*Plagusia*			
11°	7	61,524	1,483	41,984	0,426	N.S.	0,19
16°	7	26,858	14,972	77,537	1,634	0,2	0,59
21°	5	154,290	-4,799	69,651	-0,585	N.S.	-0,32
26°	7	99,470	31,916	165,671	1,857	0,2	0,64
b)				*Hymenosoma*			
11°	13	0,828	6,025	4,759	2,883	0,02	0,66
16°	13	3,186	32,789	11,041	4,778	0,001	0,82
21°	13	11,510	13,656	3,814	2,795	0,02	0,64
26°	11	20,448	2,714	9,519	0,577	N.S.	0,19
c)				*Cyclograpsus*			
11°	13	1,653	-0,376	0,735	-0,939	N.S.	-0,27
16°	12	10,759	5,482	9,118	2,228	0,05	0,58
21°	13	15,249	14,696	23,175	1,425	0,2	0,39
26°	13	7,358	11,818	14,609	2,911	0,02	0,66

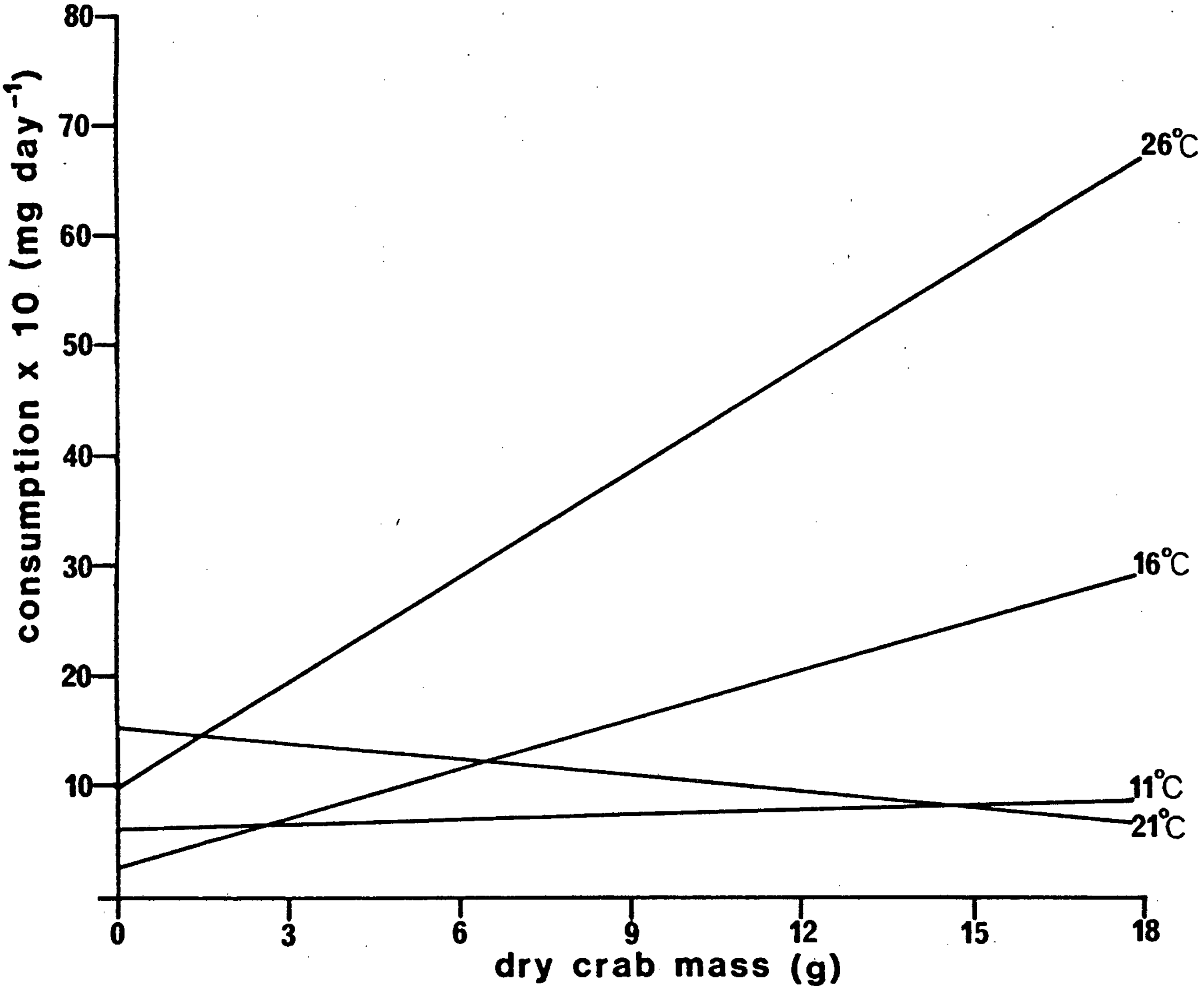


Fig. 7a The linear relationship between crab dry mass (g) and food consumption (mg day^{-1}) for Plagusia at the four temperatures.

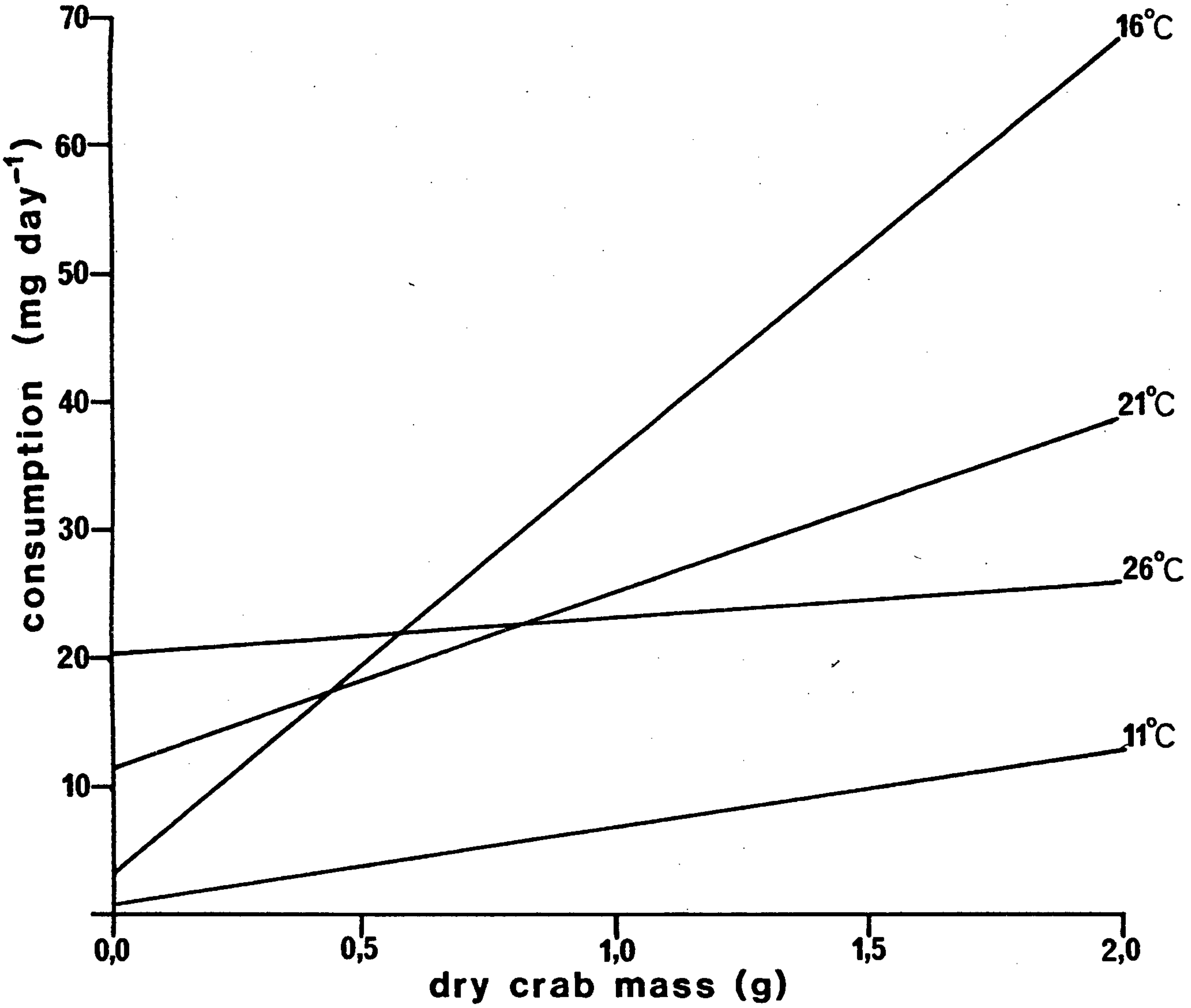


Fig. 7b The linear relationship between crab dry mass (g) and food consumption (mg day^{-1}) for Hymenosoma at the four temperatures.

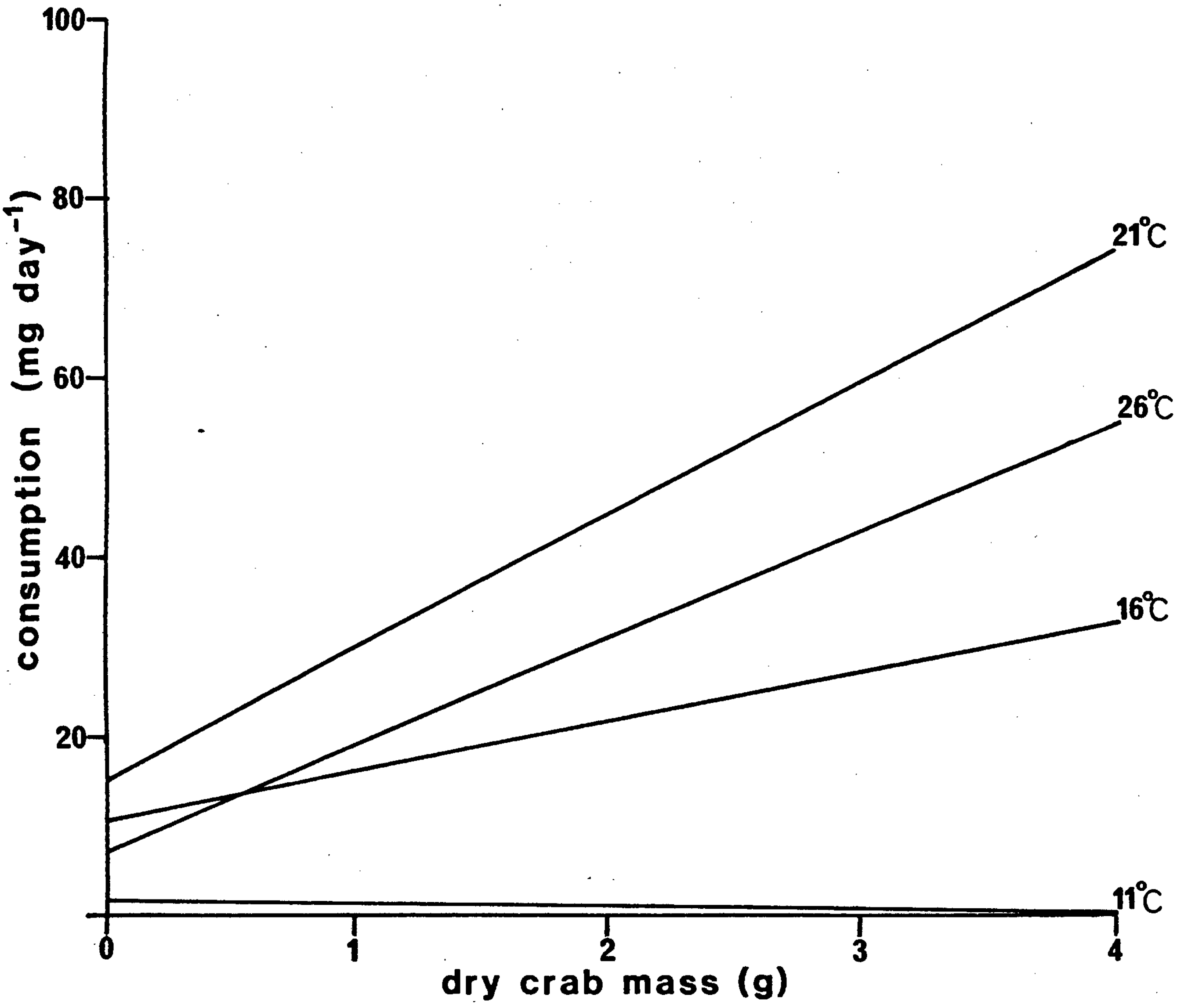


Fig. 7c The linear relationship between crab dry mass (g) and food consumption (mg day^{-1}) for Cyclograpsus at the four temperatures.

TABLE 8 Parameters of the linear regression equations obtained for crab dry mass (g) against faeces produced (mg day^{-1}). $Y = a+bX$; Syx is the standard error of the estimate; r is the correlation coefficient; P is the significance level in a two-tailed hypothesis.

Temp C°	n	a	b	±Syx	t	P	r
a)			Plagusia				
11°	7	19,28	-0,595	9,009	-0,796	N.S.	-0,34
16°	7	27,73	0,530	18,310	0,245	N.S.	0,11
21°	5	47,61	0,213	23,577	0,065	N.S.	0,04
26°	7	70,56	2,433	53,207	0,441	N.S.	0,19
b)			Hymenosoma				
11°	13	1,735	-0,736	1,720	-0,974	N.S.	0,00
16°	13	4,804	14,744	11,045	2,140	0,1	0,54
21°	13	5,055	-2,149	2,384	-1,625	0,2	0,00
26°	11	0,424	8,817	3,103	5,748	0,001	0,89
c)			Cyclograpsus				
11°	13	0,000	0,000	0,000	+ +	0,001	1,00
16°	12	2,066	-0,197	2,492	-0,292	N.S.	-0,09
21°	13	3,135	8,916	10,159	1,972	0,1	0,51
26°	13	2,583	3,610	5,407	2,403	0,05	0,59

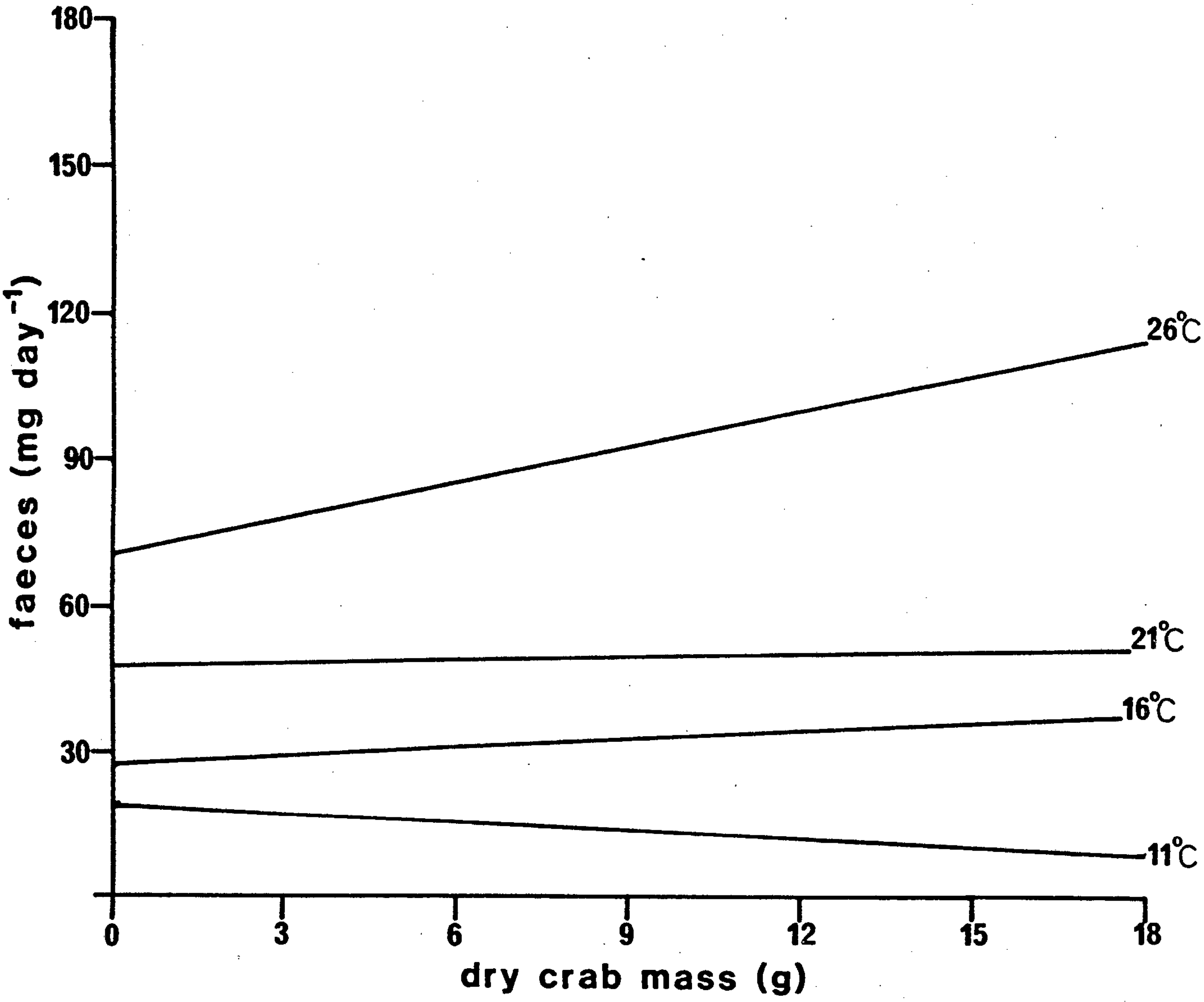


Fig. 8a The linear relationship between crab dry mass (g) and faeces production (mg day^{-1}) for Plagusia at the four temperatures.

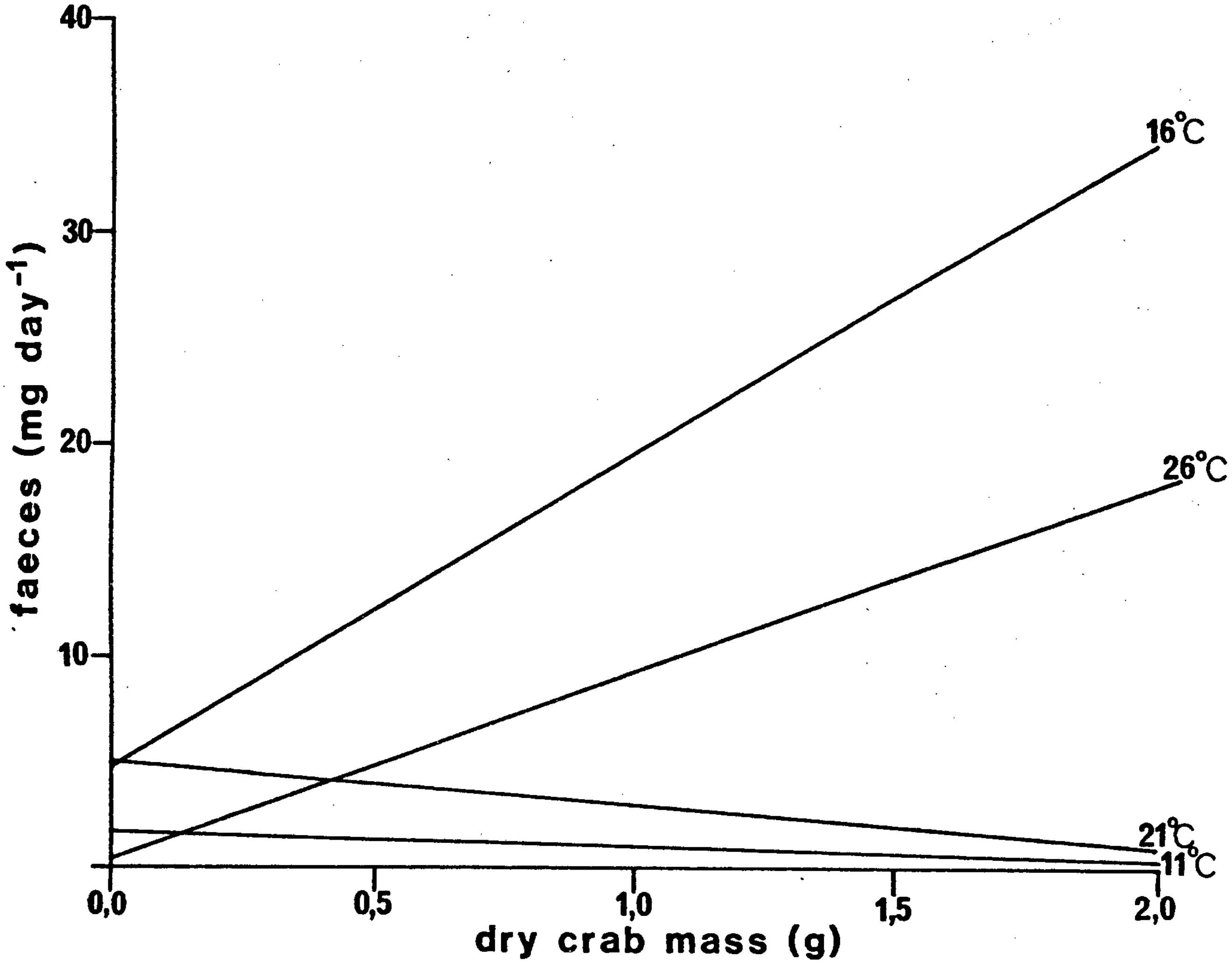


Fig. 8b The linear relationship between crab dry mass (g) and faeces production (mg day^{-1}) for Hymenosoma at the four temperatures.

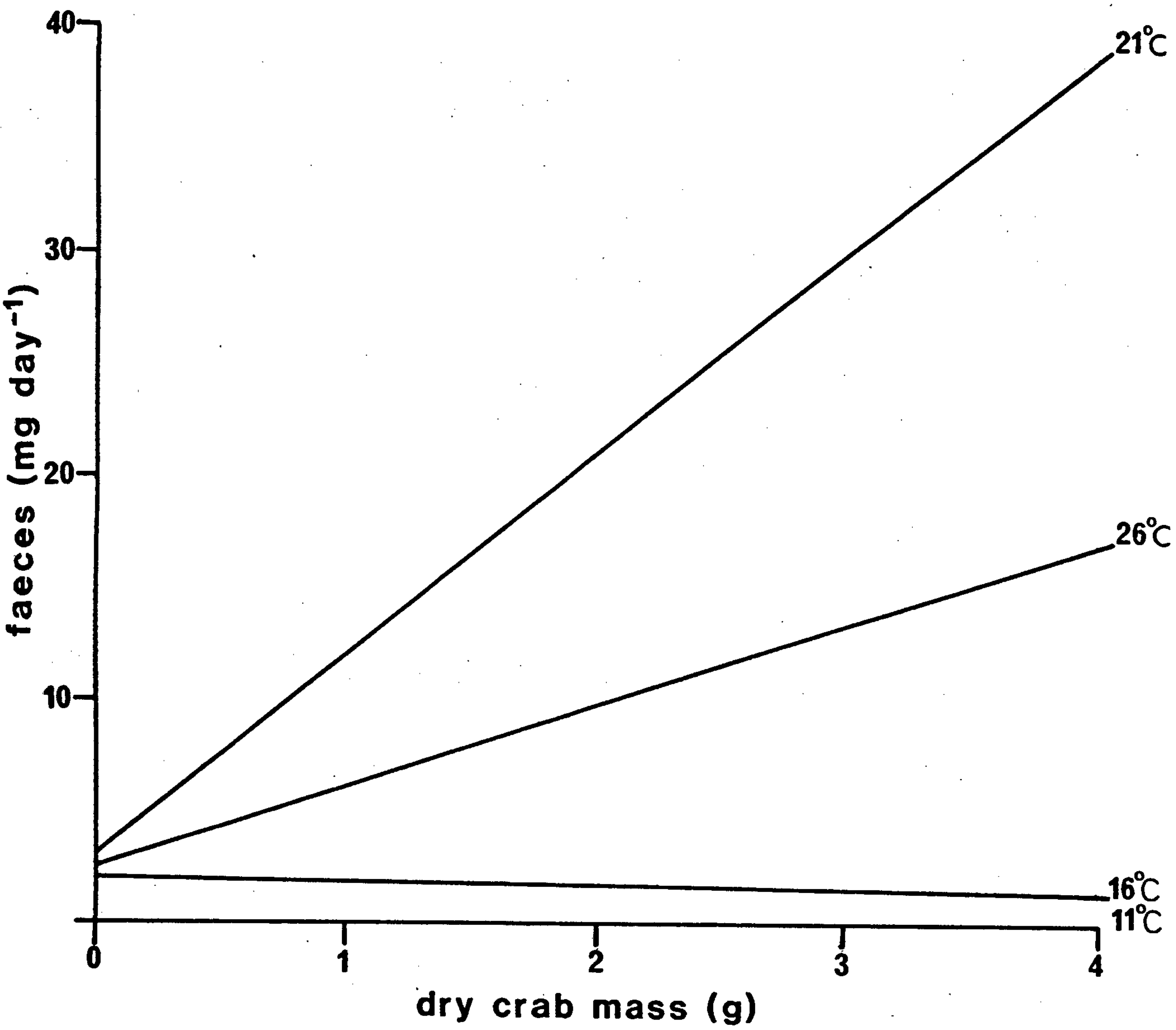


Fig. 8c The linear relationship between crab dry mass (g) and faeces production (mg day^{-1}) for Cyclograpsus at the four temperatures.

TABLE 9 The means and standard deviation of dry crab mass (g), food consumption (kJ day^{-1}) and faecal production (kJ day^{-1}) of P. chabrus. ANOVA showed the means of the dry mass of the crabs to have no significant difference between the values. $F_{(0,5;\ 3,22)} = 2,28$.

	$\bar{x}$	s	n	Σx	Σx^2
11°c					
Mass	8,431	5,822	7	59,02	700,98
Food Consumption	1,419	0,885	7	9,934	18,797
Faeces Produced	0,179	0,130	7	1,256	0,327
16°C					
Mass	8,579	4,087	7	60,05	615,37
Food Consumption	2,977	1,988	7	20,84	85,75
Faeces Produced	0,294	0,181	7	2,056	0,801
21°C					
Dry Mass	6,234	5,481	5	31,17	314,47
Food Consumption	2,384	1,576	5	11,93	38,35
Faeces Produced	0,480	0,306	5	2,398	1,524
26°C					
Dry Mass	6,691	4,66	7	46,83	443,36
Food Consumption	6,000	4,460	7	42,00	371,35
Faeces Produced	0,981	0,662	7	6,869	9,369

TABLE 10 Results of the student's t-test (for *P. chabrus*) and ANOCOVA test (for *H. orbiculare* and *C. punctatus*) between the means of food consumption and faecal production (mg day^{-1}) and linear regression lines between crab dry mass (g) and food consumption and faecal production (mg day^{-1}) ($p > 0,05$). F_s-test between slopes. F_e-test between elevations.

a *Plagusia* (t-test)

	▨	11°	16°	21°	26°	
	11°	▨	t=0,050 Not Sig	t =1,617 Not Sig	t=2,652 Sig	
Food	16°	t=1,443 Not Sig	▨	t=1,702 Not Sig	t=2,787 Sig	Faeces
	21°	t=2,560 Sig	t=1,626 Not Sig	▨	t=1,429 Not Sig	
	26°	t=5,478 Sig	t=4,318 Sig	t=1,920 Sig	▨	

b <u>Hymenosoma</u> (F-test)

	▨	11°	16°	21°	26°	
	11°	▨	F_s=6,590 Sig	F_e=7,447 Sig	F_s=34,815 >> Sig	
Food	16°	F_s=17,134 >> Sig	▨	F_s=6,414 Sig	Not Sig	Faeces
	21°	F_e=24,406 >> Sig	Not Sig	▨	F_s=29,062 >> Sig	
	26°	F_e=27,837 >> Sig	F_s=13,299 >> Sig	Not Sig	▨	

c <u>Cyclograpsus</u> (F-test)

	▨	11°	16°	21°	26°	
	11°	▨	F_e=5,785 Sig	F_e=19,899 >> Sig	F_e=16,900 >> Sig	
Food	16°	F_e=31,760 >> Sig	▨	F_e=16,725 >> Sig	F_e=11,219 >> Sig	Faeces
	21°	F_e=20,595 >> Sig	Not Sig	▨	F_e=6,061 Sig	
	26°	F_e=19,192 >> Sig	Not Sig	Not Sig	▨	

given in Tables 7 and 8 show better correlation coefficients than those obtained for P. chabrus. The regression lines and not the mean values will therefore be considered for these two species. Logarithmic values given in Tables III and IV (appendix) are of little significance and the graphs at 11°C were not obtained because of zeros in the original data. For H. orbiculare, the percentage of faeces produced of the total mass of food consumed, varies considerably from 16% at 26°C and 27% at 21°C, to 52% and 69% at 11°C and 16°C respectively. This shows an increase in assimilation efficiency at the higher temperatures. Food consumption increases up to the maximum temperature (Fig. 7c, Table 10) with a 5,6-fold increase between 11°C and 21°C and a 1,5-fold increase between 16°C and 26°C. These results indicate that the higher temperatures are favourable for consumption and assimilation in H. orbiculare.

A wide variation in percentage of faeces produced to total food consumed is also observed for C. punctatus, the values being <1% at 11°C, 11% at 16°C, 41% at 21°C and 32% at 26°C. A peak in food consumption is reached at 21°C followed by a decline at 26°C, but the assimilation efficiency is lower at 21°C than at 26°C. Johns (1982) also found a peak in the amount of food consumed by Cancer larvae followed by a decline in consumption with continued increase in temperature but this was not significantly lower. However, in his work Johns found that larvae had a significantly lower feeding rate at 10°C - 30$‰_0$ salinity than larvae at 15°C - 35$‰_0$S and 15°C - 24$‰_0$S. The assimilation efficiency was also lowest at 15°C - 35$‰_0$S when consumption peaked.

Table 10 shows consumption rate to be significantly higher at 16°C, 21°C and 26°C than that at 11°C. Within the 16°C to 26°C range, however, the difference is not significant. Faecal production increases significantly with temperature except between 11°C and 16°C, and 21°C and 26°C. The increase in food consumption between 11°C and 21°C is 24,1-fold and between 16°C and 26°C only 1,2-fold. The results may indicate that C. punctatus feed around temperatures of 21°C, i.e. at low tide, and digestion takes place at the lower temperatures experienced at high tide.

3.4 Excretion

The principal waste product of crustaceans is ammonia, although other nitrogenous losses such as urea, uric acid and amines incompletely broken down, are also constituents of excretion (Warner 1977). The quantity of nitrogenous waste varies between species and from one animal to the next, and depends on the diet, salinity, temperature, injury, moulting and the proximity of other animals (Parry 1960). Excretion can occur through all permeable parts of the integument, and in some crustaceans especially through the gills.

In this study only ammonia excretion was measured so the results may be lower than expected for total excretion. For example, the percentage of total excretion accounted for by ammonia in certain subtidal marine Crustacea was found to be 48% for Cancer pagurus, 85 to 100% for Carcinus maenas and 93% for Eriocheir sinensis. The percentage for littoral Crustacea is 85% for Orchestia sp. and 93% for Ligia oceanica (Parry 1960). The results presented in this study may therefore be an underestimate of the true excretory rate.

Table 11 and Figs 9a, b and c give the results obtained for the excretory rate against the dry mass of the crabs at the four temperatures. Table 12 gives the results of the analysis of covariance tests performed between the slopes and elevations of the lines. Significant differences are few and are between the elevations of the lines at 11°C and 26°C, and 16°C and 26°C for P. chabrus, between 11°C and 21°C, and 16°C and 21°C for H. orbiculare and the slopes of the 16°C and 21°C lines for C. punctatus. Excretion is maximum at 26°C for P. chabrus but for H. orbiculare and C. punctatus maximum excretion occurs at 21°C with the rates decreasing at 26°C. On the whole, however, the excretion rate showed little significant increase with temperature (Table 12).

These results are comparable to those obtained by Macé and Ansell (1982) on work on two species of molluscs - Polineces alderi and P. catena. The relationship Macé and Ansell obtained for P. alderi suggests that the rate of $N\text{-}NH_3$ excretion increases with temperature between 10 and 20°C for large animals, but for smaller animals the maximum rate is attained at 15°C. The rate of excretion shows little change with temperature for P. catena.

Johns (1981b) also found little relationship between $N\text{-}NH_3$ production for Cancer at 10°C, 15°C and 24°C. The intercepts, however, suggest

TABLE 11 Parameters of the linear regression equations for crab dry mass (g) against excretion (kJ day^{-1}). $Y = a+bX$; Syx is the standard error of the estimate; r is the correlation coefficient; P is the significance level in a two-tailed hypothesis.

Temp' C°	n	a	b	Syx	t	P	r
a)			Plagusia				
11°	7	0,0008	0,0006	0,0000	2,161	0,01	0,69
16°	9	0,0003	0,0010	0,0033	2,151	0,01	0,63
21°	9	0,0139	-0,0001	0,0100	-0,041	N.S.	0,02
26°	8	0,0065	0,0010	0,0050	1,467	N.S.	0,51
b)			Hymenosoma				
11°	8	-0,0003	0,0017	0,0000	2,709	0,05	0,74
16°	8	-0,0010	0,0026	0,0000	4,008	0,01	0,85
21°	10	0,0004	0,0037	0,0000	3,180	0,02	0,75
26°	8	0,0007	0,0023	0,0035	0,950	N.S.	0,36
c)			Cyclograpsus				
11°	8	-0,0005	0,0007	0,0000	5,021	0,005	0,90
61°	8	0,0004	0,0004	0,0000	2,926	0,05	0,77
21°	9	-0,0021	0,0023	0,0000	4,103	0,005	0,84
26°	5	0,0002	0,0005	0,0000	3,339	0,05	0,89

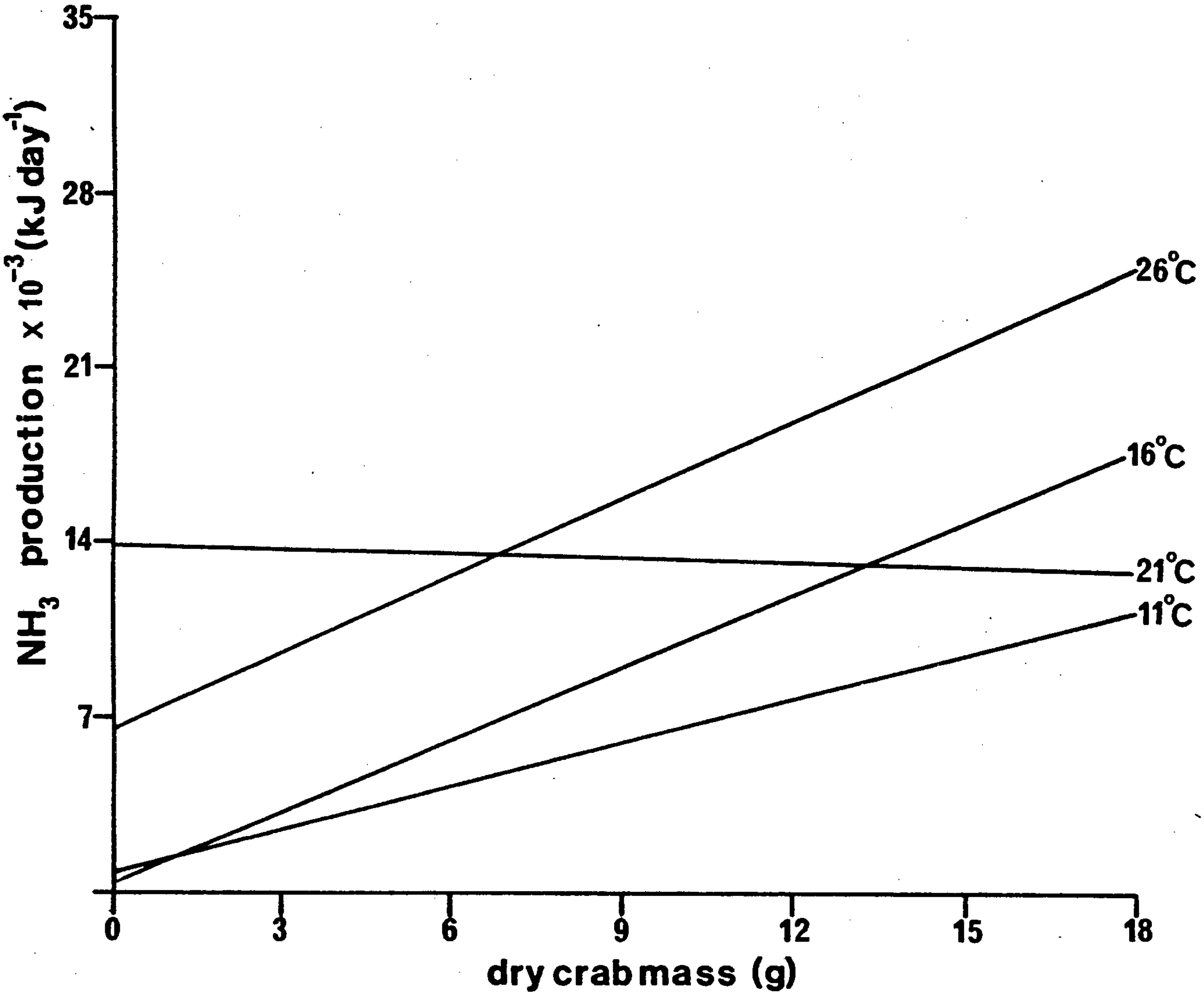


Fig. 9a The linear relationship between crab dry mass (g) and excretion (kJ day^{-1}) for Plagusia at the four temperatures.

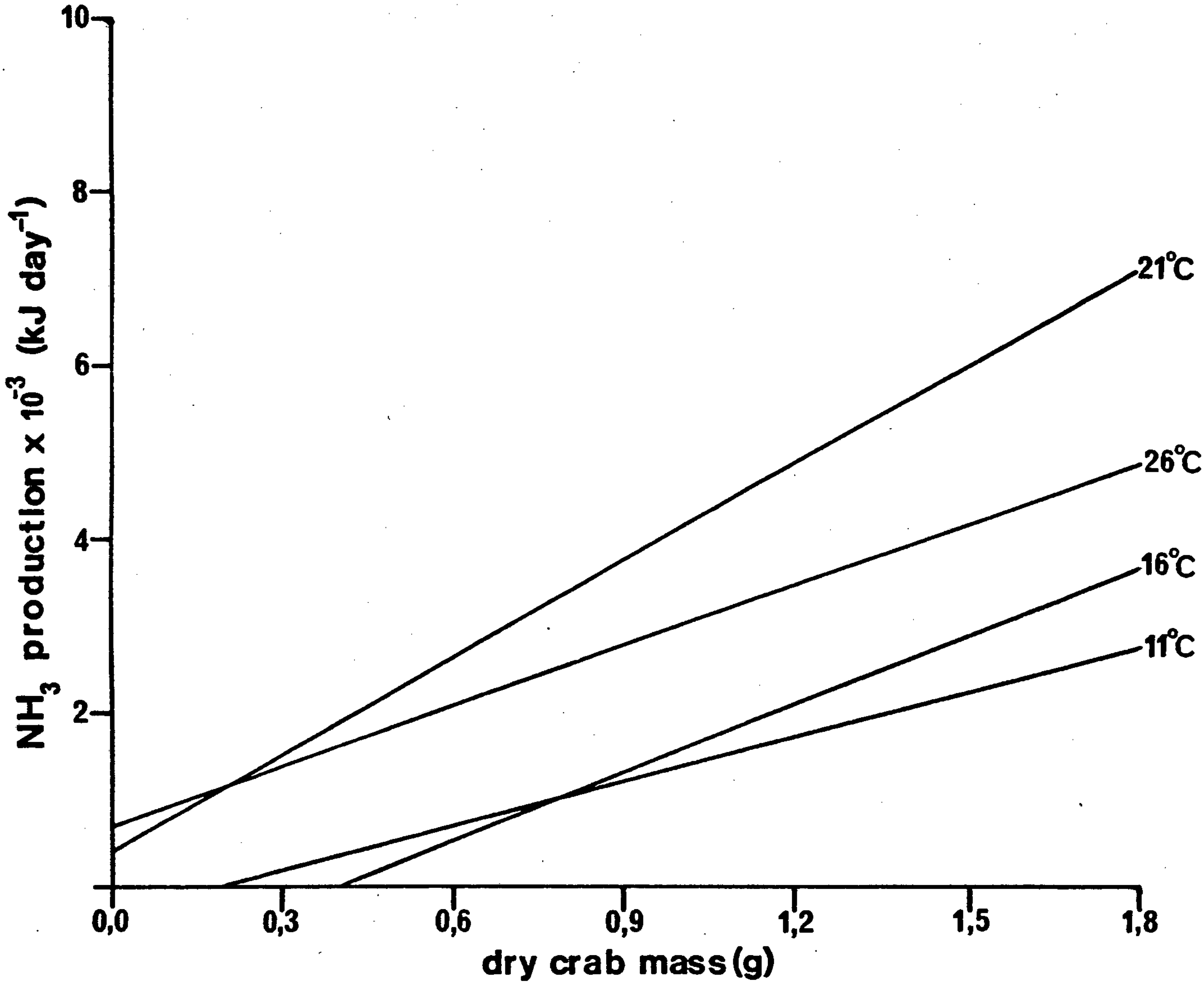


Fig. 9b The linear relationship between crab dry mass (g) and excretion (kJ day^{-1}) for Hymenosoma at the four temperatures.

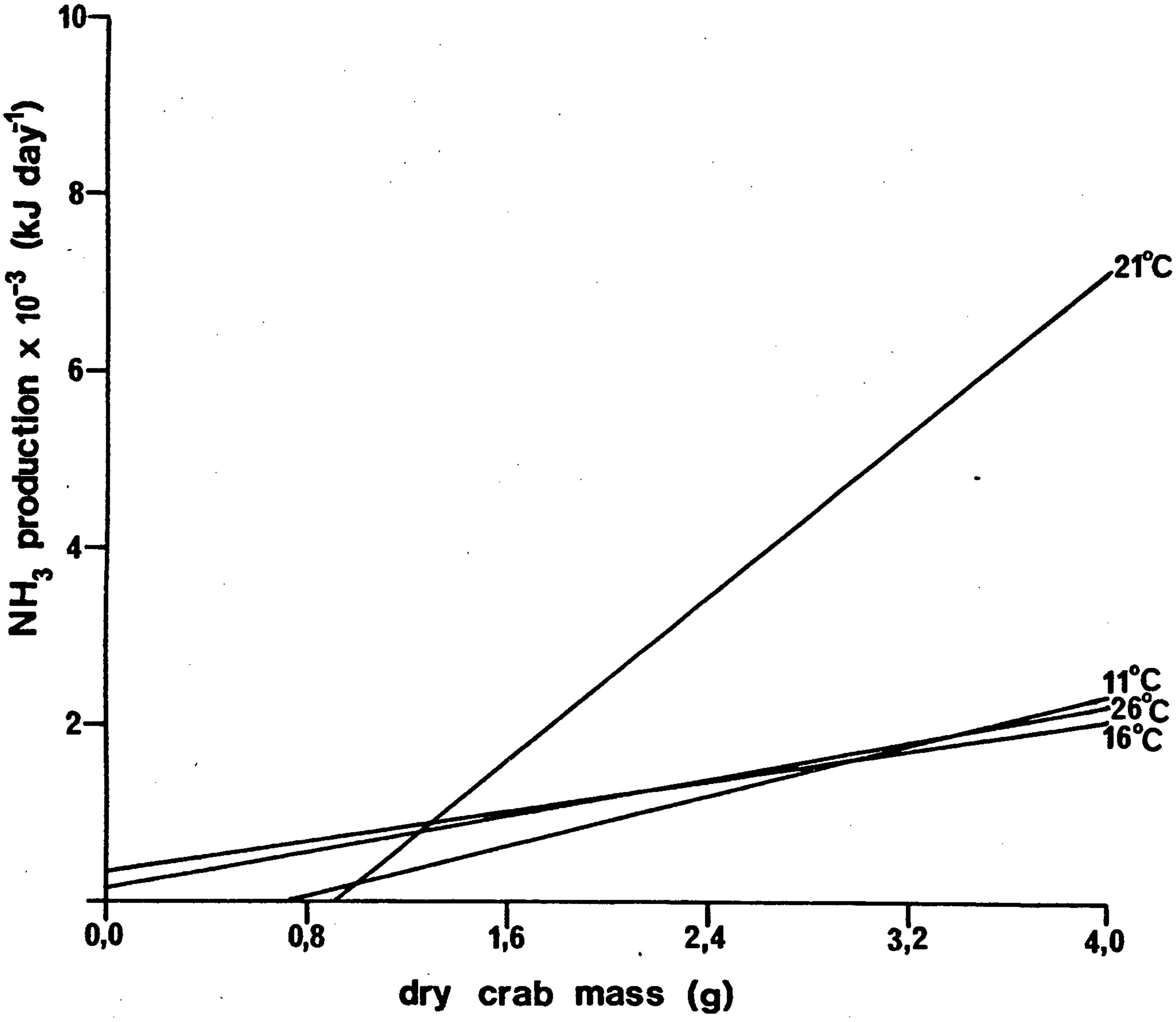


Fig. 9c The linear relationship between crab dry mass (g) and excretion for Cyclograpsus at the four temperatures.

TABLE 12 Results of ANOCOVA test between the linear regression lines obtained for crab dry mass (g) against excretion (kJ day^{-1}). F_s-test between slopes. F_e-test between elevations. ($p > 0,05$)

Hymenosoma

Plagusia

▨	11°	16°	21°	26°
11°	▨	Not Sig	F_e=7,089 Sig	Not Sig
16°	Not Sig	▨	F_e=7,960 Sig	Not Sig
21°	Not Sig	Not Sig	▨	Not Sig
26°	F_e=16,284 >>Sig	F_e=8,536 Sig	Not Sig	▨

Cyclograpsus

▨	11°				
11°	▨	16°			
16°	Not Sig	▨	21°		
21°	Not Sig	F_s=9,010 Sig	▨	26°	
26°	Not Sig	Not Sig	Not Sig	▨	

TABLE 13 Q_{10} values for nitrogen excretion of the three species of crab.

Temp. range °C	P. chabrus	H. orbiculare	C. punctatus
11 - 16	2,2	0,1	16,0
16 - 21	2,9	256*	0,1
21 - 26	1,1	0,9	5,4
11 - 21	2,5	28,4	1,5
16 - 26	1,8	225*	0,9

* The very high Q_{10} values for H. orbiculare are a result of the calculations being based on very low excretory rates (0,0001 kJ day^{-1}) where accurate measurements are difficult.

Q_{10} values show the greatest rise to be between 16°C and 21°C for P. chabrus and H. orbiculare, and between 11°C and 16°C for C. punctatus.

that Cancer larvae at 10°C and 24°C excrete significantly lower amounts of ammonia than larvae at 15C°. Both Johns (1982) and Emerson (1969) found that salinity affects the amount of ammonia produced. A rise in salinity results in a decrease in ammonia production.

Q_{10} values for nitrogen excretion are given in Table 13.

3.5 Reproduction

Fecundity, like many other biological characteristics of poikilothermic animals, is often greatly affected by temperature. Not only is it important that many eggs are laid but the eggs must be provided with the optimum amount of yolk and deposited in areas favourable for egg and larval development (Laudien 1973). Reproduction requires a more critical temperature optimum than vegetative processes (functions other than reproductive) and in many marine animals the temperature range for breeding is less than that for vegetative processes (Gunter 1957; Naylor 1965b).

Efford (1970) studied egg volume as a function of latitude (temperature) in the sand crab Emerita and observed that the volume of eggs produced was maximal at 11°C - 13°C and that the number of eggs produced per female was constant at all temperatures. In later work with Emerita, Fusaro (1980) found that females produced eggs much sooner at a higher temperature - 25,4°C than at the lower temperature - 11,5°C, and seven times as many females were ovigerous at 25,4°C than at 11,5°C. The length of time to zoeal release was also shortened at high temperatures. Fusaro suggests that it is the proportion of females in the population that are carrying eggs and the development time of the eggs which are the important factors in reproduction.

Young and Hazlett (1978) and Johns (1982) showed that larval development in the crab was faster at higher temperatures and the number of moults to the first crab stage was lower. The best developmental temperature for *Clibanarius* larvae was between 25°C and 30°C, especially at high salinities (Young & Hazlett 1978), and *Cancer* larvae showed the highest survival rate at 21°C with maximum carapace lengths obtained at 18°C.

Egg carrying in crabs from temperate regions is seasonal and often occurs in spring and summer (Warner 1977). The number of eggs laid per batch is generally very large and varies with the size of the crab. Newly-laid eggs are attached to the pleopods on the abdomen where they are held until zoeal release. The eggs are a yellow-orange colour when first laid and darken to a deep purple on maturation. The number of batches produced in a year is variable in Crustacea, with tropical crabs such as *Aratus* producing an average of six batches of eggs per year, while *Cancer* usually produces only one (Warner 1977). Reproduction in *C. punctatus* was studied by Broekhuysen (1941) who found that the female crab had one major breeding season from May to September and a minor breeding season from January to February. It seems likely from Broekhuysen's results that one female can extrude three batches of eggs between May and September and one batch in

January. The incubation period of the eggs is two months and one copulation suffices for all the egg batches. Little data is available on egg production in P. chabrus and H. orbiculare.

Sixteen berried females of P. chabrus were used to estimate the percentage mass of eggs produced to dry mass of crab. Logarithmic graphs of these parameters showed little correlation, but logarithmic graphs of the numbers of eggs produced against dry mass showed that a definite relationship existed. The regression equation for the graph of the number of eggs produced against dry mass of crab was

$$\log Y = \log 597{,}448 + 1{,}965 \log X$$

$$(r = 0{,}95)$$

From calculations of the mean masses of the eggs and females, it appears that the eggs account for an average of 10% of the dry mass of the female. The calorific value of the eggs is 25,65 kJ g^{-1} dry mass, so reproduction will account for a large part of the energy output during the breeding season.

It is not known how many batches of eggs are produced by P. chabrus in a breeding season, or how many breeding seasons the crab has a year. However, if the minimum value is considered, i.e. one batch of eggs per annum then the total energy expenditure for reproduction can be calculated as 0,053 kJ day^{-1} for the average sized crab of 7,484 g dry mass.

Nine female H. orbiculare were used to calculate the percentage of dry mass of eggs to body mass of crab. The average was found to be 21%, with the greatest value being 41%. The calorific value of the immature eggs was 24,30 kJ g^{-1} dry mass which results in a total energy expenditure for reproduction of 0,005 kJ day^{-1} for an average sized crab producing only one batch of eggs per year.

Four berried female C. punctatus were obtained in February. It appears that 11% of the dry mass of the crabs is made up of eggs. The calorific value of the immature (yellow) eggs obtained was 23,68 kJ g^{-1} dry mass and the mature (purple) eggs 18,20 kJ g^{-1} dry mass indicating a decrease in calorific value due to metabolism of the eggs with time. A batch of zoea larvae was also collected from the pleopods of one female and the calorific value found to be 5,81 kJ g^{-1} dry mass after correction for endothermy (Paine 1966). If an average production of three batches of eggs per annum is considered for a 1,033 g dry mass crab then the total energy expenditure for reproduction is 0,022 kJ day^{-1} $crab^{-1}$.

Broekhuysen (1941) and Johns (1982) state, however, that the incubation period shortens as the temperature rises. Therefore it is possible that the crabs could produce more than the average number of batches at the increased temperatures, thereby increasing energy expenditure. On the other hand, reproduction may become increasingly inhibited as temperature rises because of the unfavourable conditions for egg production and the cycle may halt at this stage. This may result in the excess energy being partitioned into growth.

3.6 Overall energy budget and energetic efficiencies

Table 14 gives the observed energy budget of the three crab species at the different temperatures. These values were calculated for the average sized animal in each of the species, the mean dry masses being 7,484 g for P. chabrus, 0,337 g for H. orbiculare and 1,033 g for C. punctatus. Energy required for reproduction was not included in the table, but it is assumed that during the reproductive season, energy usually partitioned into growth will be used for reproduction instead and consumption will increase accordingly.

The respiration values, as mentioned in Section 3.2 should be considered as routine rates because the crabs were given food ad lib. Routine metabolic rate is a measure of the average level of activity, and this is usually temperature dependent (Newell 1979). It must also be remembered that the respiration rates at the lower temperatures will probably be lower than those calculated due to long periods of cessation in branchial pumping (see Section 3.2). For respiration values of C. punctatus in air and water, it was assumed that the crab spent 12 h submerged and 12 h in air. This should bring the laboratory results obtained closer to field values, because being a littoral zone crab, it is unlikely to be submerged for as long as 12 h but the respiration rate would rise above that recorded due to an increase in activity while submerged in the field.

Ammonia is assumed to be the major excretory product, but as discussed in Section 3.4, other nitrogenous bases may also be excreted.

TABLE 14 Parameters of the energy budget equation, $C=P+R+U_{ex}+F+U_e$ measured for the three species of crab. The standard dry crab mass was used in the calculation for each of the species. Values given are in kJ (crab x day)$^{-1}$.

Temp C°	Consumption	Respiration	Growth	Moult	Faeces	Excretion
a)		Plagusia	(7,484 g dry mass)			
11°	1,260	1,251	<0,012	<0,032	0,159	0,005
16°	2,597	1,835	⩽0,138	⩽0,039	0,256	0,008
21°	2,862	1,910	0,360	0,051	0,576	0,013
26°	6,711	1,860	0,415	0,055	1,097	0,014
b)		Hymenosoma	(0,337 g dry mass)			
11°	0,055	0,174	<0,012	<0,074	0,011	0,000
16°	0,273	0,045	⩽0,043	⩽0,063	0,074	0,000
21°	0,309	0,158	0,048	0,136	0,032	0,002
26°	0,410	0,199	0,043*	0,136*	0,026	0,001

c) Cyclograpsus (1,033 g dry mass)

Temp C°	Consumption	Resp. in Air	Resp. in Water	Growth	Moult	Faeces	Excretion
11°	0,024	0,001	0,030	<0,007	<0,008	0,000	0,000
16°	0,315	0,001	0,062	0,027*	0,008*	0,010	0,001
21°	0,583	0,001	0,129	0,024*	0,012*	0,071	0,000
26°	0,375	0,001	0,157	0,041*	0,012*	0,036	0,001

* Intermoult period was taken to be the same as that at 21°C for H. orbiculare (32 days) and for C. punctatus, the results from Broekhuysen's study (1941) were used (93 days at 11°C and 16°C and 69 days at 21°C and 26°C).

TABLE 15 The percentage gross growth, assimilation and net growth efficiencies for the three crab species calculated from Table 14.

Temp.	Gross Growth Eff. G/C	Assimilation Eff. $\frac{G + R}{C}$	Net Growth Eff. $\frac{G}{G + R}$
		Plagusia	
11°C	<3,5	<103,0	3,4
16°C	<6,8	<77,5	8,8
21°C	21,2	81,1	17,7
26°C	7,0	34,7	20,2
		Hymenosoma	
11°C	<156,4	<472,7	33,1
16°C	38,8	55,3	1,6
21°C	59,5	110,7	53,8
26°C	43,7	92,2	47,4
		Cyclograpsus	
11°C	<62,5	<191,7	32,6
16°C	10,8	30,8	35,1
21°C	6,2	28,5	21,7
26°C	13,6	55,7	24,4

Nitrogen could also be lost as glucosamine (chitin) at each moult (Logan & Epifanio 1978). Therefore excretion values measured may be an underestimate of the true value.

The largest energy expenditure was used in growth and metabolic maintenance (Table 14). In all cases, except for H. orbiculare at 16°C and 21°C more energy was used in metabolic processes than was converted into new tissue. These high respiration rates at all temperatures may also be partly due to excitement from handling (Aldrich 1979), although as mentioned before, the animals were conditioned to the laboratory.

Table 15 gives the gross growth, assimilation and net growth efficiencies obtained for the three species. The assimilation efficiencies varied from 28,5% for C. punctatus at 21°C to 'over' 100% for P. chabrus at 11°C, H. orbiculare at 11°C and 21°C and C. punctatus at 11°C. The > 100% values are either due to the low consumption values obtained at these temperatures, or increased respiration values because of handling and other factors mentioned above. At 11°C the consumption values may be lower than usual because the experimental period was five days and at these temperatures crabs may only feed every 10 to 14 days due to slower digestion rates. Therefore total crab consumption may not have been recorded in the short experimental period. Conover (1966) suggests an assimilation efficiency of at least 60% and greater for crustaceans, but this value is known to differ very much amongst crustaceans (Sushchenya 1973; Klein-Breteler 1975c) and a general relationship is difficult to define. If these exceptional assimilation efficiency values are ignored, it can be seen that the highest efficiency is at 21°C for *P. chabrus* (81,1%) and 26°C for *H. orbiculare* (92,2%) and *C. punctatus* (55,7%). Net growth efficiency is greatest at 26°C for *P. chabrus* (20,2%) and *H. orbiculare* (53,8%) and at 16°C for *C. punctatus* (35,1%).

4. CONCLUSION

Organisms can often adjust the rate of their physiological processes in response to environmental conditions. These responses have been categorized into five main types by both Precht (1958) and Prosser (1973). In concluding this study, the classification devised by Precht will be used. A brief description of each response type follows. The response is classified as Type 1 if the reaction rate shows excess compensation; Type 2 if there is a complete return to the initial reaction rate at a different temperature (Prosser (1973) calls this lateral translation of the response curve); Type 3 occurs when there is partial acclimation and the reaction rate approaches but does not reach the initial reaction rate; Type 4 - there is no further change following the initial response to a new temperature (no acclimation) and Type 5 in which inverse compensation occurs and the new rate of reaction diverges even further from the original rate during acclimation. A general environmental change can affect different physiological rates in a combination of these patterns. For instance there may be no compensation for feeding rate at a new temperature yet a considerable change in metabolic rate.

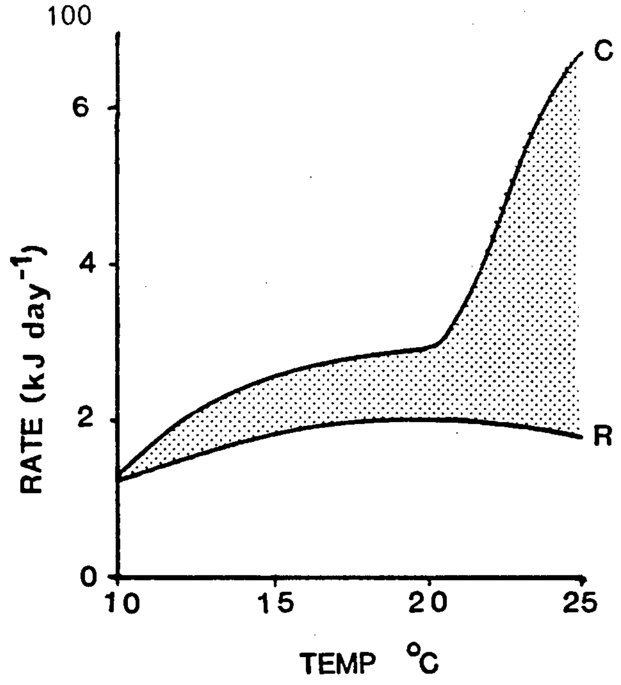
Although no acute rates (observed rates when an animal is placed in temperatures different to that at which it was acclimated) have been determined for the species studied, it appears from the data that either Type 3 or Type 4 response has been adopted for consumption rates of P. chabrus and H. orbiculare, because the rates show significant differences between the four temperatures. It can be concluded that partial acclimation has occurred if the acute rate changes are greater than those observed here, a Type 3 response. If acute rates are the same, then no acclimation has occurred and the response is Type 4. Similar results are obtained for C. punctatus up until 16°C and then from 16°C to 26°C it appears that there is a greater degree of acclimation with the rate of consumption rising to a maximum at 21°C and then decreasing to 26°C, but showing no significant differences.

Respiration rates show a better compensation to the higher temperatures than food consumption rates. The rates for P. chabrus increase up until 21°C and then stabilize between 21°C and 26°C, but the difference is small and the response is probably Type 3 or Type 2 between the temperatures 16°C and 26°C. H. orbiculare shows little compensatory changes between the four temperatures, with the rate of metabolism decreasing from 11°C to 16°C and then increasing steadily to 26°C. The response may be Type 3 or Type 4. C. punctatus also shows a Type 3 or Type 4 response with respiratory rates increasing significantly from 11°C to 26°C.

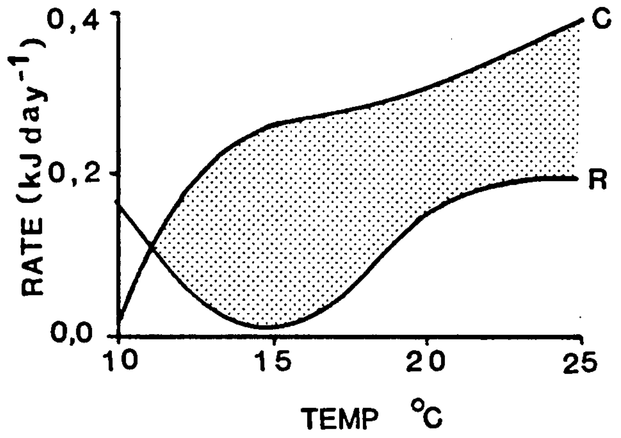
The results imply that an increase in water temperature will result in an overall increase in metabolic rates and growth processes but this will be compensated for by an increase in the consumption rate, provided there is available food. It appears that the most favourable temperatures for the three species of crabs are between 16°C and 21°C. Growth and moulting can proceed normally at these temperatures whereas at 26°C death during or after moults is common especially in P. chabrus and H. orbiculare. Figure 10 shows the difference between the food consumption rates and respiration rates at each temperature. This difference is termed the 'scope for growth'. From Figure 10a it appears that the maximum 'scope for growth' for P. chabrus is at 26°C. However, as moulting often results in death, temperatures around 21°C are the optimum. Figures 10b and c show the maximum 'scope for growth' to be around 16°C for H. orbiculare and 21°C for C. punctatus.

Long-term changes in environmental temperature, operating over many generations of the species may favour the appearance of genetic variants (Newell & Branch 1980) if reproduction continues at the increased temperatures. This may result in a gradual shift in the rate-temperature response curves, back to the original values (Type 2 response).

It appears therefore that Plagusia chabrus, Hymenosoma orbiculare and Cyclograpsus punctatus are eurythermal species and are capable of becoming acclimated to the warmer temperatures that will be experienced around Koeberg Power Station. The results indicate that the three crab species should not experience any adverse physiological effects from the increased temperature per se. However, in a *Plagusia*



b *Hymenosoma*



c *Cyclograpsus*

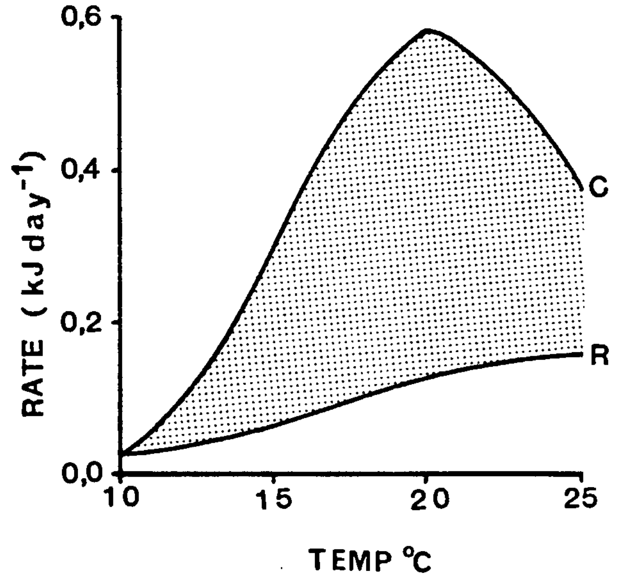


Fig. 10 Rate-temperature curves showing the 'scope for growth' for the three crab species. C is the consumption rate; R is the respiration rate.

considering whether or not the thermal effluent from the power station will have any overall effect on the crab population, other factors such as:

i) temperatures detrimental to egg and larval development;

ii) the abundance of food in the warmer waters; and

iii) any increase in competition from immigrant species

would also have to be considered.

5. SUMMARY

1. In the three crab species studied, *Plagusia chabrus*, *Hymenosoma orbiculare* and *Cyclograpsus punctatus*, growth rate increases with an increase in temperature from 11°C to 26°C.

1. There was little or no increase in width increment at each moult at the higher temperatures and the increase in growth rate is achieved by decreasing the intermoult period in *P. chabrus* and *H. orbiculare*. No intermoult period was obtained at any temperature for *C. punctatus*, but more crabs moulted at the higher temperatures and it was assumed that the intermoult period is shortened.

3. Little relationship was found between linear regressions of the initial width and percentage growth in any of the species.

4. Mortality is particularly high during ecdysis at 26°C for *P. chabrus* and *H. orbiculare* (73% and 100% mortality respectively).

5. Linear regression lines fitted the data in this study better than a logarithmic regression and it is assumed that the size range of crabs used was too small to determine a good exponential fit.

6. Linear regression lines for respiration showed significant differences between 11°C and 16°C, and 16°C and 21°C for *P. chabrus*, between 11°C and 16°C, 16°C and 21°C and 16°C and 26°C for *H. orbiculare* and between all the temperatures except 21°C and 26°C for *C. punctatus*.

7. Respiration of *C. punctatus* in air was found to differ only between the elevation of the slopes of 11°C and 26°C. Respiration in air was much lower than in water (e.g. 93% lower at 21°C and 26°C).

8. Mean consumption and faecal production rates increased significantly with temperature for *P. chabrus*. Linear regressions were obtained for *H. orbiculare* and *C. punctatus* between consumption rates and dry mass of the crabs and between faecal production and dry mass. Both consumption and faecal production increased with increasing temperatures. However, consumption rate for *C. punctatus* peaked at 21°C and then declined at 26°C.

9. Excretion rates (ammonia production) showed little significant difference between the four temperatures and it was concluded that temperature was not a major influencing factor on excretion in these species.

10. Reproduction was not studied at the four temperatures, but collections of ovigerous females showed the percentage dry mass of eggs over body mass to be 10% for *P. chabrus*, 21% for *H. orbiculare* and 11% for *C. punctatus*.

11. The overall energy budgets and energetic efficiencies showed that P. chabrus, H. orbiculare and C. punctatus will be able to survive in water up to approximately 21°C. Therefore the cooling water from Koeberg Nuclear Power Station should present no adverse physiological effects to adults of the three crab species.

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8. APPENDIX

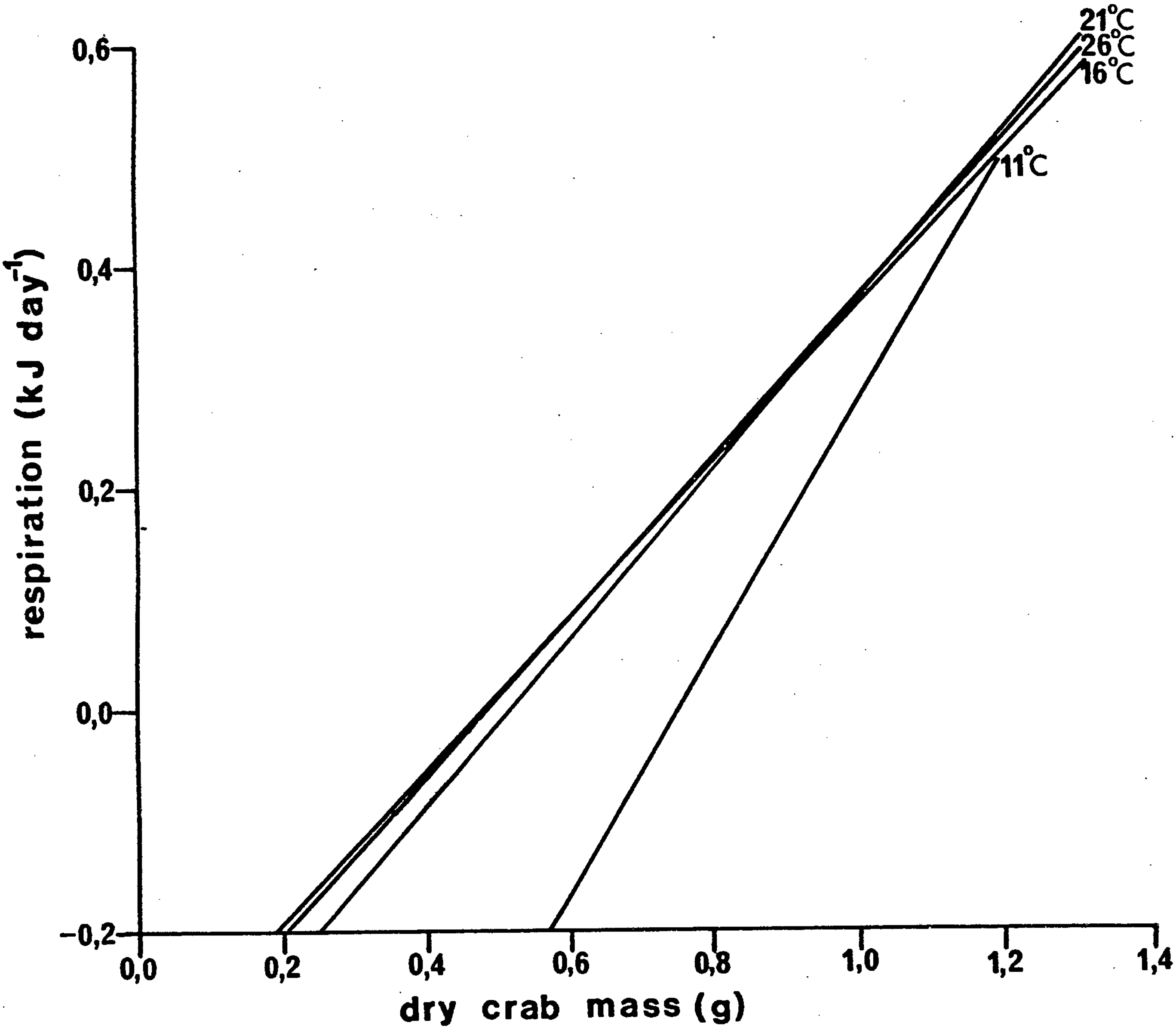
8.1 Further Data

Tables Index: Page

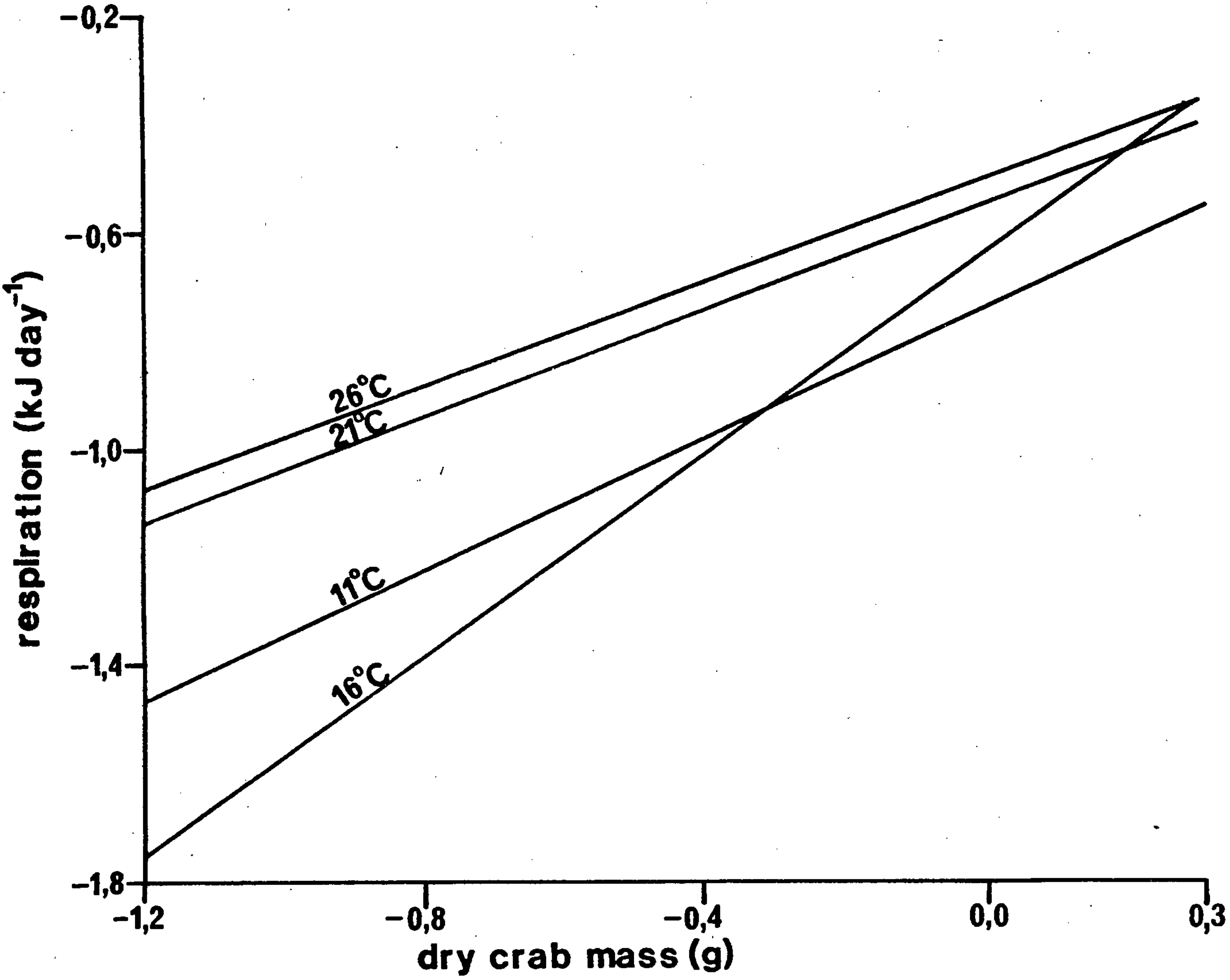
Figures Index:

TABLE I Parameters of the logarithmic regression equations for crab dry mass (g) against respiration (kJ day^{-1}). $Y = \alpha W^{\beta}$; $\log Y = \log\alpha + \beta \text{Log } W$; Syx is the standard error of the estimate, r is the correlation coefficient; P is the significance level in a two-tailed t-test.

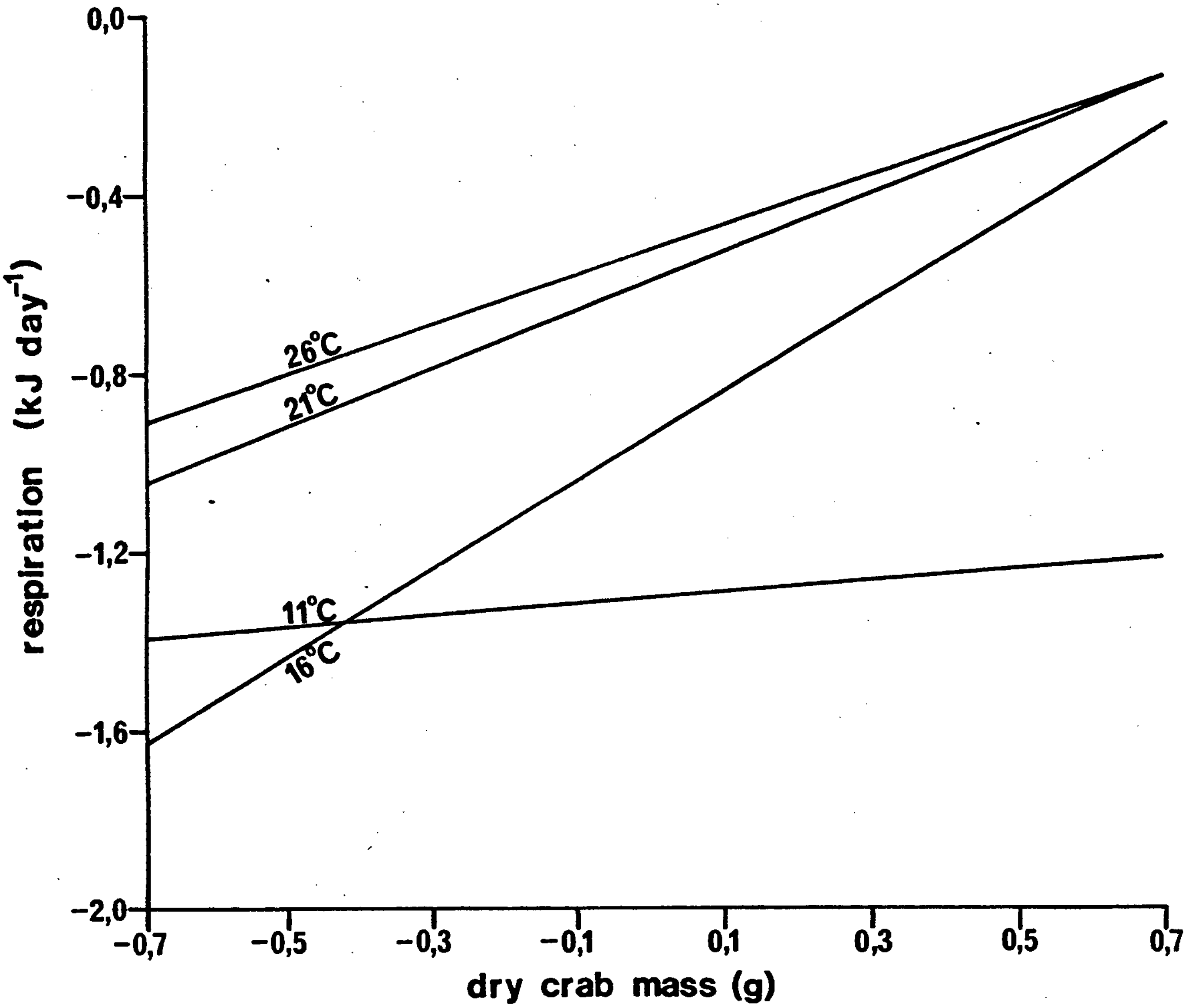
Temp C°	n	logα	β	±Syx	t	P	r
a)			Plagusia				
11°	7	-0,968	1,190	0,120	4,035	0,01	0,87
16°	8	-0,388	0,753	0,050	8,161	0,001	0,96
21°	8	-0,345	0,715	0,084	2,727	0,05	0,74
26°	8	-0,333	0,695	0,061	5,809	0,001	0,92
b)			Hymenosoma				
11°	10	-0,737	0,600	0,440	1,170	N.S.	0,38
16°	12	-0,639	0,921	0,202	2,666	0,05	0,64
21°	10	-0,548	0,488	0,219	2,329	0,05	0,64
26°	6	-0,500	0,475	0,141	1,641	0,20	0,63
c)			Cyclograpsus				
11°	9	-1,307	0,130	0,310	0,289	N.S.	0,11
16°	12	-0,941	0,995	0,155	8,226	0,001	0,93
21°	9	-0,598	0,652	0,091	4,212	0,005	0,85
26°	10	-0,525	0,558	0,173	2,216	≤0,05	0,62
d)			Cyclograpsus (Air)				
11°	10	-2,942	0,891	0,186	3,400	0,01	0,77
16°	7	-2,848	0,388	0,254	1,152	N.S.	0,46
21°	8	-2,771	0,660	0,074	4,921	0,002	0,90
26°	12	-2,675	0,071	0,208	0,234	N.S.	0,07



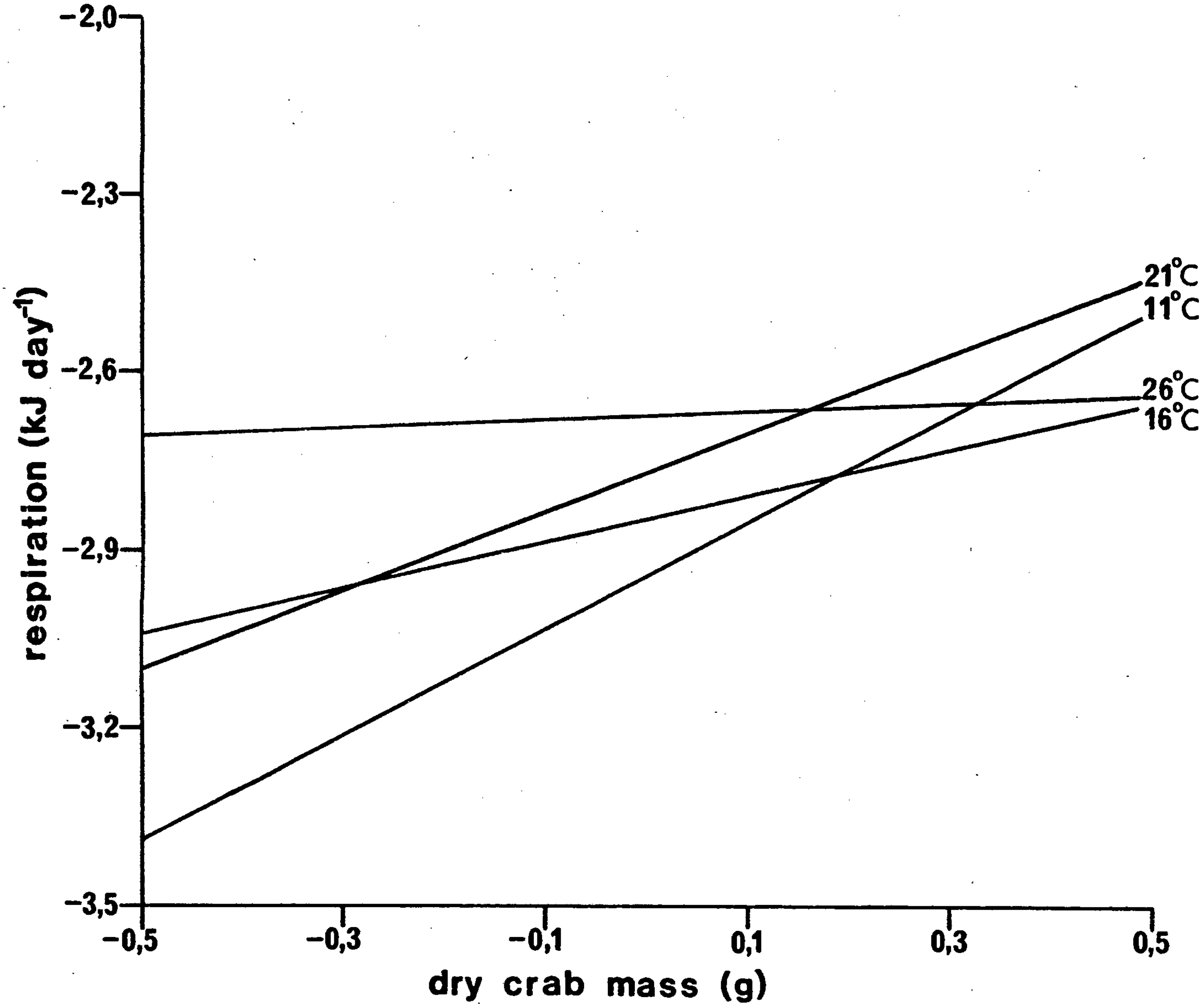
Graph 1a The logarithmic relationship between crab dry mass (g) and respiration (kJ day^{-1}) for Plagusia at four temperatures.



Graph 1b The logarithmic relationship between crab dry mass (g) and respiration (kJ day^{-1}) for Hymenosoma at four temperatures.



Graph 1c The logarithmic relationship between crab dry mass (g) and respiration (kJ day^{-1}) for Cyclograpsus at four temperatures.



Graph 1d The logarithmic relationship between crab dry mass (g) against respiration in air (kJ day^{-1}) for *Cyclograpsus* at four temperatures.

TABLE II Results of ANOCOVA test between the logarithmic regression lines obtained for crab dry mass (g) against respiration (kJ day^{-1}). ($p > 0,05$) F_s - F-test between the slopes F_e - F-test between the elevations

Plagusia

▨	11°	16°	21°	26°
11°	▨	Not Sig	Not Sig	Not Sig
16°	Not Sig	▨	Not Sig	Not Sig
21°	Not Sig	Not Sig	▨	Not Sig
26°	Not Sig	Not Sig	Not Sig	▨

Hymenosoma

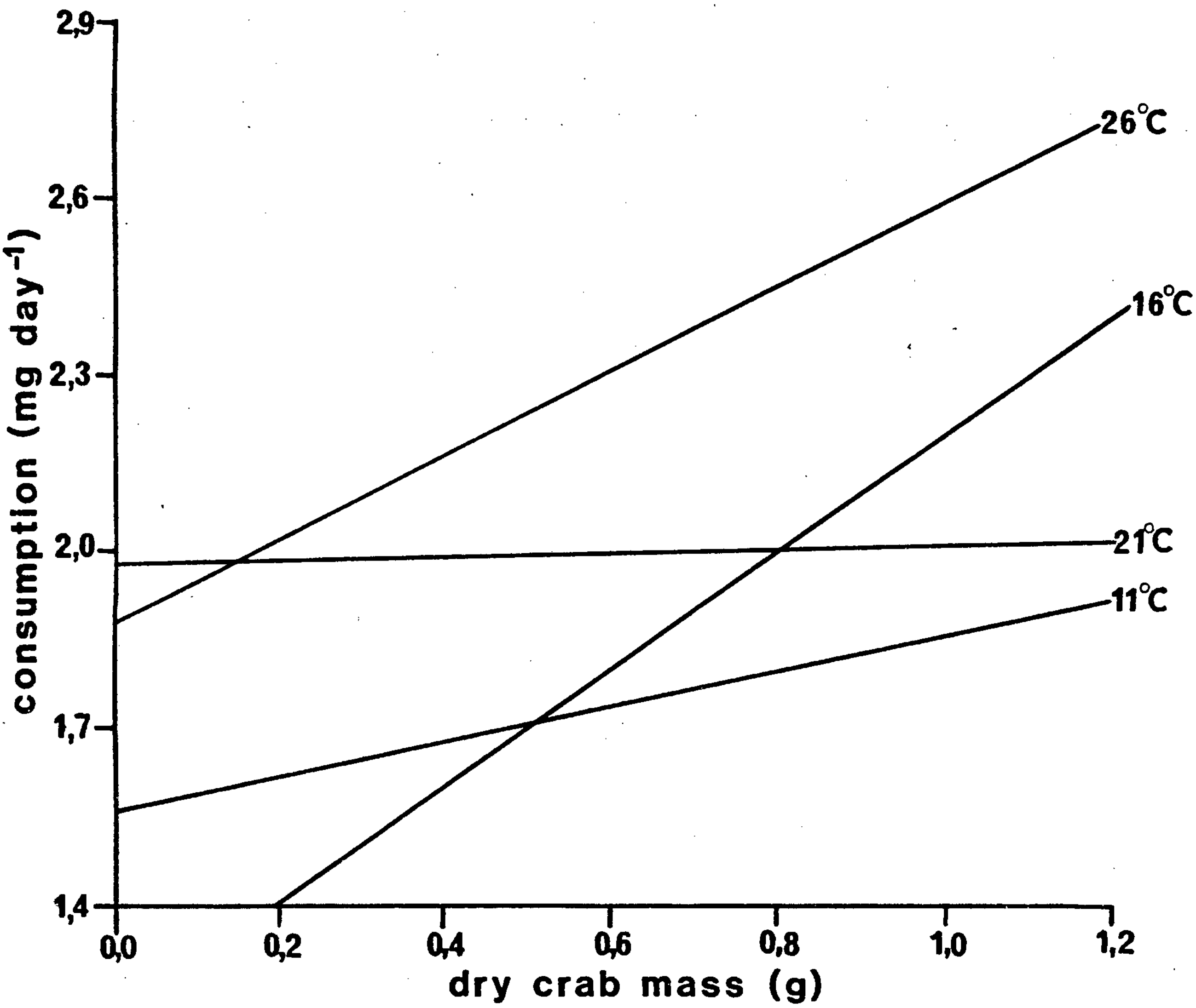
Cyclograpsus (Water)

▨	11°	16°	21°	26°
11°	▨	Not Sig	Not Sig	F_e=6,918 Sig
16°	Graph Not Sig	▨	Not Sig	Not Sig
21°	Graph Not Sig	F_e=22,228 $\gg$ Sig	▨	Not Sig
26°	Graph Not Sig	F_e=15,521 $\gg$ Sig	Not Sig	▨

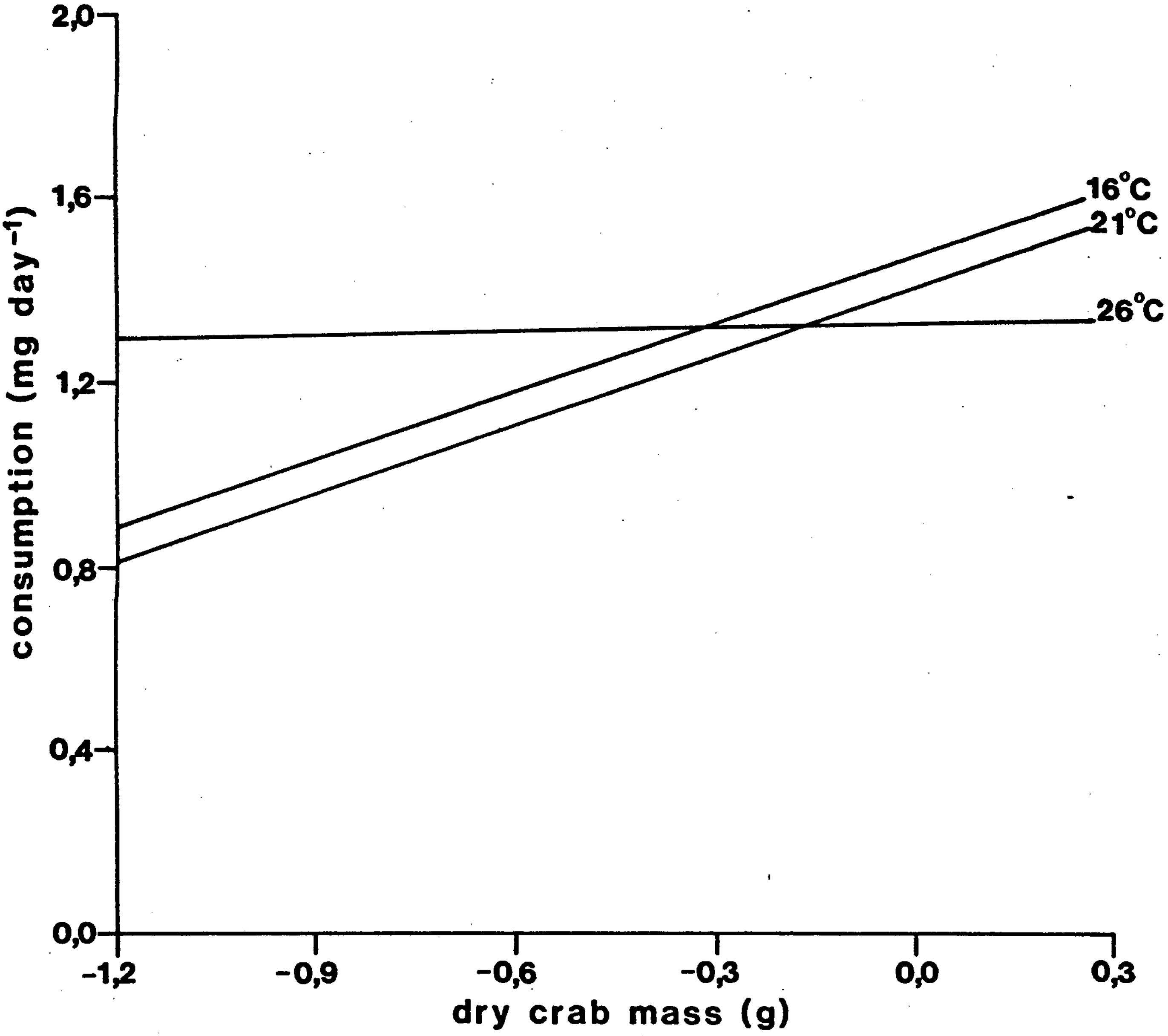
Cyclograpsus (Air)

TABLE III Parameters of the logarithmic regression equations obtained for crab dry mass (g) against food consumed (mg day^{-1}). Log C = log α′+ β′ log W; Syx is the standard error of the estimate; r is the correlation coefficient; P is the significance level in a two-tailed hypothesis.

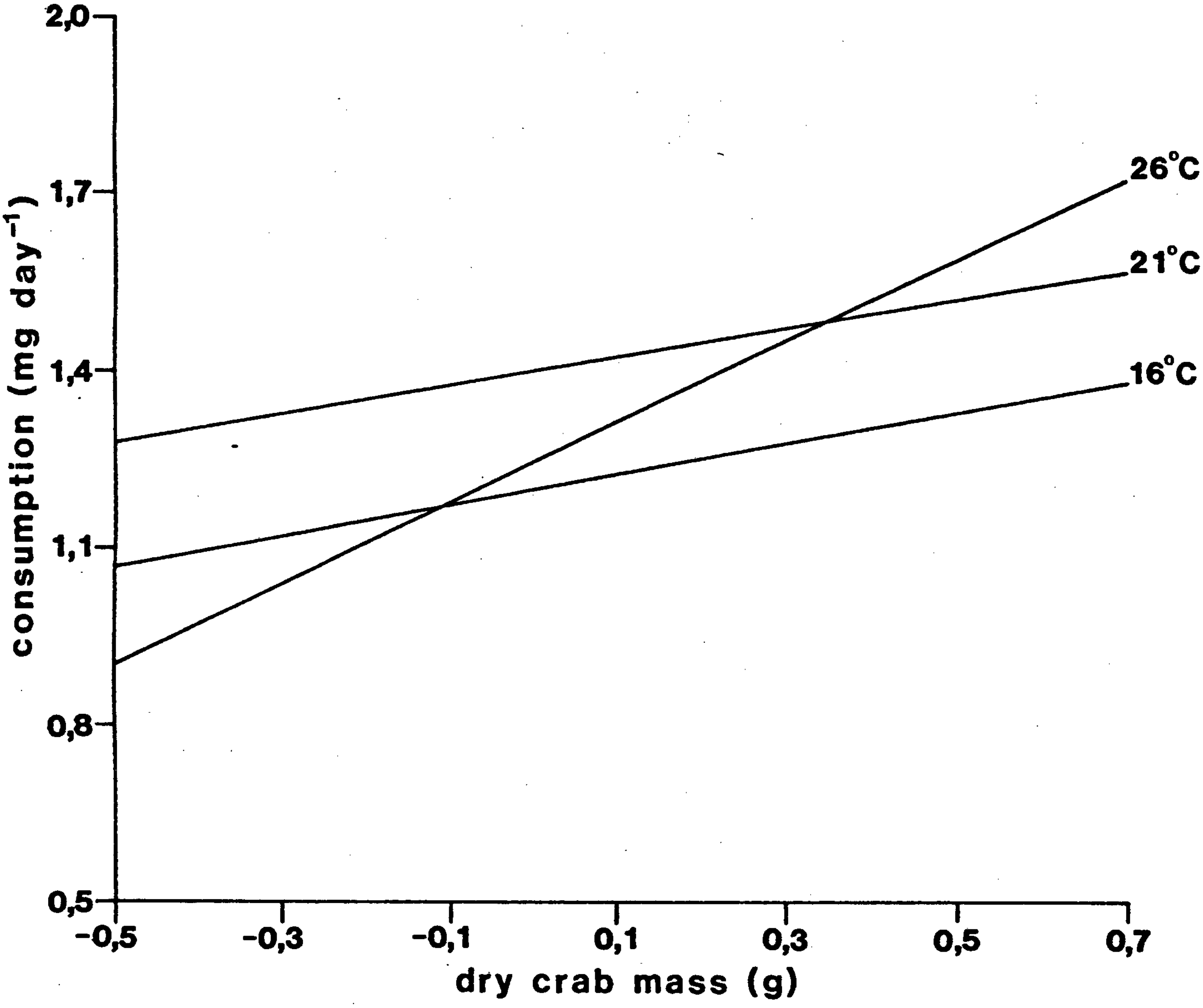
Temp C°	n	log α′	β′	± Syx	t	P	r
a)				Plagusia			
11°	7	1,558	0,305	0,199	1,126	N.S.	0,45
16°	7	1,207	0,999	0,239	2,137	0,10	0,69
21°	5	1,975	0,039	0,299	0,081	N.S.	0,05
26°	7	1,876	0,725	0,165	2,522	0,05	0,75
b)				Hymenosoma			
11°	13	No log graph					
16°	13	1,475	0,493	0,184	2,788	0,02	0,64
21°	13	1,407	0,498	0,308	2,443	0,05	0,59
26°	11	1,325	0,027	0,172	0,201	N.S.	0,07
c)				Cyclograpsus			
11°	13	No log graph					
16°	12	1,197	0,262	0,242	1,217	N.S.	0,36
21°	13	1,397	0,242	0,401	0,431	N.S.	0,13
26°	13	1,242	0,683	0,219	3,058	0,01	0,68



Graph 2a The logarithmic relationship between crab dry mass (g) and food consumption (mg day^{-1}) for Plagusia at four temperatures.



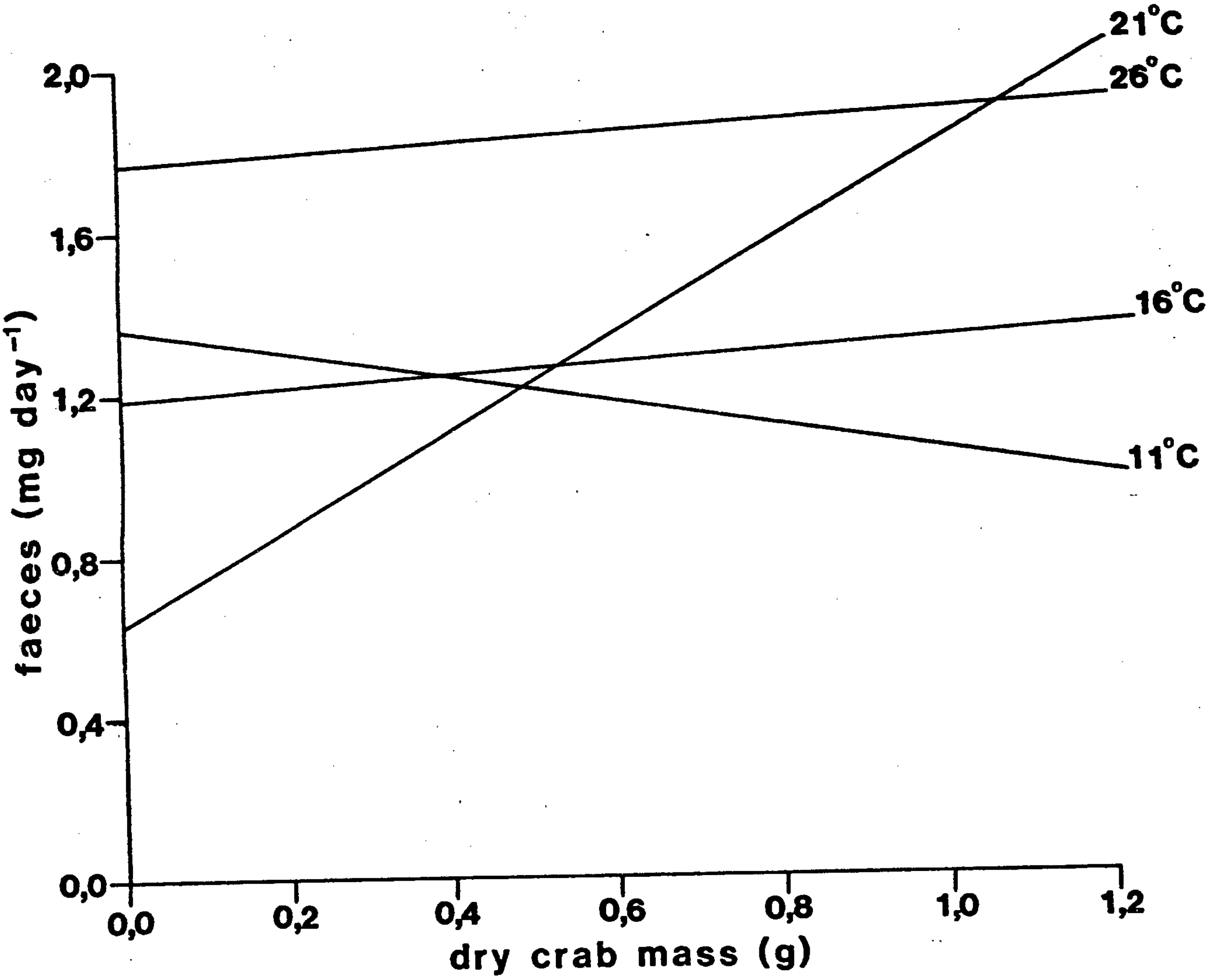
Graph 2b The logarithmic relationship between crab dry mass (g) and food consumption (mg day^{-1}) for Hymenosoma at three temperatures.



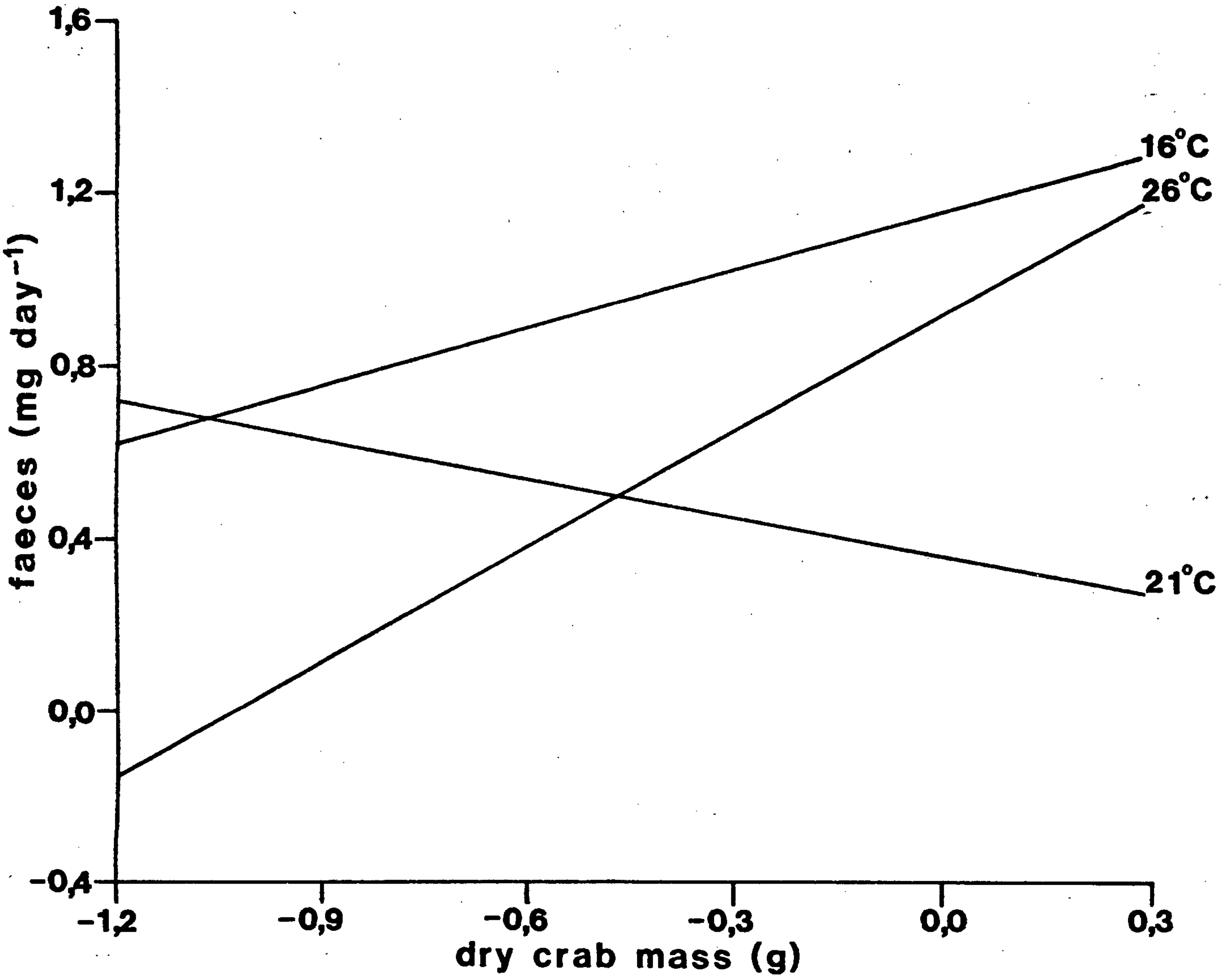
Graph 2c The logarithmic relationship between crab dry mass (g) and food consumption (mg day^{-1}) for Cyclograpsus at three temperatures.

TABLE IV Parameters of the logarithmic regression equations for crab dry mass (g) against faeces produced (mg day^{-1}). Syx is the standard error of the estimate; r is the correlation coefficient; P is the significance level in a two-tailed hypothesis; $\log F = \log \alpha' + \beta' \log W$.

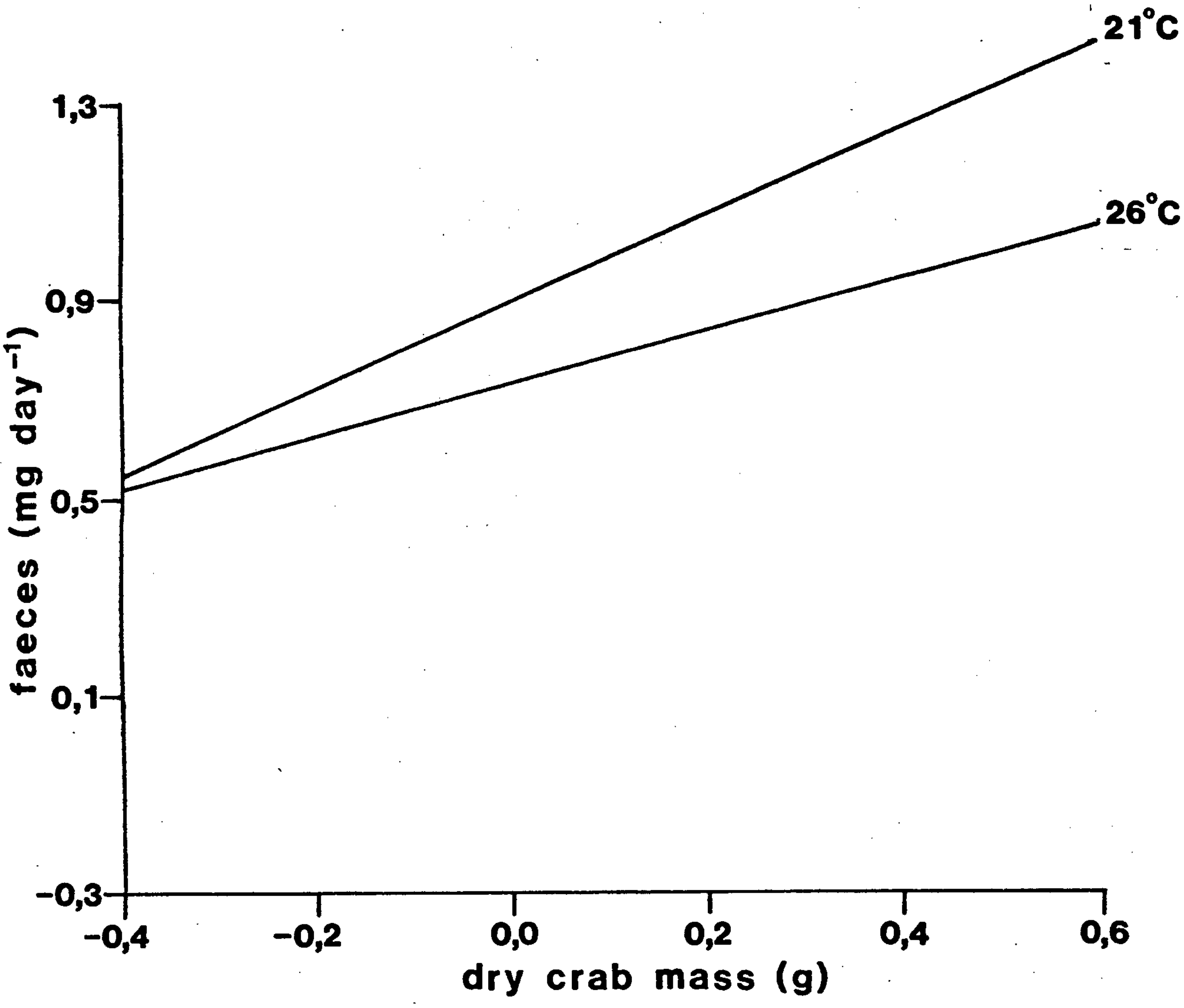
Temp C°	n	$\log \alpha'$	β'	Syx	t	P	r
a)			Plagusia				
11°	7	1,318	-0,309	0,251	-0,901	N.S.	-0,37
16°	7	1,281	0,137	0,337	0,208	N.S.	0,09
21°	5	0,695	1,179	0,416	1,763	0,20	0,71
26°	7	- 1,767	0,120	0,265	0,259	N.S.	0,11
b)			Hymenosoma				
11°	13	No log graph					
16°	13	1,160	0,451	0,316	1,487	0,20	0,41
21°	12	-0,294	0,365	0,300	-1,351	$\leqslant$0,20	-0,39
26°	11	0,921	0,895	0,258	4,448	0,002	0,84
c)			Cyclograpsus				
11°	13	No log graph					
16°	7	0,337	-0,001	0,119	-0,002	N.S.	-0,00
21°	13	0,898	0,885	0,475	1,328	N.S.	0,37
26°	13	0,734	0,539	0,351	1,505	0,20	0,41



Graph 3a The logarithmic relationship between crab dry mass (g) and faecal production (mg day^{-1}) for Plagusia at four temperatures.



Graph 3b The logarithmic relationship between crab dry mass (g) and faecal production (mg day^{-1}) for Hymenosoma at three temperatures.



Graph 3c The logarithmic relationship between crab dry mass (g) and faecal production (mg day^{-1}) for Cyclograpsus at 21°C and 26°C.

TABLE V Results of ANOCOVA test between the logarithmic regression lines obtained for crab dry mass (g) and food consumption (mg day^{-1}) and faeces produced (mg day^{-1}). $(p > 0,05)$ F_s-test between slopes. F_e-test between elevations.

a <u>Plagusia</u>

	▨	11°	16°	21°	26°	
	11°	▨	Not Sig	Not Sig	$F_e=23,360$ $\gg$Sig	Faeces
Food	16°	Not Sig	▨	Not Sig	$F_e=6,176$ $\leqslant$Sig	
	21°	Not Sig	Not Sig	▨	Not Sig	
	26°	$F_e=30,281$ $\gg$Sig	$F_e=11,728$ Sig	Not Sig	▨	

b Hymenosoma

	▨	11°	16°	21°	26°	
	11°	▨	No log Graph	—	—	
Food	16°	No log Graph	▨	F_e=18,359 $\gg$ Sig	F_e=7,216 Sig	Faeces
	21°	—	Not Sig	▨	F_e=16,130 $>$ Sig	
	26°	—	Not Sig	Not Sig	▨	

c Cyclograpsus

	▨	11°	16°	21°	26°	
	11°	▨	No log Graph	—	—	
Food	16°	No log Graph	▨	F_e=5,715 $\leqslant$ Sig	F_e=6,773 Sig	Faeces
	21°	—	Not Sig	▨	Not Sig	
	26°	—	Not Sig	Not Sig	▨	

8.2 Recommendations for Further Study

1. Egg and larval development of each crab species should be studied over a range of temperatures. Development of eggs must be studied with regard, not only to the developmental time, but also egg volume and numbers.

   A shortened larval developmental rate, together with maximum percentage survival, will indicate the optimum temperature for propogation of the species.

2. The experiments carried out in this study should be repeated with larvae and smaller sized crabs to cover the complete size range of animals likely to experience the heated effluent. Energetic efficiencies should also be evaluated at each temperature.

3. Acclimation time varies between species and it may take up to a number of weeks before a particular species becomes fully acclimated. The crabs used in this study may have required a longer acclimation period than 10 days, hence the increase in rates with increase in temperatures. In order to verify if the rates measured in this study were acute rates or acclimated rates, a number of experiments to determine the acute rates could be carried out, after acclimation at certain temperatures for a few weeks.

4. Monthly samples of crabs from the field could be examined for a minimum period of 12 months to establish reproductive cycles as Broekhuysen (1941) did with C. punctatus. This will determine the number of egg batches likely to be produced per annum and thus the energy requirement for reproduction.