AUSTRALIAN MUSEUM MEMOIR 18

Papers from the Conference on the Biology and Evolution of Crustacea

HELD AT THE AUSTRALIAN MUSEUM
SYDNEY, 1980

Edited by

JAMES K. LOWRY

The Australian Museum, Sydney

Published by order of the
Trustees of the Australian Museum

Sydney, New South Wales, Australia
1983

Manuscripts accepted for publication 1 April, 1982

STRATEGIES OF CRUSTACEAN GROWTH

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SUMMARY

The various species of Crustacea display great differences in maximum size, and the means by which this is delimited have been investigated. Two distinct strategies of growth exist. Some species have indeterminate growth and continue moulting indefinitely. In these the percentage moult increment declines and the intermoult period increases with size, thereby limiting growth: the respective rates of decline and increase determine the final size. Others have determinate growth and eventually cease moulting, usually at the time of maturity: this termination of moulting stops growth, and in such species the percentage moult increment does not decline appreciably with size. The advantages and disadvantages of the two strategies of growth are discussed.

Introduction

There is great variation in maximum size both within the Crustacea as a whole, and within restricted taxa of the class. Thus within the Crustacea there is a range from small copepods with a length of the order of a millimetre to the giant Japanese spider crab *Macrocheira,* with a carapace length of 400 mm and a chelar span of nearly 4 m. Within the Brachyura sizes range from *Macrocheira* down to the ectocommensal *Dissodactylus* with a carapace length of 3 to 4 mm, or the males of some Hapalocarcinidae with a carapace length of only 1 mm. Within the Majidae there is a range from *Macrocheira* to species of *Eurynome, Pelia* and *Thoe* with carapace lengths of 10 to 12 mm. There is also variation in the relationship between maximum size and the size at sexual maturity. Some species become sexually mature and then continue moulting (and growing) for prolonged or indefinite periods afterwards. Others cease moulting and growth at the time when sexual maturity is achieved.

Clearly the Crustacea employ diverse strategies of growth, and two questions can be asked in relation to this diversity:

1. How are the strategies effected? What are the patterns of growth which produce the desired end results?
2. Why do the various strategies exist? What are the selective advantages of one strategy over another?

This paper is mainly directed towards answering the first of these questions, and consists essentially of an analysis of the patterns of growth. At the present it is not possible to say much concerning the more fundamental subject of the physiological mechanisms which underlie these patterns. The second of the questions is dealt with only briefly. As necessary prerequisites some further detail must first be provided on the form of growth, and on the components of which growth is composed.

The pattern of growth

Although tissue growth is essentially a continuous process in Crustacea, the accompanying increase in external dimensions is discontinuous. This proceeds by a series of moults or ecdyses, when the old integument is cast off and a rapid increase in size occurs before the new integument hardens and becomes inextensible. These moults are separated by intermoults, periods when the integument is hard and no external growth occurs. During periods of growth the intermoults are relatively short, and are termed diecdyses. Between two growing seasons there is a prolonged intermoult known as an anecdysis. If moulting ceases altogether the condition is a terminal anecdysis. There are three main variables in the pattern of crustacean growth:

1. Is moulting continued indefinitely, or is there a terminal anecdysis?
2. If there is a terminal anecdysis, is the onset of sexual maturity before or after the start of the terminal anecdysis?
3. In the event of a terminal anecdysis is it preceded by a fixed or variable number of instars?

Given these variables, then the following hierarchy of patterns becomes possible. Examples are given for those patterns which are known to exist.

- Indeterminate growth, no terminal anecdysis (*Daphnia, Balanus, Homarus*)
- Determinate growth, with terminal anecdysis
  - Maturity before final moult
    - Instar number variable (*Carcinus, Portunus*)
    - Instar number fixed
  - Maturity after final moult
    - Instar number variable (*Corystes, Maja*)
    - Instar number fixed (Ostracoda, Copepoda)

There is no clear relation between taxonomic groups and growth pattern: both determinate and indeterminate growth occur in a wide range of primitive and advanced taxa, and both can occur within the same small taxon. If indeterminate growth is primitive, as seems likely, then determinate growth must have evolved independently on a number of occasions.

The components of growth

The growth rate in Crustacea results from the interaction of the two variable components of growth. One is the interval separating successive moults—the intermoult period. This can vary from less than a day in the early instars of the ostracod *Cyprinotus* (Kurata, 1962) to two to three years in mature females of large decapods such as *Cancer* (Pearson, 1908). The period is markedly affected by extrinsic factors, notably temperature and food supply, but in the present context it is the influence of intrinsic factors that is more relevant. In general the intermoult period becomes longer with increasing size, and the duration may be further extended by sexual maturity: this intrinsic variation will be analysed in detail in later sections.

The second component is the increase in size that occurs at a moult—the moult increment. This may be expressed in absolute or relative terms, and the most convenient is to present it as a percentage of the pre-moult dimension. It varies from as much as 83% in *Daphnia* (Green, 1956) to as little as zero at the moult preceding laying in some female decapods (Mauchline, 1977). Within a species the percentage moult increment usually decreases with increasing size.

In the two following sections the interaction of intermoult period and moult increment will be analysed to see how growth is regulated. This will be done first for Crustacea showing indeterminate growth, and secondly for those with determinate growth.

Regulation of indeterminate growth

The fact that growth is indeterminate in many Crustacea, in the sense that moulting does not stop, does not mean that size is unrestricted. Far from it. The changes in intermoult period and moult increment with size interact to set an upper limit which will not be appreciably exceeded in practice. However the nature of this interaction differs markedly from species to species, and so very different maximum sizes are attained. Thus indeterminate species range from *Daphnia* spp with maximum lengths of 2.5 mm (Anderson, 1932; Green, 1956) to *Homarus americanus* which exceeds 900 mm (Wilder, 1957). Exactly how is this brought about?

The intermoult period tends to increase with size, this being a very consistent phenomenon throughout the Crustacea (Hartnoll, 1982) with only a few exceptions. Several proposals have been put forward to describe the relationship of intermoult duration to size, namely the linear regressions of:

1. Intermoult period on length (Mauchline, 1977)
2. Intermoult period on length^3 (Kurata, 1962)
3. Log intermoult period on $\sqrt[3]{\text{weight}}$ (Hewett, 1974) or, much the same, log intermoult period on length (Mauchline, 1976, 1977).

There is no *a priori* reason to favour any particular regression, so the one which provides the best fit to a wide range of observations is to be preferred: this is the regression of log intermoult period on length. The slope of this regression for a selection of species is presented in Table 1, and there is great variation. Some have a steep slope which indicates a rapid lengthening of the intermoult as size

Table 1. The slope of the regression of $\log_{10}$ intermoult period (days) on reference length (mm) for various Crustacea with indeterminate growth. In the last column one, two and three asterisks indicate significance at the 5%, 1% and 0.1% levels respectively.

Species	Source	Reference dimension	Maximum size	Slope and significance
Porcellio scaber Latreille	Kurata, 1962	Head width	2 mm	0.41***
Daphnia longispina Müller	Ingle *et al.*, 1937	Total length	3 mm	0.22***
Daphnia carinata King	Navaneethakrishnan & Michael, 1971	Total length	4 mm	0.27**
Metamysidopsis elongata (Holmes)	Clutter & Theilacker, 1971	Total length	7 mm	0.085***
Rhithropanopeus harrisii (Gould)	Hartnoll, 1978	Carapace width	10 mm	0.25***
Cyclograpsus punctatus Milne-Ed.	Broekhuysen, 1941	Carapace width	25 mm	0.036***
Hemigrapsus sanguineus (de Haan)	Kurata, 1962	Carapace width	26 mm	0.025***
Crangon crangon (L.)	Meixner, 1969	Total length	55 mm	0.011***
Jasus lalandei (H. Milne Edw.)	Fielder, 1964	Carapace length	90 mm	0.007*
Panulirus argus (Latreille)	Travis, 1954	Carapace length	90 mm	0.004***
Cancer anthonyi Rathbun	Anderson & Ford, 1976	Carapace width	110 mm	0.023***
Homarus americanus Milne Edw.	Templeman, 1948	Carapace length	130 mm	0.013***

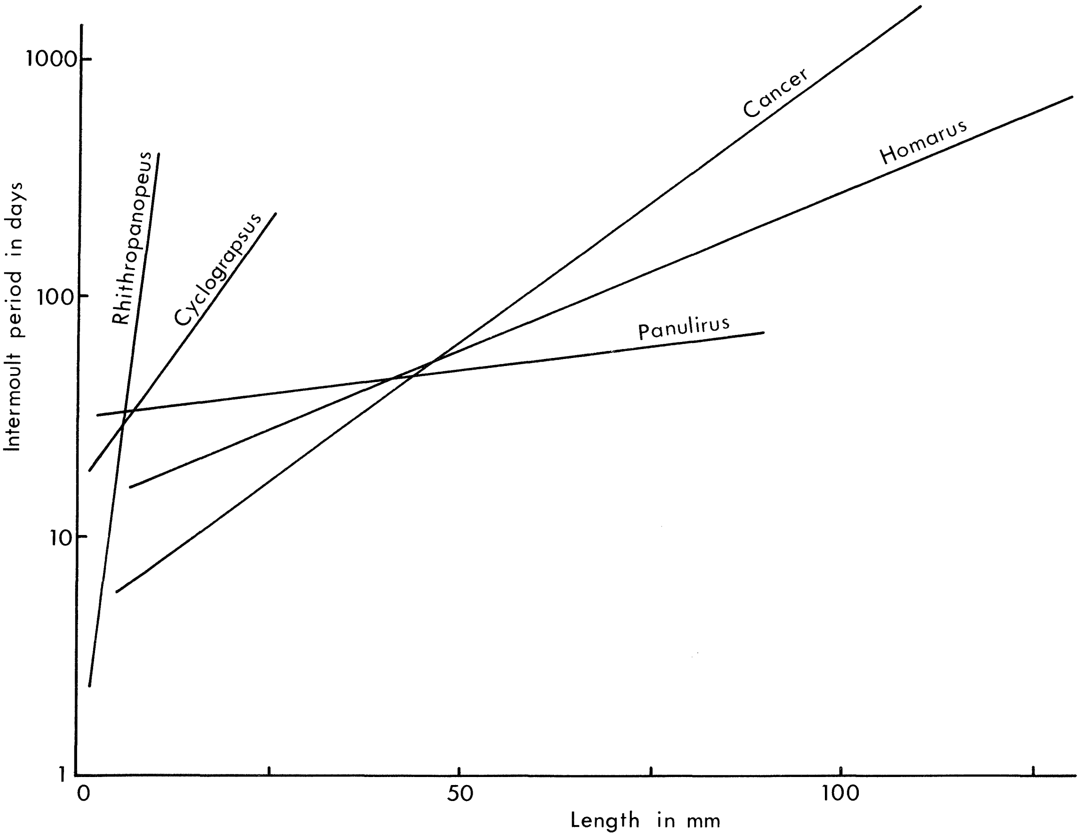

Fig. 1. The regressions of log intermoult period on carapace size for *Rhithropanopeus harrisii, Cyclograpsus punctatus, Cancer anthonyi, Homarus americanus* and *Panulirus argus.* Sources of data in Table 1.

Table 2. The slope of the regression of $\log_{10}$ percentage moult increment on reference length (mm) for various Crustacea with indeterminate growth.

Species	Source	Reference dimension	Maximum size	Slope and significance
Porcellio scaber	Kurata, 1962	Head width	2 mm	−0.37***
Daphnia pulex (de Geer)	Anderson *et al.*, 1937	Total length	2 mm	−1.72***
Gastrosaccus vulgaris Nakazawa	Matsudaira *et al.*, 1952	Carapace length	5 mm	−0.18***
Rhithropanopeus harrisii	Hartnoll, 1978	Carapace width	10 mm	−0.14**
Hymenosoma orbiculare Desm.	Broekhuysen, 1955	Carapace width	25 mm	−0.026*
Pachygrapsus crassipes Randall	Mauchline, 1976	Carapace width	38 mm	−0.019***
Crangon crangon	Lloyd & Yonge, 1947	Total length	68 mm	−0.019***
Panulirus homarus (L.)	Mauchline, 1977	Carapace length	94 mm	−0.014***
Jasus lalandei	Newman & Pollock, 1974	Carapace length	105 mm	−0.004***
Homarus americanus	Templeman, 1948	Carapace length	130 mm	−0.005***
Cancer pagurus L.	Mauchline, 1977	Carapace width	150 mm	−0.002***
Cancer magister Dana	Poole, 1967	Carapace width	190 mm	−0.002***

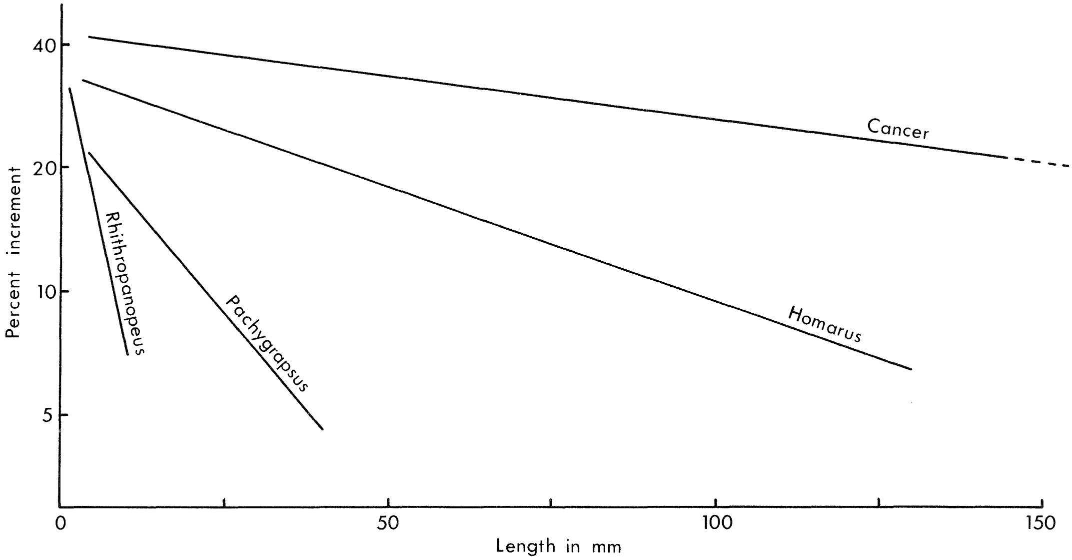

Fig. 2. The regressions of log percentage moult increment on carapace size for *Rhithropanopeus harrisii, Pachygrapsus crassipes, Homarus americanus* and *Cancer magister.*

increases, others a gentle slope. Small species (in terms of the reference dimension) generally have steep slopes, large species gentle ones (Fig. 1).

The percentage moult increment tends to decrease with size, and although not as universal a trend as the increase in intermoult period, this is the prevalent condition (Hartnoll, 1982). Since first pointed out by Olmstead & Baumberger (1923) it has been observed in many species from all crustacean groups. Various approaches have been adopted to try and quantify the relationship of moult increment to size. One was to plot post-moult against pre-moult size (Hiatt, 1948; Kurata, 1962) to produce a 'Hiatt growth diagram': when a linear relationship exists it is expressed by the equation:

$$L = a_{n+1} + b.L._n$$

b is known as the growth coefficient, but it is not easily interpreted. Also the method is unsatisfactory in that L_n is contained within L_{n+1}, making a degree of correlation inevitable. A more rigorous approach is to examine the relationship between percentage moult increment and pre-moult length

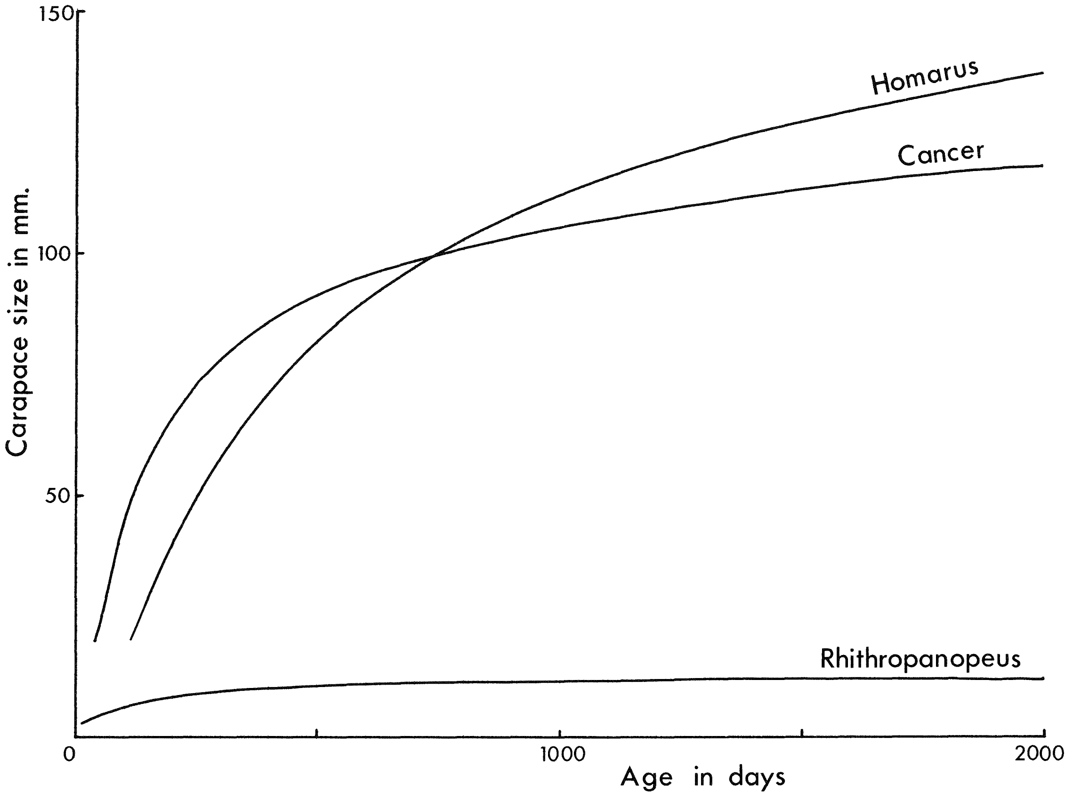

Fig. 3. Growth curves for *Homarus americanus, Cancer anthonyi* and *Rhithropanopeus harrisii* generated from the regressions of log intermoult period and log per cent increment on carapace size.

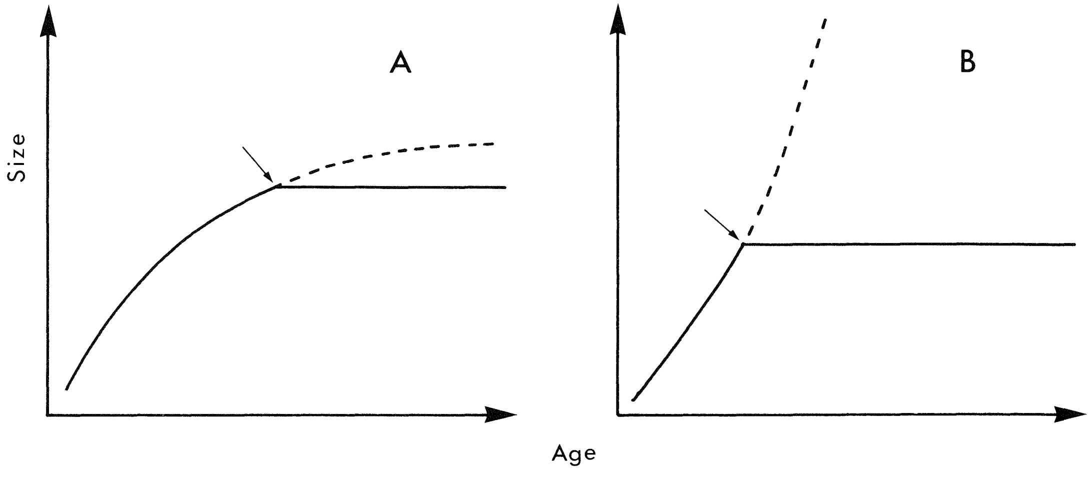

Fig. 4. Two possible formats for Crustacea with definitive growth, showing actual (solid line), and potential growth (broken line) if the terminal anecdysis did not occur. The start of the terminal anecdysis is arrowed.

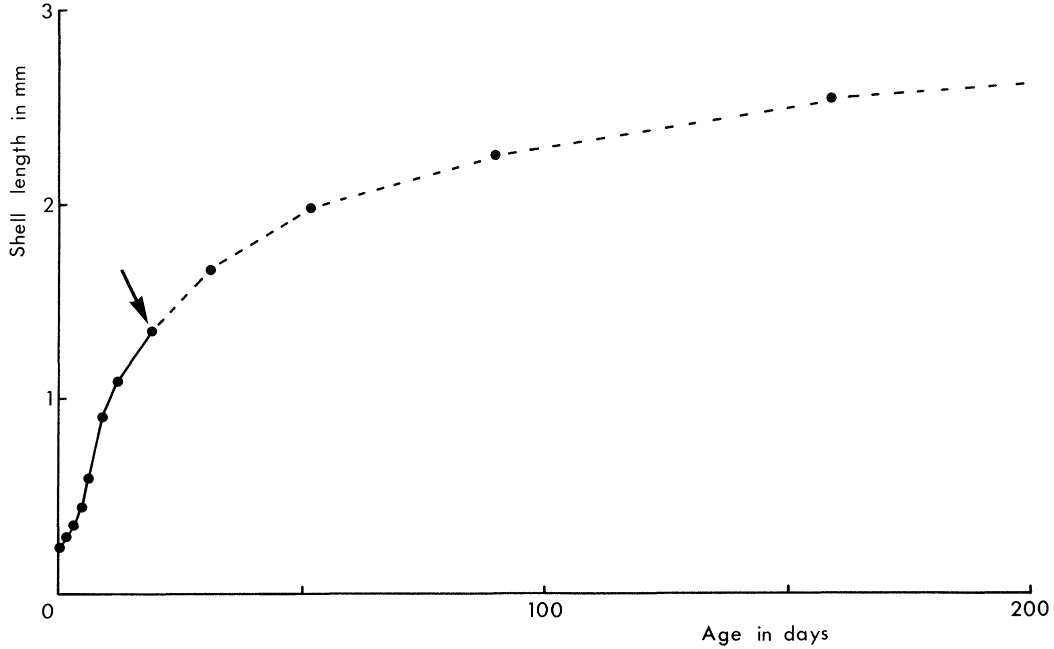

Fig. 5. Actual (solid line) and extrapolated (broken line) growth of *Cyprinotus* sp. at 21°C: the eighth and final instar is arrowed. Data from Kurata (1962).

(Mauchline, 1976), best expressed as the linear regression of log percent increment on pre-moult length (Mauchline, 1977). The slopes of this regression for a series of species with indeterminate growth are listed in Table 2, and several species compared in Fig. 2. The regression has a negative slope, since increment decreases with size. As in the case of intermoult period, small species tend to have a steep slope and large species a gentle one.

It is apparent that in species with indeterminate growth there is a measure of correlation between the slopes of intermoult period and moult increment on size: for a given species both slopes tend to be either steep or gentle (or intermediate). In the former event intermoult period will increase and moult increment decrease rapidly with size, so that however long the species lives it can never reach a very large size. On the other hand, if both slopes are gentle, then growth will continue at an appreciable rate, permitting a large maximum to be attained. Thus in twenty moults from hatching *Porcellio scaber* reaches a body length of 11 mm, compared with 180 mm for *Homarus americanus* after the same number of moults. If the regressions for both log intermoult period and log per cent increment on size are available they can be used to generate growth curves. These are highly simplified in that they ignore seasonal influences and the effects of sexual maturity, but they are adequate to indicate the maximum size attainable. Such curves have been produced for one small and two large species (Fig. 3). Despite the simplifications the indicated maximum sizes are well in agreement with those which occur.

Thus in crustacean species with indeterminate growth the regulation of size is brought about through the mediation of both components of growth. These are regulated in such a way as to set a size limit beyond which the species is effectively unable to grow, irrespective of how long it survives. These growth tendencies are identifiable even in the early post-larval instars, and regressions calculated from such instars can, when extrapolated, give acceptable estimates of maximum size (Hartnoll, 1978).

Regulation of determinate growth

In determinate species, which eventually cease moulting after either a fixed or variable number of moults, the limitation of growth appears extremely simple at first sight: a series of moults occur until the required size is attained, whereupon moulting and growth stop. There is, however, considerable

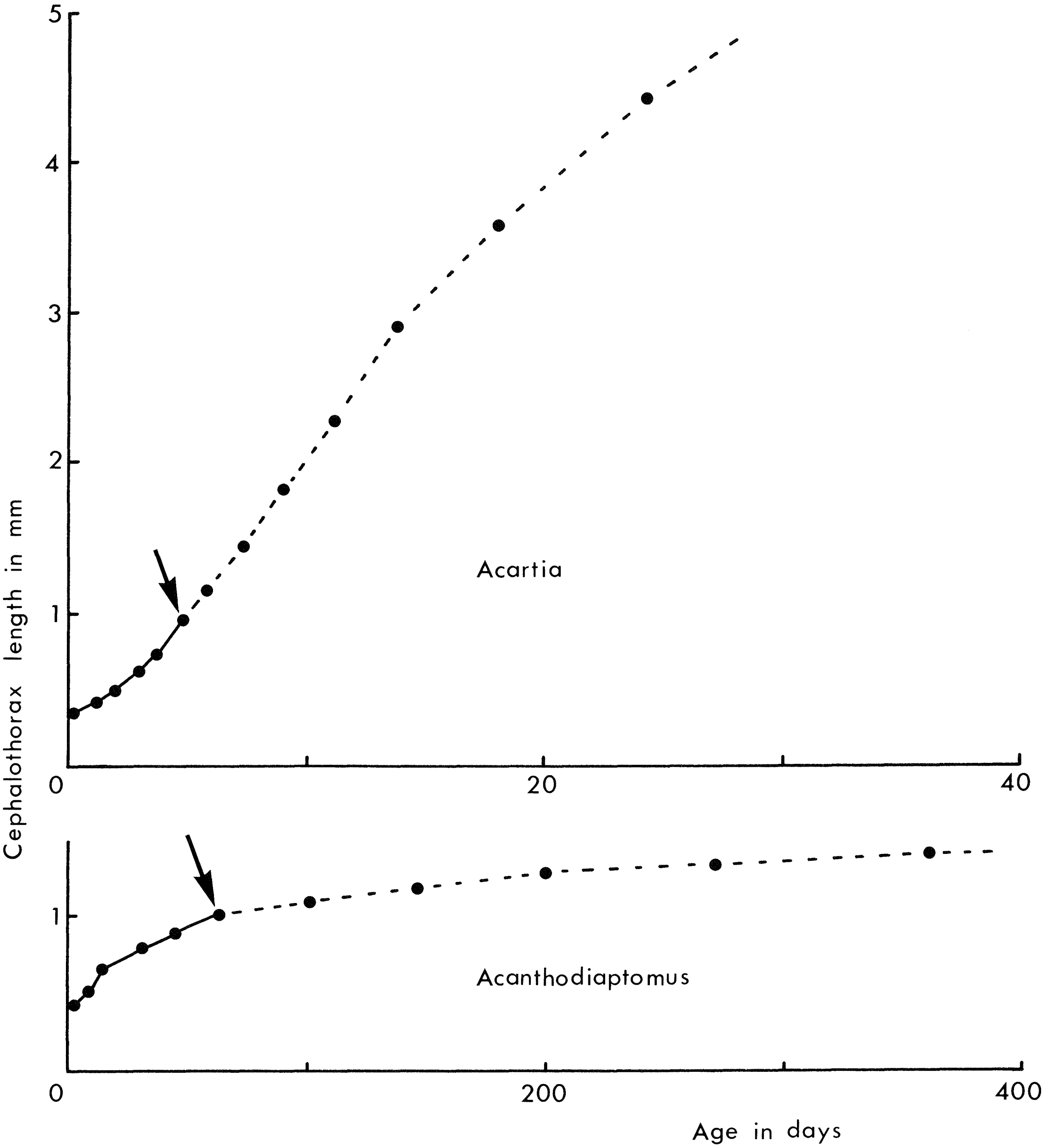

Fig. 6. Actual (solid lines) and extrapolated (broken line) growth for *Acartica tonsa* (data from Miller *et al.*, 1977) and *Acanthodiaptomus denticornis* (data from Ivanova, 1973). Final instar arrowed.

variation in the pattern of growth which precedes the terminal moult, and this deserves closer examination. Do the components of growth respond to increasing size in a similar way to that seen in indeterminate species, or are they freed from such restraints, and does the limitation of size depend entirely upon the terminal anecdysis? The two possible situations are shown in Fig. 4. The pattern of growth in Fig. 4A is similar to that already observed in indeterminate species, and the intervention of the terminal anecdysis causes only a modest truncation of the potential growth. That shown in Fig. 4B is unrestricted, and the terminal anecdysis is the important limiting factor. The pattern of determinate growth will be examined in Ostracoda, Copepoda and certain Brachyura, to see how it relates to the two alternatives.

Table 3. The slopes of the regressions of $\log_{10}$ percentage moult increment and $\log_{10}$ intermoult period (days) on carapace size (mm) for several crabs with determinate growth.

Species	Source	Maximum size	Slope and significance
Increment			
Pisa tetraodon (Pennant)	Vernet-Cornubert, 1960	45 mm	- 0.002 ns
Carcinus mediterraneus Czerniavsky	Veillet, 1945	50 mm	- 0.003***
Carcinus maenas (L.)	Crothers, 1967	50 mm	♂ - 0.003 ns ♀ - 0.005**
Callinectes sapidus Rathbun	Tagatz, 1968	140 mm	♂ - 0.0004 ns ♀ 0.0011***
Intermoult period			
Pisa tetraodon	Vernet-Cornubert, 1960	45 mm	0.010*
Carcinus maenas	Meek, 1918	70 mm	0.020***
Callinectes sapidus	Tagatz, 1968	140 mm	0.005***

Cyprinotus sp. is an ostracod with a fixed number of eight instars (Kurata, 1962). The intermoult period lengthens sharply with size, the regression of log period on body length having a slope of 0.76 to 1.14 depending upon temperature: a comparison with Table 1 shows this slope to be steep. On the other hand the percentage moult increment does not decline consistently with size—it in fact increases for the first five moults, and only declines over the final two. Fig. 5 is an extrapolated curve for growth at 21 °C calculated from the observed relationships of moult increment and intermoult period with size. This indicates a levelling off at about 2.5 mm, compared with an actual length in the terminal instar of 1.35 mm. The terminal anecdysis obviously truncates growth to a degree, though it would apparently cease eventually in any case.

The Copepoda have a fixed sequence of six post-larval instars, but display considerable variation in the pattern of growth. In species such as *Acanthodiaptomus denticornis* (Wierzejski) (Ivanova, 1973) the increment declines and the intermoult lengthens with size, and the extarapolated growth curve (derived similarly to Fig. 5) flattens off in typical fashion (Fig. 6). The potential maximum of 1.5 mm cephalothorax length is not greatly in excess of the actual final instar length of 1.0 mm, and growth is of the pattern depicted in Fig. 4A. In other species such as *Acartia tonsa* Dana the per cent increment and intermoult period both change little with increasing size, giving 'isochronal development' (Miller *et al.,* 1977). The extrapolated growth curve is still rising sharply at 5 mm cephalothorax length (Fig. 6), whilst the length of the final instar is only 0.93 mm: this is a marked truncation of growth by the terminal anecdysis as in Fig. 4B.

In crabs with definitive growth there is a tendency, as in *Acartia,* for the percentage moult increment not to decrease with size. This is true of *Carcinus maenas* (Crothers, 1967; Hogarth, 1975; Meek, 1918; Needham, 1950), *Carcinus mediterraneus* (Veillet, 1945), *Maja squinado* (Carlisle, 1957) and *Pisa tetraodon* (Vernet-Cornubert, 1958). In *Callinectes sapidus* the increment is constant in males, but even increases with size in females (Haefner & Shuster, 1964; Leffler, 1972; Tagatz, 1968). The slopes of the regressions of log percentage moult increment on size are gentle, and sometimes not significant (Table 3), and clearly nowhere near as steep as those of indeterminate species of comparable size (Fig. 7). On the other hand the intermoult period increases with size in the normal way, and the slopes of the regressions of log intermoult period on size (Table 3) are comparable with indeterminate species of similar size. The overall effect is that growth is not as potentially unrestricted as in 'isochronal' copepods, but does eventually level off. In *Callinectes sapidus* the extrapolated curve flattens at a carapace width of about 250 mm, whereas specimens in the final instar may measure only 100 mm (Tagatz, 1968).

So although maximum size in determinate species is controlled by the termination of moulting, there is considerable variation in the extent to which this truncates the potential growth were moulting to continue indefinitely. Where, as in 'isochronal' species, the components of growth change little with size, the truncation of potential growth is extreme. However, this situation is unusual in determinate

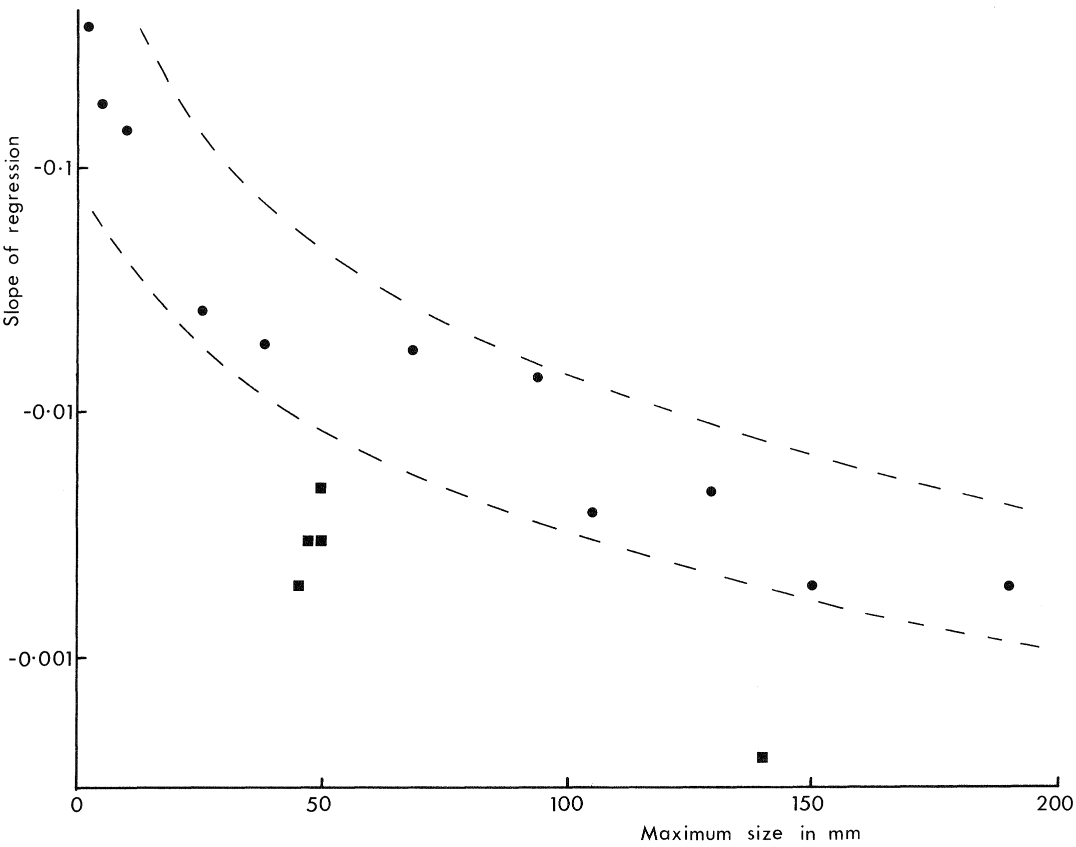

Fig. 7. The log of the slope of the regression of log per cent moult increment on length plotted against maximum size. ●—species with indeterminate growth listed in Table 2. ■—species with determinate growth listed in Table 3.

species, for although the per cent increment tends not to decline with size as it does in indeterminate ones, the intermoult period does lengthen. So the growth curve levels off in due course, and the truncation of growth can be quite modest.

DISCUSSION

It has been shown that there are various patterns of growth in Crustacea which can be responsible for determining the size which a species attains. It must be emphasised that this account has been limited to a description of the patterns of growth as they have been observed, and there has been no attempt to explain the underlying physiological mechanisms. That would be exceedingly difficult. Something is known of the endocrinal control of the terminal anecdysis in crabs (Carlisle, 1957; Hartnoll, 1972), but nothing of that in other determinate Crustacea. Nothing is known of the mechanisms which cause intermoult period and moult increment to change with size.

It remains to consider briefly the adaptive advantage of the alternative strategies of growth which have been described. Assuming that a particular maximal size is optimal for a species which fills a given ecological niche, there are basically two alternative ways by which this size can be assured. One is by indeterminate growth, with the growth rate levelling off in response to changes in the components of growth operative from the early post-larval stages (Fig. 8A). The other is determinate growth, levelling off more slowly, and with growth stopped at a certain size by the cessation of moulting (Fig. 8B). What are the advantages of each strategy?

Indeterminate growth:

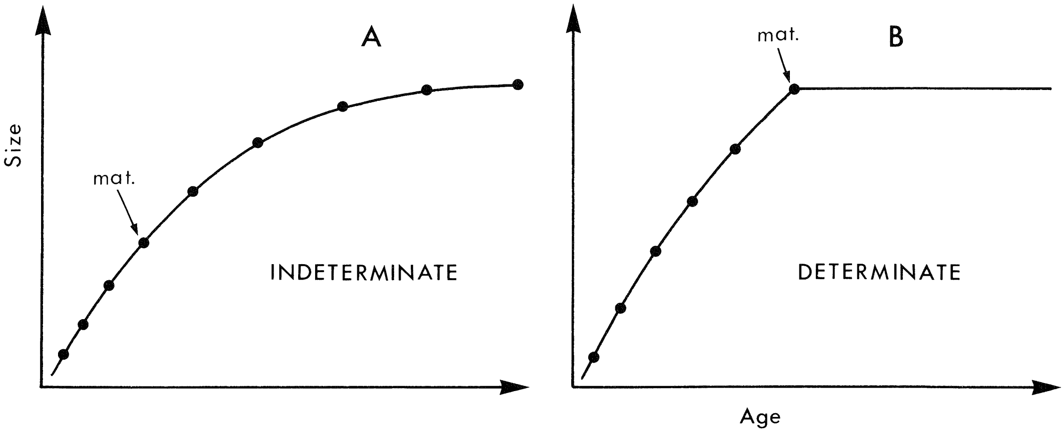

Fig. 8. Growth curves indicating the sequence of instars for species with A, indeterminate, and B, determinate growth. Onset of maturity arrowed.

1. Sexual maturity is early, so there is an ability to reproduce even if mortality occurs before full size is reached.
2. The mature phase is prolonged by post-pubertal moulting, which allows the repair of damage, regeneration of appendages and elimination of metabolites.
3. A pre-ovigerous moult, providing a clean surface for the attachment of eggs, can precede each incubation.

Determinate growth:

1. Growth to full size can be faster.
2. In the mature phase all resources can be concentrated on reproduction, and none diverted to growth. Moulting does not interrupt breeding.
3. During the mature phase there is no mortality induced by moulting.

The selection of one strategy in preference to the other presumably depends upon the balance of the cost-benefit effects of these various factors. At present the information is not available in order to attempt such an analysis.

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