

The life history patterns of brachyuran crabs.

A thesis submitted in accordance with the regulations
of the University of Liverpool for the degree of
Doctor of Philosophy.

By

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In memory of my Aunt, Eunice Skirrow (1925-1991).

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Abstract.

The life history patterns of the majid crabs *Hyas coarctatus* Leach and *Inachus dorsettensis* (Pennant) were studied in populations off the Isle of Man (54°N, 4°30'W) and in the laboratory. Both species grow through a number of juvenile instars, then moult to a terminal, sexually mature instar. In *H. coarctatus* the ovaries of the female develop before this moult, and mating and then egg laying follow almost immediately afterwards. Due to a long diapause the egg batch is carried for 9-11 months, after which another batch may be laid. In *I. dorsettensis* females the ovaries develop only after the terminal moult so there is a short delay at the start of the terminal instar before the first batch of eggs is laid. Several batches may be laid per year, and development is not synchronised with the seasons, as it is in *H. coarctatus*.

Population structure was studied by a programme of regular sampling at two sites. Adult (terminal instar) modal size, of both sexes of both species, differed between populations. Sex ratios were biased in favour of males in the juveniles, especially so for *Inachus dorsettensis*, and in favour of females in the adults (except for *Hyas coarctatus* at one of the sites). Lower abundances were found for both species at one site than were found in a study conducted thirty years earlier (Hartnoll 1961, 1963). A lower maximum size was found in *Hyas coarctatus*, especially in the females, relative to the earlier study. It is suggested that these temporal differences are related to disturbance by commercial scallop dredging in the area.

Growth of the two species was studied in the laboratory. Relative growth analysis of the chelae of the males indicated a clear morphometric difference between juveniles and adults. Percentage increment was smaller at the terminal moult than at the juvenile moults in both sexes of *Hyas coarctatus*. In the females this difference was thought to be due to pre-terminal moult allocation of resources to ovarian development. An opposite result was found in female *Inachus dorsettensis*. Intermoult period increased with body size in *H. coarctatus* and, in the females, decreased with temperature. A decrease in intermoult period with temperature was shown in female *I. dorsettensis*, but no relationship with body size was found. The results suggest that *H. coarctatus* spends only one year as a juvenile (5-10 instars), and that *I. dorsettensis* females spend two to three years (8-11 juvenile instars).

Brood size was strongly related to body size in both species. The first-laid batch of eggs was smaller than those laid subsequently in *Inachus dorsettensis*. There was no intraspecific trade-off between egg size and number per batch, and no variation of egg size with body size. Reproductive allocation by weight was similar for both species and similar to that reported for other brachyurans (brood mass = 10% of body mass). Energetic allocation was three to four times higher than allocation by weight. Reproductive effort was greater in *I. dorsettensis* than in *Hyas coarctatus*.

A simulation model was developed to predict optimal precocity and longevity in response to postlarval survival rates. It was applied to the life histories of four brachyuran species, using data from the literature and from other parts of the present study. Pubertal and terminal moulting were predicted to be delayed in response to increasing postlarval survival. For *Carcinus maenas* and *Cancer pagurus*, both of which continue moulting after puberty, the model predicted a flat peak in lifetime egg production with respect to terminal instar number. Thus, a near-optimal lifetime egg production could be attained by early terminal moulting. The near-optimal tactic corresponded well to that observed in the field for *C. pagurus*, but not for *C. maenas*. Low lifetime egg production was predicted by the model for *Hyas coarctatus* and *Inachus dorsettensis*. Predicted optimal tactics agreed with those which were observed for the former species, but not for the latter. The model suggested lower postlarval survival rates for the majids than for the other two brachyurans.

Chapter 1.

General Introduction.

1.1. Life history patterns.

The life history of an organism comprises its pattern of growth, differentiation, reproduction and storage over the entire lifetime. In recent years life history variation has become a very active field of research (eg. Stearns 1976, 1989, Calow 1978, Begon *et al.* 1990). Experimental work has involved detailed investigation of species' life histories in natural populations and in the laboratory. Comparisons of life histories have been made across taxa and efforts have been made to relate life history patterns to habitat (Southwood 1977, 1988). In addition to the empirical work a considerable body of theory has been developed. This has involved prediction of the life histories which may evolve in organisms in response to specific habitats, and of the population consequences of the evolved patterns (Stearns 1976).

Life history patterns are variously referred to as strategies and tactics in the literature. 'Strategy' refers to the overall, genotypic pattern, whereas 'tactics' are the traits or sets of traits which make up the strategy (see also section 5.1). Stearns (1976) defined the term tactic as 'a set of coadapted traits designed, by natural selection, to solve particular ecological problems'. Both terms emphasise the adaptive significance of life history patterns.

One important component trait of the life history strategy is the age distribution of reproductive effort. This comprises the age at the onset of maturity (the time delay before reproduction) and the pattern of reproduction during maturity. Two classes have been used to describe this pattern: semelparity and iteroparity (Cole 1954). Semelparity describes the condition of multiplying only once in a lifetime. Iteroparity represents a more restrained reproductive pattern, in that episodes of reproduction are several and spread over the lifetime of the organism. Parity, that is the number of reproductive episodes in a lifetime, may vary between and within iteroparous species. An overall conclusion of modelling work on this topic (Sibly and Calow 1983, Stearns 1983) is that iteroparity, late in life, will be selected for when juvenile survival is variable or low (relative to adult survival). The opposite scenario, with juvenile survival equalling or

exceeding adult survival, especially if the latter is variable, will lead to decreased parity, early in life. The semelparity / iteroparity difference is discussed in section 5.4 with reference to benthic marine invertebrates, particularly the brachyuran crabs which are modelled in that chapter.

Other relevant traits are the size and number of offspring produced by an organism in each reproductive episode. Size and number of offspring are considered to be balanced, or 'traded-off' against each other. These two traits, and the mode in which offspring develop, have been of particular interest in marine invertebrates. Marine invertebrate species may be classified into three basic types with respect to mode of larval development (Thorson 1946, 1950, Mileikovsky 1971, Grahame and Branch 1985). The most common type (Thorson 1946) have long-lived planktotrophic larvae which swim in the plankton for weeks or several months, feeding on other plankton, and are hatched from numerous, small eggs. Less common are species with short-lived planktotrophic larvae which spend one week or less in the plankton, having an apparently functional gut but feeding little or not at all, and changing little between hatching and settlement. Finally, some species have lecithotrophic pelagic larvae, whose energy requirements are met by yolk rather than by feeding, and are hatched from larger (yolky), less numerous eggs. Other species have no larval phase and develop directly from egg to juvenile. Various forms of brooding are employed by some species, irrespective of development mode.

Thorson (1946, 1950) noted that pelagic larval development is less common towards the poles and in deeper water. The adaptive significance of development mode has been considered theoretically, firstly by Vance (1973a,b). That author predicted optimal resource allocation between the extremes of many small and few large eggs, with the assumption that smaller larvae spend longer in the plankton. Two distinct optimal strategies were suggested: one with tiny planktotrophic larvae and another with direct development. These ideas have been variously developed (reviewed by Strathmann 1985) and one recent model has considered the entire life cycle rather than just the larval phase (Roughgarden 1989). The significance of dispersal in species with pelagic larvae has been investigated also, and has been considered to be of secondary importance in the

evolution of this development mode (Palmer and Strathman 1981, Roughgarden 1989). Other possible factors in the evolution of mode of development are settlement timing (Todd and Doyle 1981) and the irreversibility of the evolution of lecithotrophy due to the loss of feeding structures (Strathmann 1978).

The concept of reproductive effort has been important in the theoretical literature on life history strategies (Stearns 1976). Hirshfield and Tinkle (1975) defined reproductive effort as the proportion of the total energy budget that is devoted to reproduction. It has been predicted that reproductive effort should be correlated with residual reproductive value (negatively, Pianka 1976), with the r/K characteristics (see below) of an organism (Gadgil and Solbrig 1972), with parity (eg. Calow 1979) and with development mode (eg. Day and McEdward 1984, Grahame and Branch 1985, see also Havenhand and Todd 1989). It is debatable whether all of these correlations do actually occur, however. In studying littorinids and reviewing literature on other intertidal prosobranchs, Hughes and Roberts (1980) found no general relationship between reproductive effort and either development mode or population ecology. Havenhand and Todd (1989) investigated reproductive effort and development mode in nudibranchs and concluded that data in the literature were not sufficiently comparable to enable general conclusions to be made. In both studies the results differed depending upon which measure of reproductive allocation was used.

The r/K scheme, originally due to MacArthur and Wilson (1967), was important in the early development of life history theory. This offered an explanation of life history patterns which was alternative to the survivorship-based explanations following on from Cole (1954). The letters are the parameters of the logistic equation, with 'r' representing the intrinsic rate of population increase and 'K' the carrying capacity of the environment (eg. Begon *et al.* 1990). The scheme was modified considerably following its inception (Pianka 1970, 1972, Gadgil & Solbrig 1972), becoming broader than the original (Parry 1981). Species living in environments which induced instability in population numbers were supposed to be 'r-selected', with early maturation and senescence, reaching a small adult size,

producing many small offspring and exerting a large reproductive effort. More stable environments were considered to be 'K-selecting', leading to a life history pattern at the opposite extreme with respect to the variables described above for r-selected organisms.

The scheme shows a poor fit to the data. From 35 published studies, Stearns (1977) found 18 in which the organisms fit the 'accepted' scheme and 17 in which the scheme was contradicted. Schaffer (1979) considered it inappropriate to associate specific life history attributes with these two selective regimes. Experimental studies (eg. Raffaelli and Hughes 1978, Hart and Begon 1982) have suggested that reference to a species' detailed ecology is required in order to explain life history variation. The latter study considered the intertidal gastropod *Littorina rudis* in a loose boulders habitat and a rock crevice habitat. These two may be considered r-selecting and K-selecting respectively, according to the r/K scheme. A mixture of r and K characters was found in each population, which could be explained by detailed consideration of habitat. In the boulders habitat, for example, the observed large sizes and thick shells (K characters) were considered to be adaptations to avoid shell damage. Small size (an r character) in the crevice habitat was considered to be an adaptation to the small (and limiting) size of crevices.

Over several decades, the theory has been refined to provide reasonable explanations of observed life history patterns. At the outset explanations were based on simple, fixed mortality assumptions (Cole 1954) and, as an alternative, the idea of a hypothetical r/K dichotomy or continuum was explored. The focus of attention is now upon age-specific survival and fecundity schedules and the trade-offs between life history variables (Stearns 1983, 1989).

1.2. Brachyuran life histories.

The Brachyura (true crabs) are a sub-order of the order Decapoda (Ingle 1980). Among the four or five sections of the Brachyura (Ingle 1980 and Warner 1977 respectively) there are 4500 species, which makes them the largest group of the Decapoda, indeed one of the largest crustacean groups, in terms of species number. In all Crustacea the outward manifestation of growth is discrete, occurring as a series of moults (ecdyses) separated by intermoult periods (instars). Growth rate is thus determined by the size increment at ecdysis and the duration of each instar. Reviews have been published on the analysis of crustacean growth (Hartnoll 1982) and on the patterns of growth and reproduction within the Crustacea (Hartnoll 1985).

The sexes are separate in most Crustacea and all Brachyura (Hartnoll 1985). In general the postlarvae of both sexes become mature at a particular moult, termed the puberty or maturity moult. Pre- and post-puberty individuals are referred to as juvenile and adult or mature respectively. Copulation (in Crustacea) is followed by storage of the spermatozoa by the female for a short period at least before egg laying and fertilization. Normally, all ripe ova are expelled at laying. Some species are semelparous, with the females laying a single egg batch, but iteroparity is more common. In some species the females can mate only during the period immediately following the moult, whilst the carapace is still soft. This is common but not exclusively the case (Hartnoll 1969, 1985). Typically, the egg batches are carried on the abdominal appendages until hatching.

The Decapoda show a great diversity of life history patterns when compared to other crustacean groups of equivalent rank (Hartnoll 1985). In the swimming decapods (Natantia: Bruce *et al.* 1963, Barnes 1987) growth is indeterminate, that is there is no morphologically or endocrinologically distinct terminal instar (Hartnoll 1985). Following the puberty moult there is an indefinite series of instars, with mating occurring shortly after the female has moulted. Only one batch of eggs is produced per ovigerous instar. Many, perhaps all, species have some morphologically distinct non-

ovigerous instars after puberty. The pattern for the lobsters (Astacidea and Palinura: Barnes 1987) is more regular. In most species growth occurs indeterminately after puberty, mating follows ecdysis and the female carries one batch of eggs in each mature instar. Less is known of the Anomura, the squat lobsters and hermit crabs. Moulting is known to continue after puberty, but no further generalisations are possible (Hartnoll 1985).

The Brachyura are unusual crustaceans in that spermatozoa are stored after copulation in internal, non-integumental spermathecae (Hartnoll 1985). These are not shed at ecdysis, so a single mating may be sufficient to fertilize several egg batches in several instars. In many species mating is restricted to the period following the moult. Because of sperm storage in the spermathecae however, this does not necessarily limit the subsequent pattern of egg production. In general, more than one batch of eggs is laid in each mature instar and there is great variation in the patterns of post-puberty growth and reproduction (Hartnoll 1985). In some species growth proceeds through an indefinite series of instars and is said to be indeterminate. Other species grow determinately to a definite terminal moult and final instar, the terminal anecdysis (Carlisle 1957, Hartnoll 1972).

The experimental work of the present study considered two species of brachyuran crab, *Hyas coarctatus* Leach and *Inachus dorsettensis* (Pennant) (Ingle 1980), in populations off the Isle of Man (54°N, 4°W). *H. coarctatus* is a boreal-arctic species, extending from the arctic circle down to about 45°N; *I. dorsettensis* is boreal and extends from about 70°N to the Mediterranean (Christiansen 1969, 1973, Ingle 1980). Both are spider crabs (Majidae), a family which belongs to section Oxyrhyncha of the Brachyura. These species, and probably all of the Majidae, have only a single mature instar, the terminal anecdysis (Hartnoll 1963, 1985). This has been established for the British spider crabs by several lines of evidence (Hartnoll 1963). There is some doubt, however, regarding this life history feature in males of the west North Atlantic and Bering Sea *Chionoectes* species (Conan *et al.* 1990, see also sections 3.1 and 3.4.2). The puberty moult is discernable morphologically in spider crabs, as it is in many brachyurans. In the male, the shape and relative size of the chelae changes at puberty. In females, there are changes in the abdomen shape, the pleopods and the thoracic

sternae. The males undergo some development of the sperm ducts before the puberty moult. Copulation, in the females at least, is possible only after the puberty moult. After the eggs are laid by the female, they are carried on the endopodites of her pleopods until hatching.

The Majidae are mostly subtidal. *Hyas coarctatus* has been recorded from 2m to 457m depth (Ingle 1980), on a wide range of bottom types including stones, muddy sand and sand (Hartnoll 1963). *Inachus dorsettensis* has also been reported over a wide depth range (4-256m, Ingle 1980) but is slightly more limited in habitat, being found mainly on muddy sand (Hartnoll 1963). Spider crabs are slow moving relative to other brachyurans and do not burrow. As a group, they also have extensive epifauna. Their integument has various setae, some of which are specially hooked, which facilitate attachment, and the animals have been observed deliberately attaching organisms to the carapace (Hartnoll 1963). They are thus considered to be cryptic.

Stomach content analysis of the British spider crabs (Hartnoll 1963) has shown that diet is heavily influenced by the food available, but some selectivity is shown. The gut contents comprised a high proportion of crustacea, little algae, some bivalve and some ophiuroid. *Hyas coarctatus* was found to feed very generally, eating almost any available food. *Inachus dorsettensis* fed less generally. As may be expected of these sluggish species, predatory feeding behaviour follows a sit-and-wait pattern. Tactile stimulus is required after which the crabs grab at prey either with the chelae or, as with *H. coarctatus*, with all legs to form a cage (Hartnoll 1963).

Hartnoll (1963) also studied the growth-reproduction patterns of the Majidae, around the Isle of Man. The three most abundant species, *Hyas coarctatus*, *Inachus dorsettensis* and *Macropodia rostrata*, were considered in most detail. The results from that earlier study, for *H. coarctatus* and *I. dorsettensis*, constitute introductory material for Chapters two and four. Chapters two and three are discussed partly in the context of the earlier study. The model of Chapter five is applied to the species *Carcinus maenas* and *Cancer pagurus*, using data from the literature, and to *H. coarctatus* and *I. dorsettensis* using results from the earlier chapters.

As the basic biology of local populations of spider crabs has been covered in some depth already (Hartnoll 1961, 1963), the two species may be considered a good choice for an investigation of life history patterns. One disadvantage however, which applies to all Crustacea, is the difficulty in ageing the animals. At each moult all hard structures are lost, eliminating any possibility of determining the exact age. Moreover, successive instars of Crustacea are usually similar and rarely is it possible to distinguish exactly which instar a specimen is in. These difficulties will tend to complicate any study of the population biology of this group.

Overall, crustacean reproduction and life histories have received far less attention than for example the insects, a class of comparable adaptive diversity and economic importance (Adiyodi & Subramoniam 1983). Insects, with their short breeding cycles, short life-spans, small size and robustness in the laboratory are ideal model animals in many ways for demographic study. Crustacea are slower breeders generally and the marine environment in which most species live is relatively inaccessible for study. Despite these difficulties, which may have limited interest in the past, there remains one reason for studying this group: simply the fact that knowledge of them is limited. Life history studies seek to explain the variation in individual strategies observed in natural populations. Any general theory of life history variation must be able to explain the patterns observed in a diverse range of organisms. The search, then, must include many species, not just those which are ideal laboratory models.

Chapter 2.

**Population structure of
Hyas coarctatus and *Inachus dorsettensis*.**

2.1. Introduction.

This population study of *Hyas coarctatus* and *Inachus dorsettensis* draws upon and enlarges some of the results of Hartnoll's (1963) study of the Majidae around the Isle of Man. His observations on postlarval life cycle are of crucial importance to the present study. One observation was that these species grow determinately, reaching a terminal instar which is morphometrically distinguishable from the juvenile instars. Another was that this terminal instar is the only one in which the female can mate and lay eggs. Hartnoll (1963) also reported the basic phenology of these species in the area that is considered in the present study.

Size frequency data are used in this study, in conjunction with laboratory growth results, to investigate the species' life histories and their population structures. The population size structure of juveniles, especially during the known puberty moult season, is considered in an attempt to discriminate modes which may represent separate instars. The size increments which would be required to moult from one inferred instar to the next are compared with those found in the laboratory (Chapter three). The adult size distributions are considered in relation to those of the juveniles. Again, inferred size increments, of the terminal moult, are compared with the laboratory results. Attempts are made to determine whether there is variation within the populations in the number of juvenile instars preceding the terminal moult. Such variation would increase the variability of size in the terminal instar and could conceivably result in a multimodal adult size distribution. The number of juvenile instars and the size of individuals in the terminal instar are of especial interest as the optimality model of Chapter five makes various predictions regarding these variables.

Size frequency analysis represents an incomplete characterisation of population structure. It is used because of the impossibility of measuring age classes in most natural populations of Crustacea (Wenner *et al.* 1974, Coull and Bell 1983). If these cohorts could be recognised, aged, and the survival of each one determined, then a full species life-table could be constructed. This has been possible only in barnacles on the rocky shore (Connell 1970, Hines 1978, 1979, Coull and Bell 1983). That crustacean

group is exceptional because of the sessile lifestyle of the postlarvae, which facilitates precise study of population events over time. In other crustacean groups, in marine soft-bottom and reef habitats, demographic study is more difficult and size frequency analysis is required (Coull and Bell 1983). Much population level study has been done on Cladocera (Slobodkin 1954, Allan 1976, Hebert 1978) and Copepoda in their various planktonic habitats (Mort 1991). Again, demographic study of these groups is difficult and precise life history data exist mainly for laboratory reared rather than natural populations (Coull and Bell 1983).

Various methods have been developed for the analysis of size frequency distributions (Grant 1989). Graphical methods were described by Harding (1949), Cassie (1954) and Bhattacharya (1967) and a numerical method was described by Macdonald and Pitcher (1979). The usual aim of such methods is to discriminate year classes within a population which has seasonal recruitment. For a species which grows by moulting, however, the primary aim is to discriminate instar classes. By following changes in abundance in the recognised instars over time, it is possible in some instances to determine growth rates in the field (Hartnoll 1982). This method is generally imprecise in practice; usually a maximum of the first five to six instars will be recognised in the distribution (Hartnoll 1978, 1982) due to the cumulative increase in variance in instar size. Additionally there is almost always a size bias involved in the sampling technique, which over-estimates the importance of larger classes and may result in insubstantial sample sizes in the smaller classes. Despite these limitations instar discrimination was attempted for these two species; they have relatively few postlarval instars (Chapter three and Hartnoll 1963) and independent data exist on growth rate (Chapter three), against which inferred field growth rates may be compared.

Beside the immediate aims, stated above, of this population level study, the practical work of this chapter provided samples needed for the work described in other chapters. Sampling was undertaken regularly through a period of one year. The specimens collected were used for seasonal studies of growth in the laboratory (Chapter three), and for the study of reproductive investment (Chapter four).

2.2. Sampling: methods and areas.

All of the sampling described in this section was done from the University of Liverpool's research vessel 'Cuma'. Samples were taken by dredging, a method that Hartnoll (1963) found to be effective at catching spider crabs in the same area on all except the very fine grounds. Early, exploratory, samples were taken using a single 0.91m-wide spring-loaded dredge, without teeth, on each side of the vessel. The inner diameter of the steel rings which make up the chain belly of the dredges was 6.4cm. During the sampling period the dredging gear comprised a 'gang' of two toothless, spring-loaded, 0.76m wide dredges on each side, with ring inner-diameters of 5.7cm and 7.0cm on the port and starboard sides respectively. The design of the spring-loaded dredge, particularly in the latterly-used paired form, is described in Chapman *et al.* (1977).

The initial sampling trips were undertaken in order to locate populations of the two species to be studied. The areas investigated on these trips were those in which Hartnoll (1963) had found *Hyas coarctatus* and *Inachus dorsettensis* in abundance. In this earlier work *H. coarctatus* was found to be the most abundant majid species on all rough grounds and was especially abundant on the stony ground designated 'B' (Fig. 2.1). It was also found to be frequent on muddy sand, especially inshore (areas F, Fig. 2.1). It was found to be relatively scarce on sandy grounds in and around Port Erin Bay. *I. dorsettensis*, contrastingly, was scarce on rough ground but common on muddy sand (grounds F and G, Fig. 2.1). It was the most abundant majid species on muddy sand, found also on sand but not generally on mud.

Despite repeated sampling trips, very few spider crabs were found by dredge sampling on ground B. *Hyas coarctatus* was the most abundant of the species caught, but the samples were too small for population study. Similarly, only a very few spider crabs were found on the *Modiolus* bed (ground A), NW Calf (ground C), SW of Port Erin breakwater (part of ground F), Chicken Rock and the muddy sand further offshore to the west (ground G). It is not known why so few animals were found relative to the abundant catches, mainly by dredging, of Hartnoll (1963).

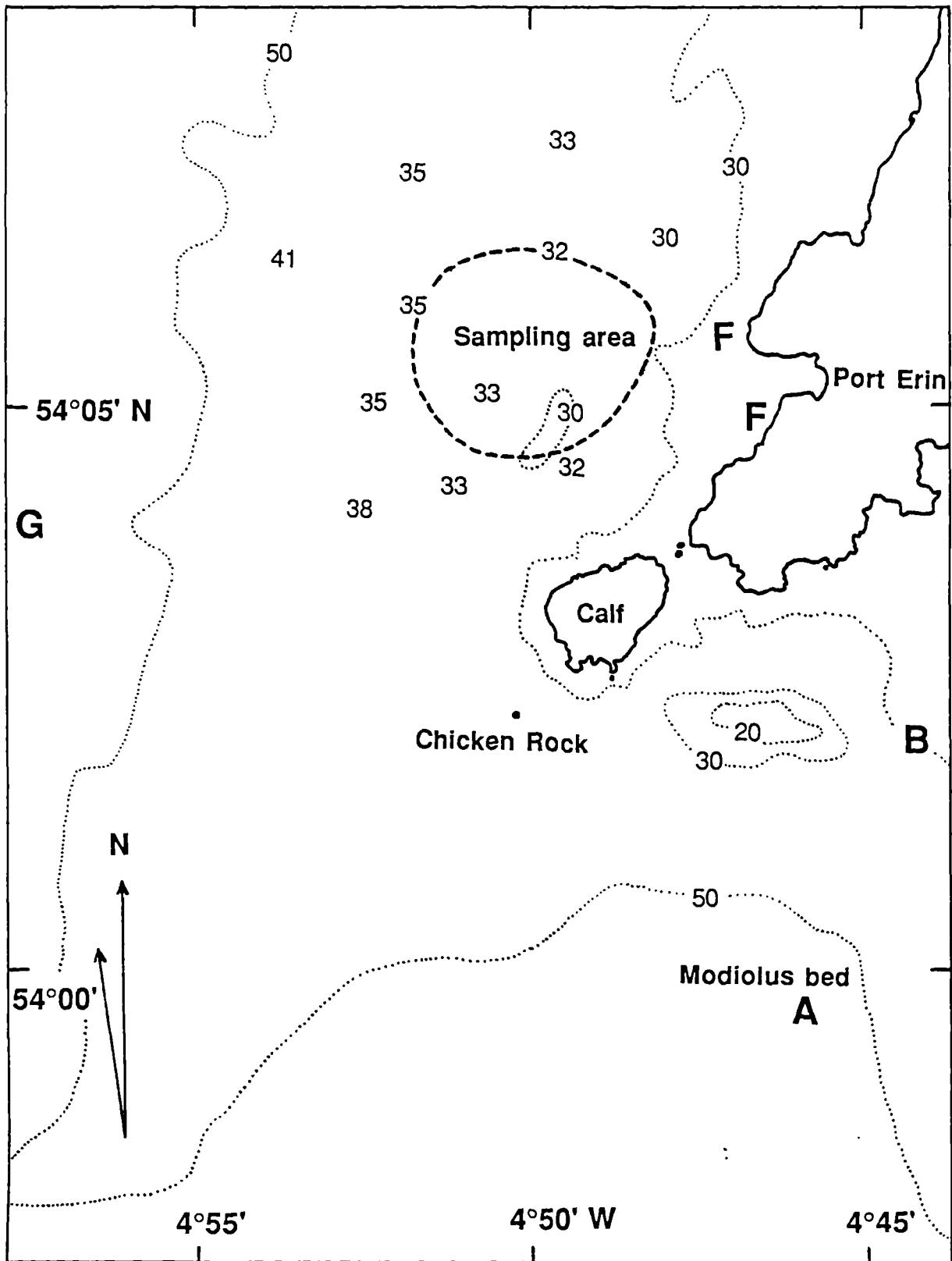


Fig. 2.1. The south west of the Isle of Man, showing the Bradda sampling area and the grounds sampled by Hartnoll (1963) (lettered A, B, F, G). Depths are in metres.

Of all the areas sampled to the south west of the Isle of Man, both species were found to be most common off Bradda Head, part of Hartnoll's (1963) ground F. This general area was therefore selected as a study site; the exact area which was sampled is shown in Fig. 2.1. The bottom of the area is muddy sand, mixed with broken shell, gravel and stones, at a charted depth of 30-35m. On the east side of the island, *Inachus dorsettensis* was found to be abundant outside Laxey Bay (Fig. 2.2). *Hyas coarctatus* was also found here but in small numbers. An area close inshore at Laxey, shown in Fig. 2.2, was selected as a second study site, for comparison with the Bradda site. The bottom here is sand-gravel with stones and broken shell, at a charted depth of 16-24m.

A sampling program was conducted between November 1988 and November 1989 in which each site was sampled once per month, as far as was possible. Weather and boat availability problems caused some irregularity in the timing of these samples. Each sample represents between two and seven tows of the dredging gear. The specific lines followed within the areas shown in Figs. 2.1 and 2.2, on any given sampling date, depended to a large extent upon tide and weather conditions. Specimens were sorted from the other benthic material on the deck of the ship then brought, in tanks filled with seawater, to the laboratory. Here they were sexed, and juveniles were discriminated from the adults (as described in Hartnoll 1963). This discrimination is obvious in females but less so in males: in a small number of male specimens no unequivocal discrimination could be made. The presence or absence of eggs was noted in the females. Carapace length was measured from the posterior margin of the carapace to the tip of the rostrum, to the nearest 0.1mm. Where there was doubt concerning male maturity, chelar propodus length and breadth were measured also (all measurements were of the same body dimensions as reported by Hartnoll 1963). The specimens were subsequently maintained in tanks with flowing seawater at a temperature near that ambient in the sea.

For the comparison of population structures, size frequency histograms of carapace length (CL) were constructed using 1mm size classes centralised on each whole millimetre through the size range. Samples from the whole sampling period were pooled for this comparison, for both the juvenile and post-puberty groups. In addition, the size structure of the

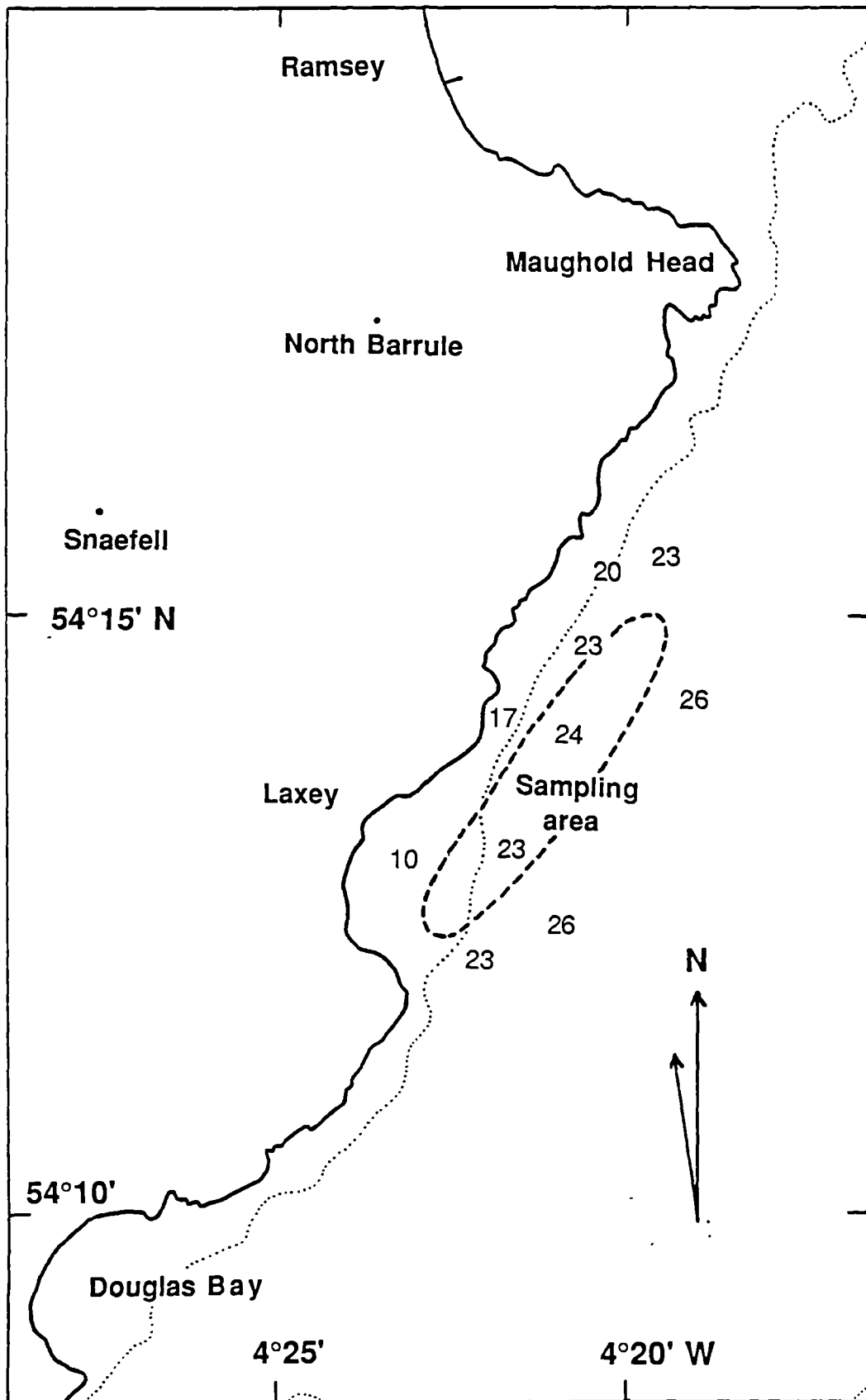


Fig. 2.2. The east of the Isle of Man, showing the Laxey sampling area. Depths are in metres.

juvenile groups during the known puberty moult season (Hartnoll 1963) was considered. This was taken to be May to September for *Hyas coarctatus* and July to October for *Inachus dorsettensis*. Where sufficiently large samples were obtained, histograms were constructed for the individual months of the sampling period. The 'laboratory growth rate' referred to in the Results section in conjunction with this size frequency analysis is that which is described in Chapter three.

For each species the adult sizes of males and females at Bradda and Laxey were compared by non-parametric two factor crossed ANOVA (Scheirer *et al.* 1976, Zar 1984), after balancing by random elimination of data. Sex ratios were compared separately for each species at each site; 2x2 contingency tables were constructed, classified by sex and life history stage (juvenile and adult). The independence of these two variables was then tested using the χ^2 statistic.

2.3. Results.

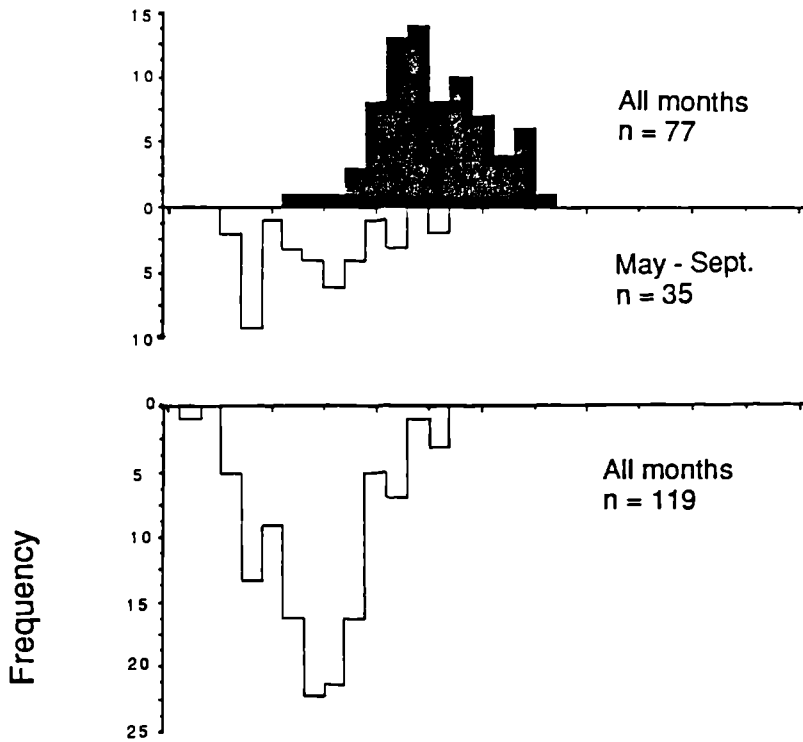
2.3.1. Size frequency distributions.

The size frequency distributions for *Hyas coarctatus* females, with all samples pooled, are shown in Fig. 2.3. There is little evidence for multiple modes within the adult groups; the Laxey distribution appears to be approximately symmetrical whilst that for Bradda shows a slight positive skew. In the Bradda juvenile distribution during the puberty moult season there is a mode at 13mm CL which may represent the penultimate instar; individuals moulting from this group to the 17mm adult modal group would have undergone a moult increment of 31%, a result which agrees well with the mean terminal moult increment found in the laboratory. Another mode, at 9mm CL, is apparent in the Bradda juvenile distributions, which may represent the instar before the penultimate instar. The moult between these two instars would be of a larger percentage increment than that of the terminal moult, which also agrees with the laboratory results.

Fig. 2.4 shows the pooled-sample distributions for *Hyas coarctatus* males. The sample sizes in the adult groups are very small, and preclude any reliable interpretation. At Bradda there appears to be an adult mode at 18mm CL, and there is a clear juvenile mode at 13mm CL. The juvenile mode is not apparent in the puberty moult season, however, so it should not be attributed necessarily to a penultimate instar group. In the Laxey juvenile group the sample size is smaller than that of the Bradda juveniles, but there are modes at 12 and 16mm CL; if these represent successive instars then the moult increment (33%) would again agree well with the laboratory results.

The sample sizes of *Inachus dorsettensis* were generally larger than those of *Hyas coarctatus*. Fig. 2.5 shows a clear unimodal, near-symmetrical distribution for *I. dorsettensis* adult females at both sites. In the Bradda juvenile samples taken during the puberty moult season there are modes at 11mm and possibly 14mm CL. A moult from the latter group to the adult modal group (18mm CL) would represent an increment of 29%,

Bradda



Laxey

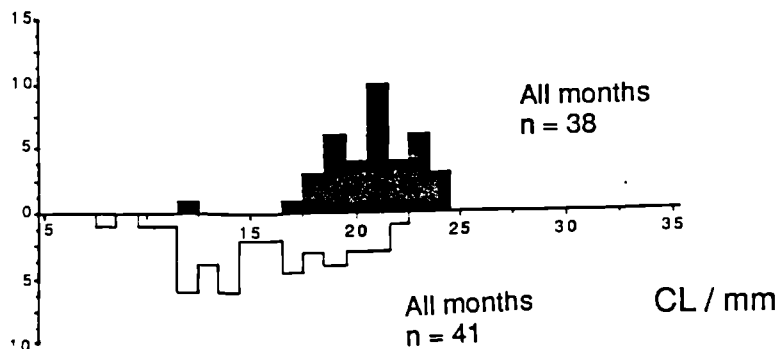


Fig. 2.3. *Hyas coarctatus* female size frequency distributions. The solid bars represent adults; the unshaded bars represent juveniles. Due to insufficient sample size the Laxey juvenile distribution during the puberty moult season is not shown separately from the all-months distribution.

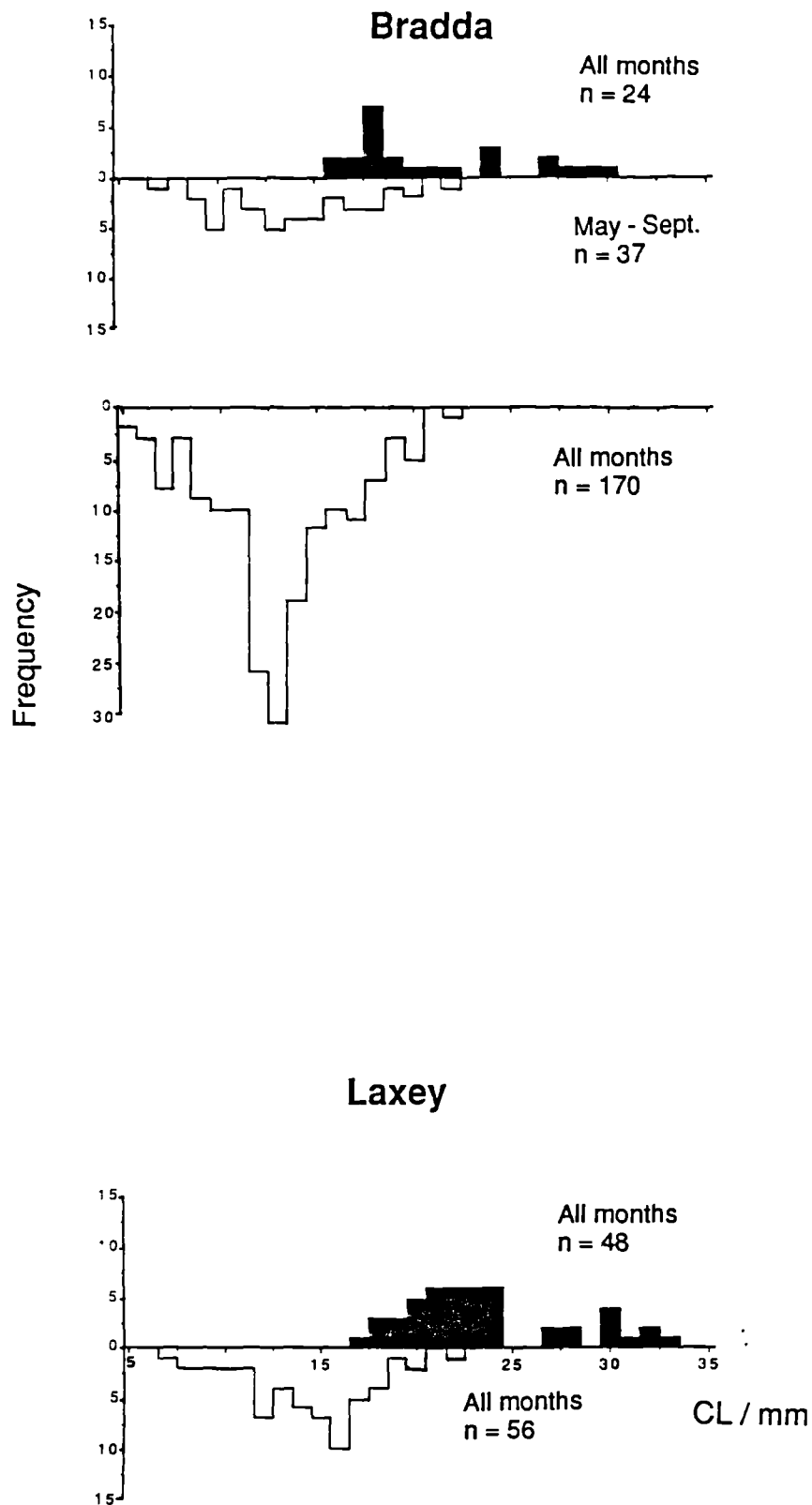


Fig. 2.4. *Hyas coarctatus* male size frequency distributions. The solid bars represent adults; the unshaded bars represent juveniles. Due to insufficient sample size the Laxey juvenile distribution during the puberty moult season is not shown separately from the all-months distribution.

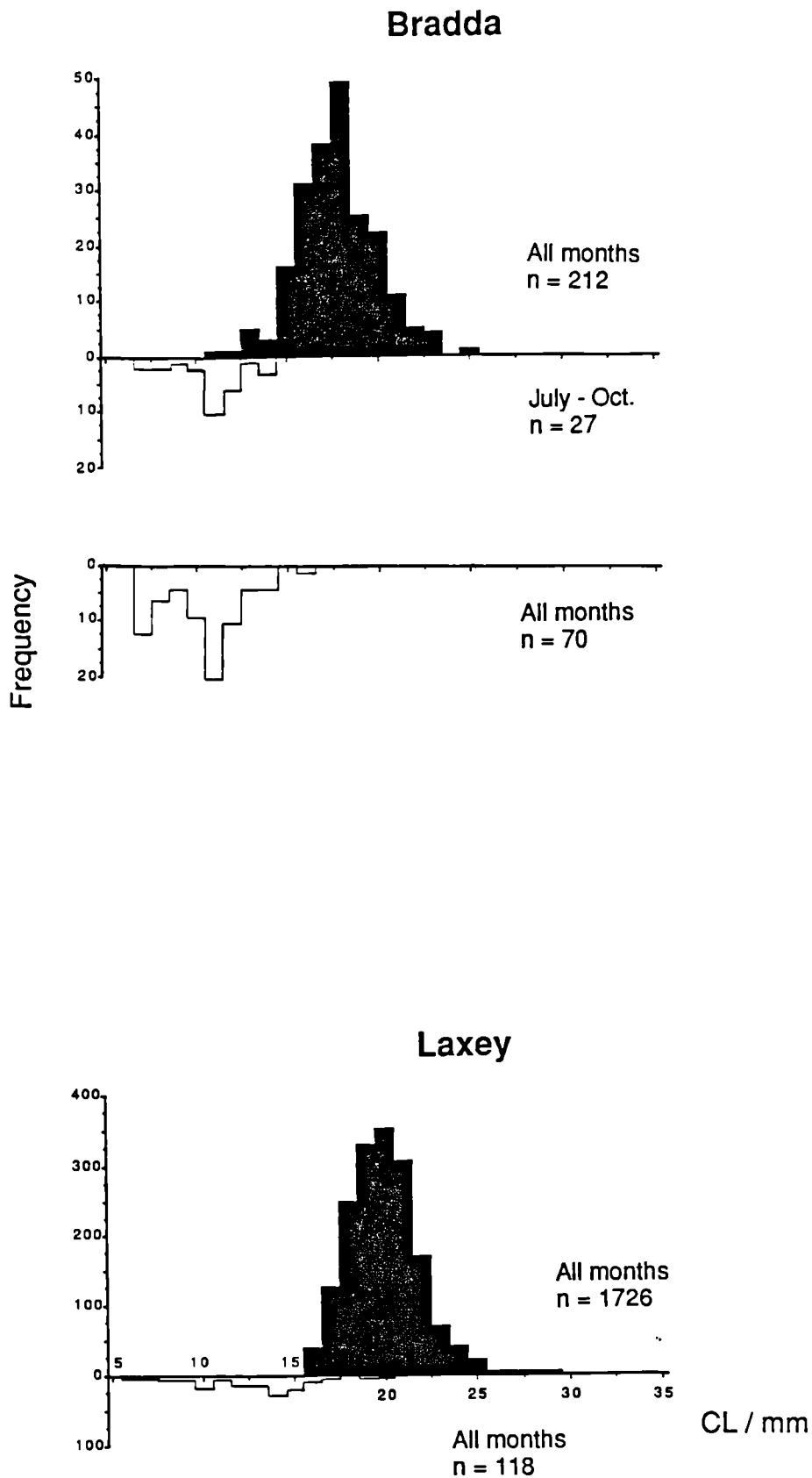


Fig. 2.5. *Inachus dorsettensis* female size frequency distributions. The solid bars represent adults; the unshaded bars represent juveniles. Due to insufficient sample size the Laxey juvenile distribution during the puberty moult season is not shown separately from the all-months distribution.

similar to that predicted by the laboratory experiment. Considering the whole sampling period at Bradda there are clear juvenile modes at 7mm and 11mm CL. It is unlikely that these represent successive instars as the increment between them, 57%, would be far larger than that found in the laboratory. In the Laxey samples there are 10mm and 14mm juvenile modes and a 20mm CL adult mode. If these are assumed to represent successive instars then the two moult increments, 40% and 43% respectively, would be larger than those found in the laboratory.

An interesting difference between Bradda and Laxey adult male size distributions is shown in Fig. 2.6. The Bradda distribution is clearly bimodal with modes at 19mm and 27mm CL, which is similar to the distribution found by Hartnoll (1963) around the south west of the Isle of Man. The Laxey distribution is negatively skewed and unimodal, with the mode corresponding to the larger of the two modes at Bradda. Within the Bradda juvenile distribution during the puberty moult season there is a mode at 15mm CL; this may represent a penultimate instar group, from which a 27% moult increment would result in the smaller of the two adult modes. There is no juvenile group apparent which could result in the larger of the two adult modes, as was found by Hartnoll (1963). Within the Laxey juvenile distributions, from both the puberty moult season and from the whole period, there is a clear mode at 18mm CL. Moults from this group would result in a smaller size than the 27-29mm CL of the observed adult modal group.

Inachus dorsettensis was present in sufficient numbers at Laxey to allow examination of distributions on a sample-by-sample basis. These distributions are shown for females and males in Figs. 2.7 and 2.8 respectively. The adult female distributions are generally similar from month to month, with the single mode at 19-20mm CL. Within these considerably sized samples there were very few juveniles (Fig. 2.7); instar peaks cannot be discriminated and there is no evidence for depletion of the larger juveniles in the puberty moult season.

In the males of these periodic samples (Fig. 2.8) there is a adult mode in most months which corresponds to that for the sampling period overall (Fig. 2.6). On three sampling occasions, the initial November, December

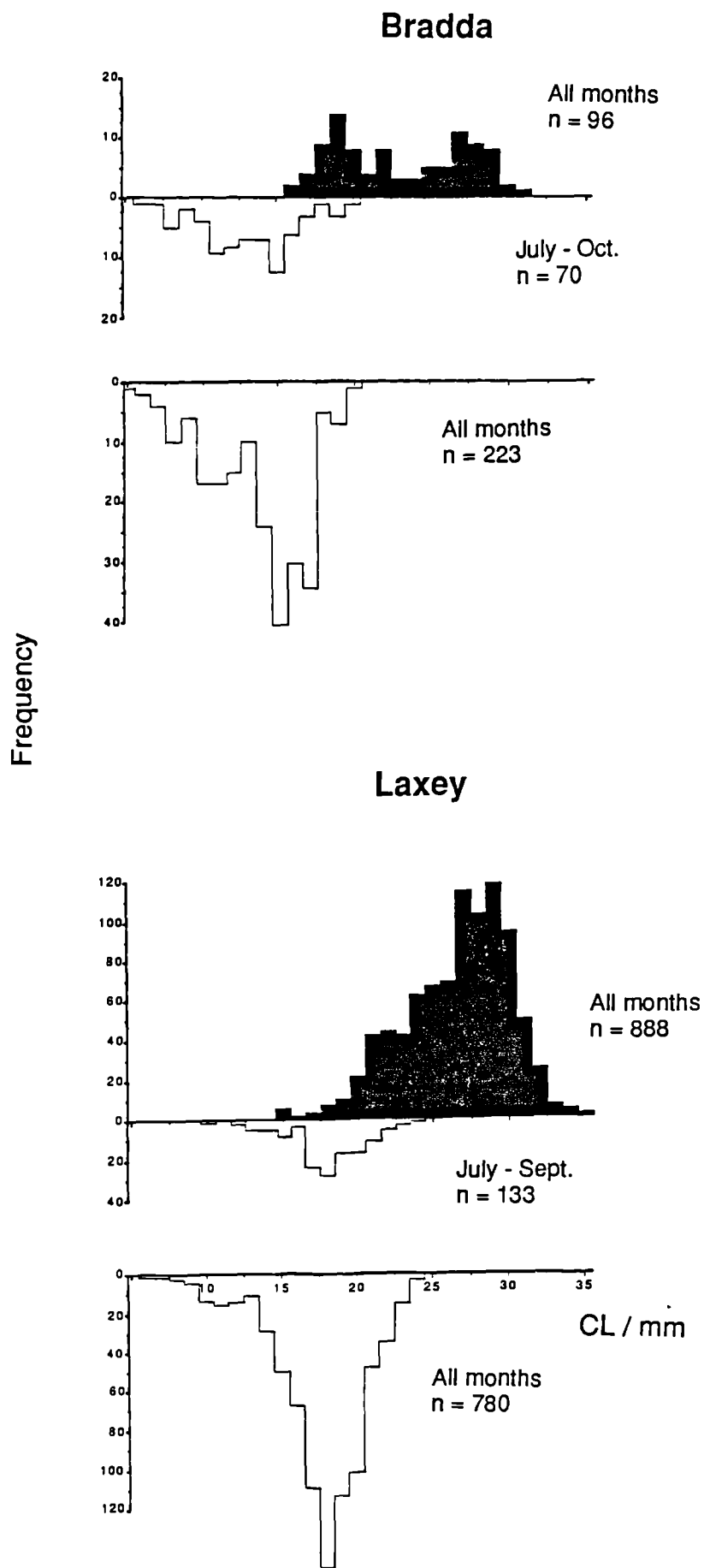


Fig. 2.6. *Inachus dorsettensis* male size frequency distributions. The solid bars represent adults; the unshaded bars represent juveniles.

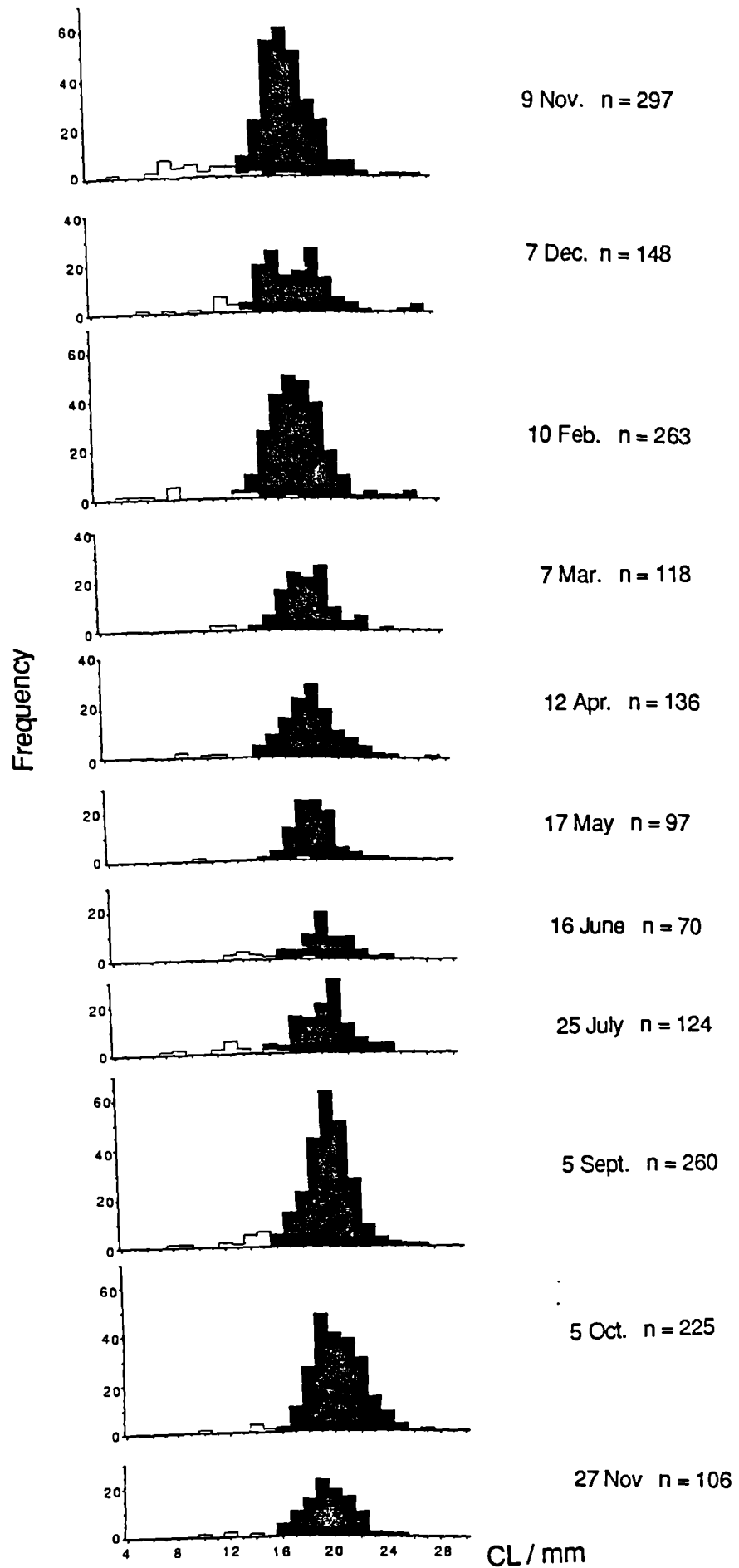


Fig. 2.7. *Inachus dorsettensis* female size frequency distributions for individual samples taken at Laxey. The solid bars represent adults; the unshaded bars represent juveniles.

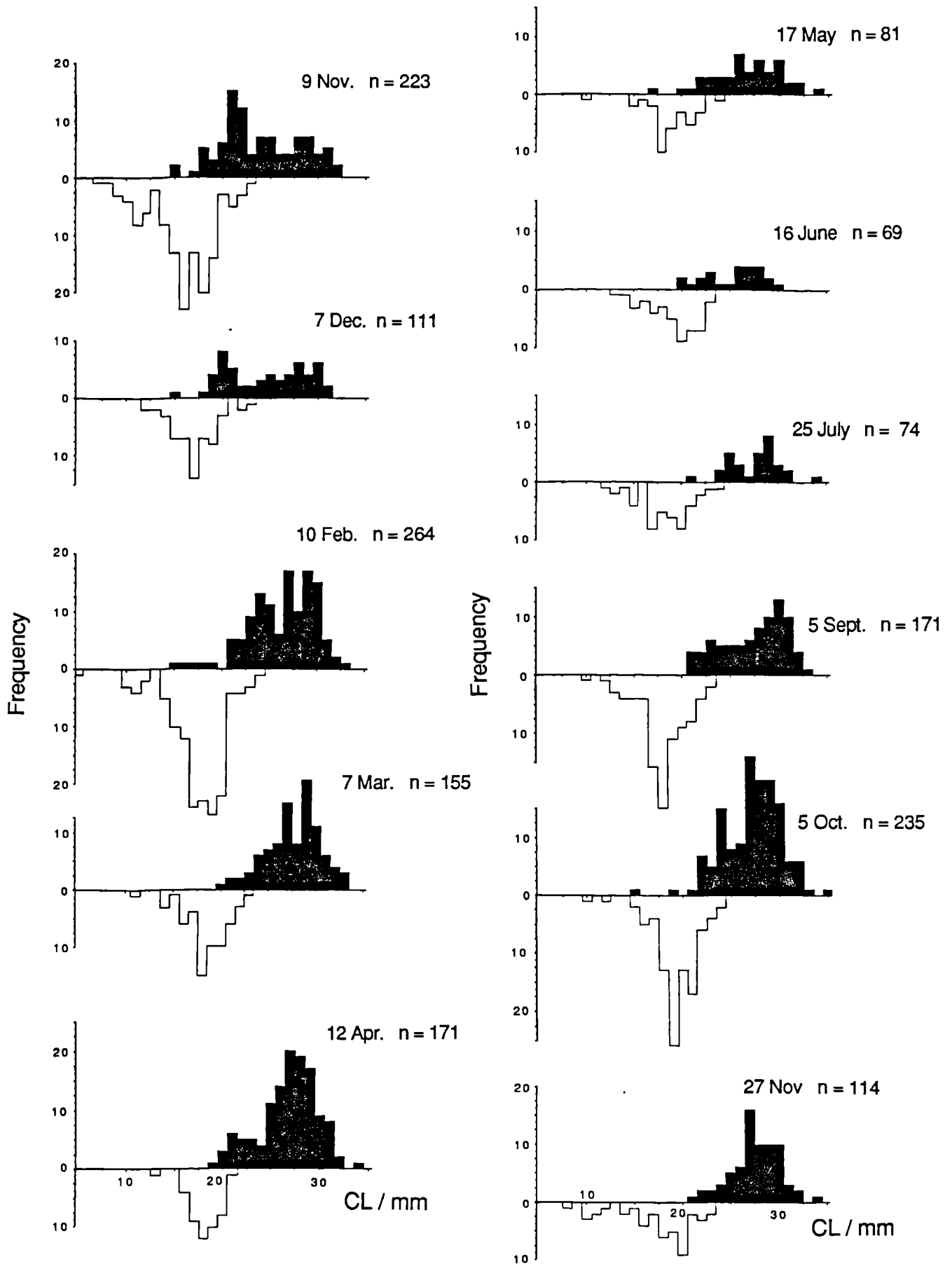


Fig. 2.8. *Inachus dorsettensis* male size frequency distributions for individual samples taken at Laxey. The solid bars represent adults; the unshaded bars represent juveniles.

and April, however, a second mode of 20-21mm CL was observed. The adult distributions observed during these months are similar to those found for Bradda (Fig. 2.6) and the south west of the Isle of Man generally (Hartnoll 1963) rather than to the pooled Laxey distribution of which they are a part. As with the females, the juvenile distributions for the males do not show clear instar modes, which precludes any inference on growth rate. There is little evidence either for the depletion of larger juveniles during the puberty moult season.

2.3.2. Adult size comparison.

The adult size of female and male *Hyas coarctatus* from Bradda and Laxey is compared in Table 2.1. Clearly, in the terminal instar, the males are larger than the females and both sexes are larger at Laxey than at Bradda. There is no significant interaction between sex and site in this analysis, indicating that each sex is affected equally, additively, by the difference in site. This could be either a habitat effect or genetic effect; the present data do not enable discrimination between these two possibilities. The size difference between Bradda and Laxey is similar to that found by Hartnoll (1963) between grounds F and B respectively. A further size difference was noted in the earlier study: *H. coarctatus* adults on ground A were considerably larger than those on either of grounds B or F.

An identical comparison, but for *Inachus dorsettensis*, is shown in Table 2.2. Again, adult males are larger than females and both are larger at Laxey than at Bradda. The levels of significance and the table of medians show that the male-female difference is greater than the site difference. Interaction between the two factors is shown to be highly significant; this non-additivity is caused by the size difference due to site being greater in males than it is in females. Due to the bimodal distribution of *I. dorsettensis* males at Bradda (Fig. 2.8), some caution must be exercised in the acceptance of these conclusions, especially that regarding interaction. As there are modes at 19mm and 27mm CL, the median size of 22.3mm, and indeed that particular rank sum used in the analysis, may be quite misleading.

Analysis of variance.

Source	d.f.	S.S.	Kruskall-Wallace H	P
Sites	1	13609	17.54	<0.001
Sex	1	8664	11.16	<0.001
Interaction	1	646	0.83	n.s.
Cells	3	22919		

Median sizes (mm CL).

		Sex	
		Female	Male
Site	Bradda	17.2	18.9
	Laxey	21.1	22.4

Table 2.1. The sizes of adult *Hyas coarctatus* females and males at Bradda and Laxey. The comparison is a non-parametric two factor crossed ANOVA of rank sums.

Analysis of variance.

Source	d.f.	S.S.	Kruskal-Wallis H	P
Sites	1	267,390	21.7	<0.001
Sex	1	1,730,308	140.4	<<0.001
Interaction	1	208,645	16.9	<0.001
Cells	3	2,206,343		

Median sizes (mm CL).

		Sex	
		Female	Male
Site	Bradda	17.7	22.3
	Laxey	19.8	27.1

Table 2.2. The sizes of adult *Inachus dorsettensis* females and males at Bradda and Laxey. The comparison is a non-parametric two factor crossed ANOVA of rank sums.

2.3.3. Sex ratio.

The sex ratios for both species at both sites, for the juvenile group and the terminal instar group, are shown in Table 2.3. It would appear from this that males dominate the juvenile samples, especially in *Inachus dorsettensis*, but females dominate the adult samples in all groups except Laxey *Hyas coarctatus*. A test of the hypothesis that there is a switch in sex ratio at the terminal moult is shown in Table 2.4. With the exception of Laxey *H. coarctatus*, non-independence is the clear result of these tests, indicating that the preponderance of one sex in the samples does switch abruptly between the juvenile and terminal instar stages. As the result for Laxey *H. coarctatus* was not significant, the two life history stages were pooled to give an overall female/total ratio of 0.43. The deviation of this from equality is near the borderline of statistical significance ($\chi^2 = 3.415$, $n = 183$, $0.10 > P > 0.05$).

Juvenile sex ratios, female / total.

		Bradda	Laxey
Species	<i>H. coarctatus</i>	119 / 289 = 0.41	41 / 97 = 0.42
	<i>I. dorsettensis</i>	70 / 293 = 0.24	118 / 898 = 0.13

Adult sex ratios, female / total.

		Bradda	Laxey
Species	<i>H. coarctatus</i>	77 / 101 = 0.76	38 / 86 = 0.44
	<i>I. dorsettensis</i>	212 / 308 = 0.69	1726 / 2614 = 0.66

Table 2.3. Sex ratios of *Hyas coarctatus* and *Inachus dorsettensis* at Bradda and Laxey.

H. coarctatus

	Bradda		Laxey	
	Female	Male	Female	Male
Juvenile	119	145	170	144
Adult	77	51	24	50
	$\chi^2 = 36.8$ P<<0.001		$\chi^2 = 0.068$ n.s.	

I. dorsettensis

	Bradda		Laxey	
	Female	Male	Female	Male
Juvenile	70	137	223	155
Adult	212	145	96	163
	$\chi^2 = 121.8$ P<<<0.001		$\chi^2 = 749.7$ P<<<0.001	

Table 2.4. Contingency tables classified by sex and life history stage of *Hyas coarctatus* and *Inachus dorsettensis* at Bradda and Laxey. The expected frequencies are shown, in small figures, next to the observed frequencies.

2.4. Discussion.

The size frequency distributions and size ranges for Bradda may be compared directly with Hartnoll's (1963) pooled data for the grounds to the south west of the Isle of Man. In *Hyas coarctatus*, especially in the females, my adult distributions are truncated relative to those of Hartnoll (1963): He found the largest terminal instar females and males to be 36mm and 42mm respectively, whereas my results for Bradda are 23mm and 30mm respectively. The sample sizes of the earlier study were much larger for this species than those reported here. However if insufficient sample size were the cause of this difference, one would expect truncation of the distribution at both extremes; this is not the case. Moreover in the growth experiments of Chapter three, also with relatively small sample sizes, I obtained the full size range reported earlier. It would appear from this that *H. coarctatus* at the Bradda site reaches a smaller terminal size than was observed in the same general area thirty years ago.

The adult size ranges for female and male *Hyas coarctatus* at Laxey were similar to those found at Bradda. The analysis of variance demonstrated a significant size difference between sites, larger at Laxey in both sexes, but this difference is small compared to the difference between these results and those of the earlier study. As Hartnoll (1963) concentrated on the south west of the Isle of Man, there is no time-lapse comparison available for the Laxey ground. As mentioned earlier, however, he did find size differences in adult *H. coarctatus* between grounds. Whilst his mean sizes for ground F were similar to my median sizes for Bradda, those for the *Modiolus* bed (ground A) were larger than the median sizes which I found at Laxey.

The adult size ranges for *Inachus dorsettensis*, both sexes at both sites, are similar to those found by Hartnoll (1963). A significant but small difference was found between sites, with larger adult sizes at Laxey than at Bradda. This difference, the same as found in *Hyas coarctatus*, could be due to differing growth increments of the juveniles, a difference in the number of juvenile instars or differential size selective predation of the adults. The results, including those of the growth experiment (Chapter three), do not allow discrimination between these factors. Neither do they

allow any conclusions to be drawn about whether the difference is habitat-related or genetic. The size difference is interesting as Chapter five is concerned partly with optimal sizes for females of these species, which are discussed in relation to those observed here. The size comparison between areas suffers the weakness, however, of not knowing whether those areas are genetically uniform or separate. Only if both sites represent the same population in both species may one attribute the difference to habitat.

A major factor affecting geographic population differentiation in these species is their possession of pelagic planktotrophic larvae. On the basis of laboratory rearing experiments *Hyas coarctatus* larvae spend around 75 days in the plankton, settling mid-June (Chapter five, using the data of Anger 1984). Applicable data are scarcer for *Inachus dorsettensis*, but one month is a likely duration for the planktonic phase (from Mohamedeen 1984). Although larval dispersal may reduce geographic variation (eg. Scheltema 1971a,b), this should not be assumed without supporting evidence; in the nudibranch *Adalaria proxima*, for example, genetic heterogeneity has been found over short distances, indicating that actual larval transport may be abbreviated relative to that expected from laboratory rearing (Todd *et al.* 1988). In congeneric littorinids Johannesson (1988) found that *Littorina littorea*, a planktonic dispersive species, was less widespread than the brooding *L. saxatilis*, again rejecting the hypothesis that a planktonic phase leads necessarily to widespread dispersal. Around the Isle of Man itself, Lewis (in prep.) found significant genetic heterogeneity between populations of the queen scallop *Chlamys opercularis*, a species with a larval life of 'about five weeks' (Macleod *et al.* 1985). Such differences may be due to restricted gene flow, differential selection or different sources of recruitment. Earlier work (Macleod *et al.* 1985) showed one allele to be restricted to a particular year class in several populations, from which it was inferred that there was temporal variation in the source of recruitment.

Further complications to the genetic uniformity hypothesis include the western Irish Sea front (Simpson 1971, 1981, Simpson and Bowers 1979) and the directional currents of the Irish Sea which, unlike the front, may be temporally unstable. On the basis of residual currents for the whole year (Ramster and Hill 1969) it has been assumed that larvae are

transported from south to north past the Isle of Man (eg. Khan and Williamson 1970, Macleod *et al.* 1985). This may be misleading however, as the residual flow for the early summer months is likely to be in the opposite direction in the western Irish Sea (unpublished predictions by Bartsch from the IfMH model: Backhaus 1985, Backhaus and Hainbucher 1987). Indeed, a southward advection of *Nephrops norvegicus* larvae has been noted in the western Irish Sea (White *et al.* 1988). In this area *N. norvegicus* larvae are in the plankton from May to August (de Figueiredo and Thomas 1967, Farmer 1973, White *et al.* 1988).

The size frequency distributions of adults in this study were in general unimodal with minimal skew. In *Inachus dorsettensis* males, however, a bimodal distribution was observed at Bradda and in certain months at Laxey. A similar result was obtained by Hartnoll (1963). This is likely to be due to variation in the number of juvenile instars rather than variation in the terminal moult increment. Whichever variable is responsible, the bimodal result indicates two consistent size classes of terminal instar males. This may be related to the reproductive activity of the adult males, although no data exist to confirm or deny such a hypothesis. In the congeneric *I. phalangium* (Diesel 1986, 1988) large males generally have higher reproductive success than small ones. Large male size, relative to the female and relative to potential competitors, is a feature of the mating behaviour of various other brachyuran species (eg. *Chionoectes bairdi*, Donaldson and Adams 1989; *Cancer magister*, Butler 1960; *Trapezia* spp., Huber 1985).

The results obtained for juveniles are of more limited value. Some modes are recognisable which, if they genuinely represent instars, indicate moult increments comparable to those found in the laboratory. This is the full extent of the information on growth that can be gained from these histograms. It was not possible to estimate growth rates due to limited sample sizes, such that pooling of periodic samples was necessary. Even if this had been possible, the results would have been affected to an unknown degree by the sampling technique. Dredges of the type used are known to select larger size classes when fishing for scallops (Chapman *et al.* 1977, Mason *et al.* 1979).

No estimates of abundance were made in this study, due to the doubts about the sampling method. Besides the known selectivity of the dredge, the catching efficiency for scallops is very low (Chapman *et al.* 1977, Mason *et al.* 1979). In addition, the composition and volume of the catch varied considerably, between successive tows and between sampling occasions. In the absence of hard data on selectivity, efficiency and variation, it was decided that abundance would not be estimated. Direct observation by diving was not attempted either; due to the cryptic habits of these species (Hartnoll 1963) sampling by this method, if possible at all, would have suffered considerable bias.

Despite the lack of quantitative abundance estimates, it is possible to make broad comparisons with the abundances reported by Hartnoll (1963). The sites in which both species had been abundant in this earlier work were selected for the present study. As described earlier very few specimens of the Majidae generally were found, on repeated occasions, using similar gear to that used by Hartnoll (1963). In the whole of this study the number of *Inachus dorsettensis* sampled was similar to that of Hartnoll (1963): 2922, of which only 308 were caught at Bradda, against his 2457. Far fewer *Hyas coarctatus* were caught in this study: 187 against Hartnoll's 3328.

Clearly, both species are far less abundant around the south west of the Isle of Man than they were thirty years ago. As these populations have not been studied in the intervening years, one cannot comment on the nature of this decline or attribute it to causative factors. It should be noted, however, that the south west grounds have been dredged extensively for the scallop *Pecten maximus* since the early 1960s (Brand *et al.* 1991, and in press). The fishery began in 1937 but fishing effort, and presumably benthic disturbance, was relatively light in the early years. The size and sophistication of the vessels increased, and the fleet size doubled between 1962 and 1969 (Brand *et al.* in press). It is known that scallop dredges lift fine sediments, bury gravel and overturn embedded rocks thus roughening the bottom, incurring lethal and sublethal damage to scallops left in the track (Caddy 1973). Bradda, where I found small numbers of spider crabs remaining, is included in these commercially dredged areas. Extensive dredging has taken place on the east coast also (Brand *et al.* 1991,

and in press), but this activity has not extended as far inshore as the area which I sampled at Laxey (P. Crebbin pers. comm.). Although no time-lapse comparison is available, *Inachus dorsettensis* was very abundant in this area in the present study. There appears to be some correlation, therefore, between disturbance and the grossly-observed patterns of spider crab abundance.

Finally, the sex ratio results merit brief discussion. Although the range of areas sampled was not exhaustive, there is little evidence for spatial segregation which would cause the observed excess of adult females. Bias in the sampling method would be expected to be in favour of the larger individuals (Chapman *et al.* 1977, Mason *et al.* 1979), thus over-representing the males. This suggests that the actual predominance of adult females may be more extreme than that observed. Biased sex ratios have been reported frequently for Crustacea (Wenner 1972). Hilsinger (1976) found that in juvenile *Chionoecetes bairdi*, caught by otter trawl, the sex ratio changed from unity to a predominance of females with increasing size; the adults were spatially segregated, precluding direct observation of their sex ratio. In *C. tanneri* (Pererya 1967, in Hilsinger 1976) adult samples had a 2.5 female/male ratio on the breeding grounds, similar to that estimated for *C. bairdi* (Hilsinger 1976). Tagging studies with *Cancer pagurus* (Edwards 1979, Bennett and Brown 1983) have demonstrated breeding-related migrations of females, which would complicate observation of the sex ratio. Jones (1980) found a greater frequency of males than females in all size classes of the estuarine grapsid *Helice crassa*. The two species studied here both show a switch in the sex ratio between the juveniles and the adults. They could therefore be classified as 'anomalous' under Wenner's (1972) scheme. It is unclear which of the possible factors - differential mortality, growth, activity or migration, or even inequality of the sex ratio very early in the life history - is responsible for this phenomenon.

Chapter 3.

**Growth of juveniles through to maturity in
Hyas coarctatus and *Inachus dorsettensis*.**

3.1. Introduction.

Crustacean growth is a much studied subject. Some of the earlier work was on the growth of one body part relative to a reference dimension of the body (eg. Huxley 1924, 1932 onwards). Crustacea are eminently suitable for this due to their rigid exoskeleton and the shape differences between the sexes and between stages of the postlarval life cycle. More recently the moult cycle, and its underlying hormonal mechanisms, have received much attention (Skinner 1985, Skinner *et al.* 1985, Fingerman 1987). Because of its outwardly-discrete cyclical nature, growth in Crustacea dominates the physiology of the animal as a whole. It is for this reason that there is currently much investigation of growth at the biochemical level. The rate of growth in terms of body length or weight has been studied in many species, especially those of commercial importance. A knowledge of growth rate is important in managing exploited populations of these species.

A further reason for studying growth, the reason that this study was made, is to attempt to understand why different growth (and reproductive) patterns have evolved in different species and groups of species (Hartnoll 1982). A diversity of growth-reproductive patterns has been observed in the Brachyura and the decapod Crustacea generally (Hartnoll 1982, 1985). The determinate and indeterminate growth formats are widespread, showing little correlation with higher taxonomic level, and it is not known why two formats should have evolved (Hartnoll 1982). As stated earlier (Chapter one), spider crab growth is determinate and reproduction, in females and probably also the males of all species, is limited to this terminal instar (Hartnoll 1963, 1982, Conan *et al.* 1990).

The primary aim of the experiment described in this chapter was to determine growth rate of *Hyas coarctatus* and *Inachus dorsettensis* in the laboratory. Maintenance conditions were designed in such a way as to perturb the animals minimally, in order to obtain growth rates as close as possible to those in the natural habitat. To this end, animals of a range of sizes were brought into the laboratory in all seasons and kept at the appropriate, gradually-changing temperature. Thus growth was measured through the juvenile instars and at the moult to maturity, in relation to temperature and season. These data are discussed in relation to studies on

other brachyuran species, referring particularly to sex differences and juvenile moult puberty moult differences. More importantly perhaps, the results for the females are used in the model described in Chapter five. This model explores the possibility of adaptive value of different growth-reproductive patterns in these and other species.

The experimental analysis of growth in Crustacea poses special problems. In many species growth in body size occurs only at the moult, although growth of the soft tissues is cyclical. To study the former one must consider the size increment at the moult and the period between moults. The effects of external factors such as temperature may affect these two elements in quite different ways (Hartnoll 1982) so they must be considered individually. Once this is done, they may be combined to show stepwise growth over time (Hartnoll 1982) or combined to fit a continuous growth function (eg. Bennett 1974, Conan and Gunderson 1979). A continuous function is not a realistic description of growth, but may be a useful descriptor of growth for, for example, the management of commercially important species.

There are additional problems, due to the difficulty in ageing crustaceans and the morphological similarity of successive instars (Chapter one). These factors tend to complicate study of population biology in the field (Chapter two) to a greater extent than the study of laboratory growth.

3.2. Materials and Methods.

A system of tanks, shown in Fig. 3.1, was constructed for this experiment. My overall aim was to house animals individually in a system which could run continuously for several months. The water system was flow-through, fed from a piped supply which was in turn pumped from the sea into holding ponds. This arrangement was such that the temperature in the experimental system was approximately the same as that of the sea in winter and slightly warmer in the summer (see Fig. 3.2). The water was filtered through polymer wool (shown in Fig. 3.1) which was cleaned or replaced every week. The incoming flow of water was continuous except for these brief filter-servicing periods. The outflow of water was periodic, effected by a syphon-type outlet, designed to ensure water flow through the solid-walled compartments. The water level oscillated through 5 cm, so that each 15 cm cubic compartment varied between near full and near two-thirds full. The compartment assemblies were raised from the bottom of the tanks in order to avoid accumulation of faeces and silt in the compartments. The total volume of each tank was 163 litres maximum, 132 litres minimum. The tanks were kept covered and the animals experienced continuous darkness.

The experiment was run continuously over a 500 day period. Individuals were kept for two moults, except when the first moult was the terminal moult or when a death occurred. Batches of animals were brought into the experiment in all seasons. Individuals of both species and of both sexes were collected as described in section 2.2. These were then kept in temporary holding tanks with running seawater for a maximum of one week. Each one was then assigned at random to one of the available compartments.

The experiment was observed daily, to check for the presence of moult casts and to measure temperature. Moult casts were dried in air at room temperature then measured using a low power microscope to the nearest 0.01mm. Temperature was recorded to the nearest 0.1°C. All animals were fed frozen adductor muscle of the queen scallop, *Chlamys opercularis*. This was done every three days, to slight excess after removal of food left over from the previous feeding. Faecal material fell through

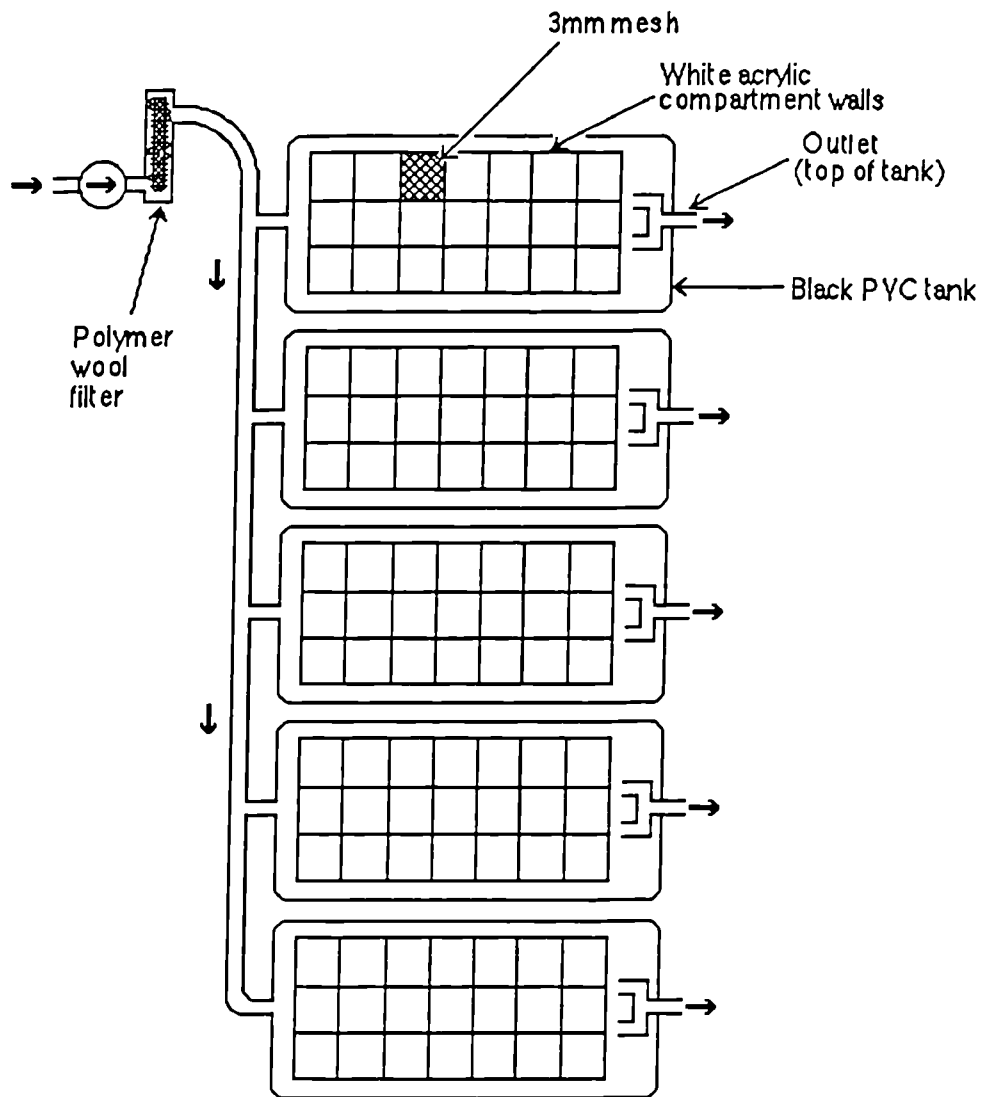


Fig. 3.1. The tank system used for the growth experiment.

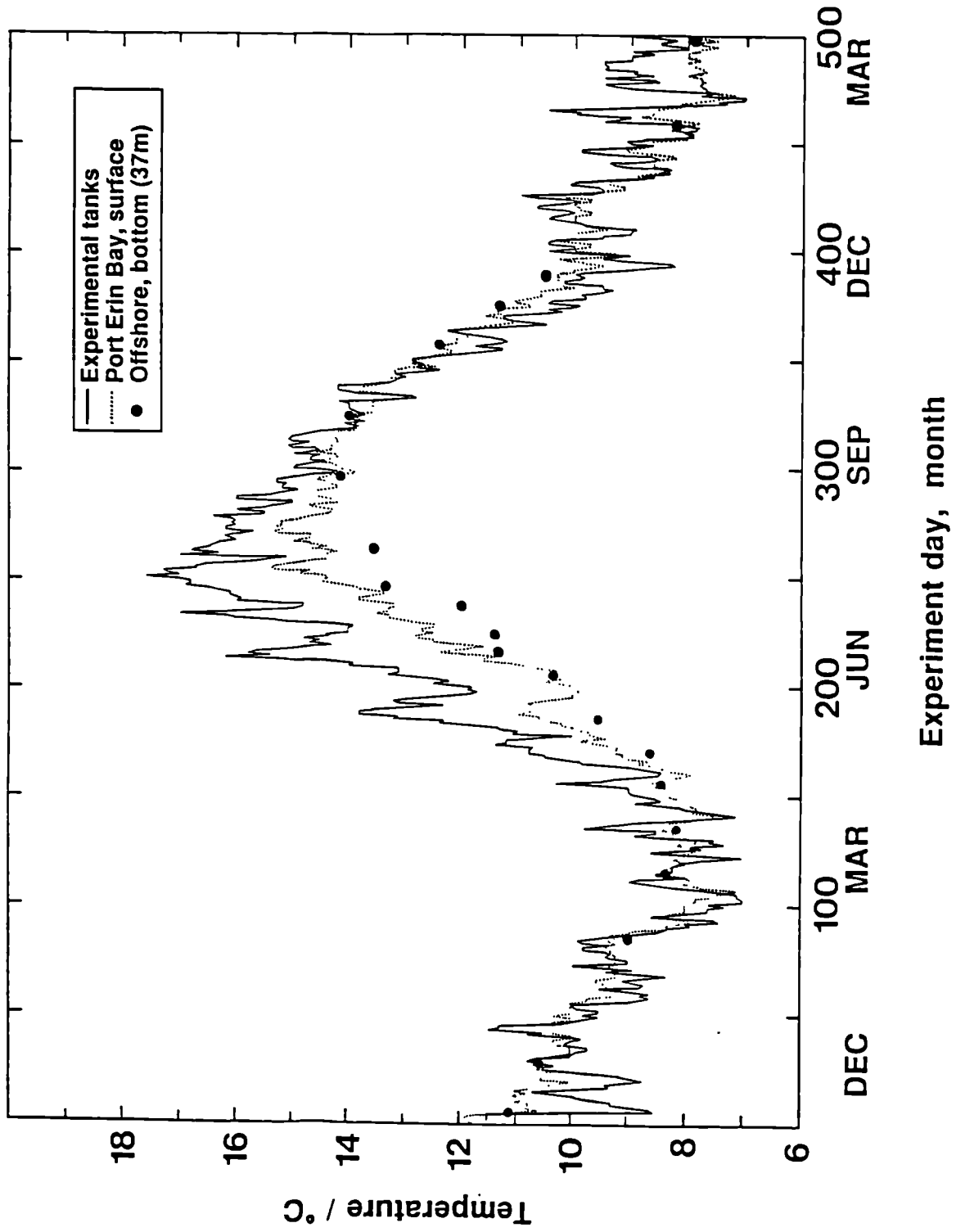


Fig. 3.2. Seawater temperature throughout the duration of the growth experiment.

the mesh bottoms of the compartments and was cleared periodically from the bottom of the tanks.

Since the temperature varied gradually, in step with the changing sea temperature through the year (Fig. 3.2), calculation of moult and intermoult temperature had to be done separately for each individual. A short computer program was written for this purpose (given in Appendix one). The program took the day, month and year of an individual's first and second moults and the daily temperature record as input data. Intermoult period to the nearest day and mean intermoult temperature were calculated. The temperature at the time of the moult was calculated as the mean of six days surrounding the moult. Further analysis of the data was performed using Minitab (Release 7.2, Minitab Inc. 1989).

Absolute growth was analysed in terms of the size increment at the moult and intermoult period (Hartnoll 1982). Moult increment was expressed as size increase as a percentage of premoult size and was angularly transformed prior to the application of parametric statistics. The relationship of these two dependent variables with carapace length (CL) and temperature was investigated. The difference between juvenile and terminal moult increments was also considered. In females, juveniles are morphologically distinct from adults (Hartnoll 1963), but the difference is less obvious in males. Relative growth of the chelae was used successfully to discriminate between these two life history stages of the male. This analysis also considered the moult of pre-puberty, using the segmented regression method of Lovett and Felder (1989). A computer program (given in Appendix two) was written for the fitting of these lines and calculation of goodness-of-fit statistics. For this analysis the data were in general not logarithmically transformed. In the absence of *a priori* justification for this commonly-used transformation (Cock 1966, Smith 1980, Lovett and Felder 1989), raw metrical data were used for these regressions. Model II regression analyses were used and are referred to in the text as geometric mean (GM) regressions (Ricker 1973). When the consideration of two predictor variables was necessary, least squares regression was used.

3.3. Results.

3.3.1. *Hyas coarctatus* females.

Preliminary analysis of percentage moult increment is shown in Fig. 3.3. As indicated, no significant correlation with CL was found for either the juveniles or the moults to maturity. A significant negative correlation is shown with temperature, but only in the juvenile group. Percentage increment thus decreases with increasing temperature in juveniles. The scatterplot indicates that moulting occurred over the full temperature range that is observed typically in the Irish Sea (see section 5.2.3), but with larger numbers of moults at the lower temperatures in both groups. However, low temperature should not necessarily be interpreted as a cause of increased frequency of moulting, as the experiment was run over a period including two winters and only one summer (Fig 3.2). Furthermore the numbers of individuals in each group was not constant over the whole period of the experiment.

The percentage increment of juveniles and individuals moulting to maturity is compared in Table 3.3. As this analysis concerns males as well as females it is described in full in the next section. For the females alone it shows that the mean increment for terminal moults is significantly smaller than that for juveniles.

Moult increment was also analysed in terms of postmoult versus premoult CL (*sensu* Hiatt 1948, Kurata 1962). This analysis is useful for comparison with other published work and is used in the construction of the model in Chapter five. Strictly, however, this analysis reveals nothing which is not shown in the percentage increment analysis, and is in some respects inferior to it (Mauchline 1977, Hartnoll 1982). Juvenile and maturity moults were treated separately, and equations were fitted by GM regression:

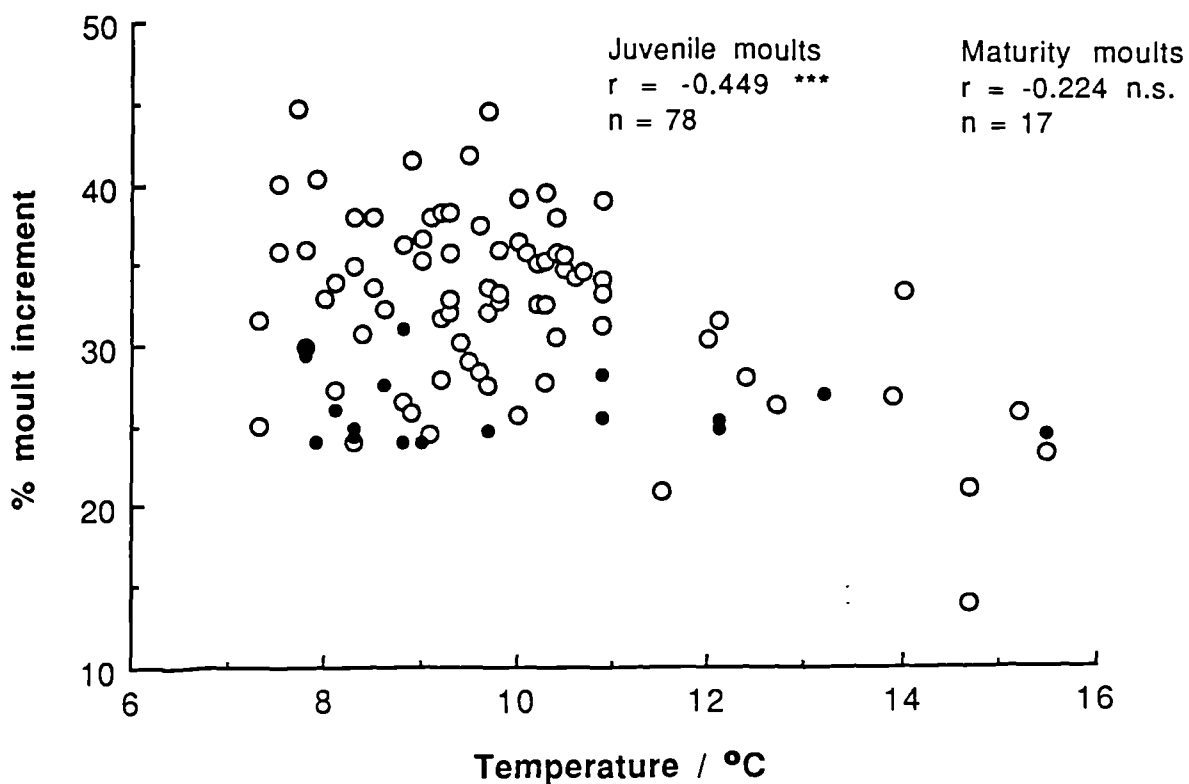
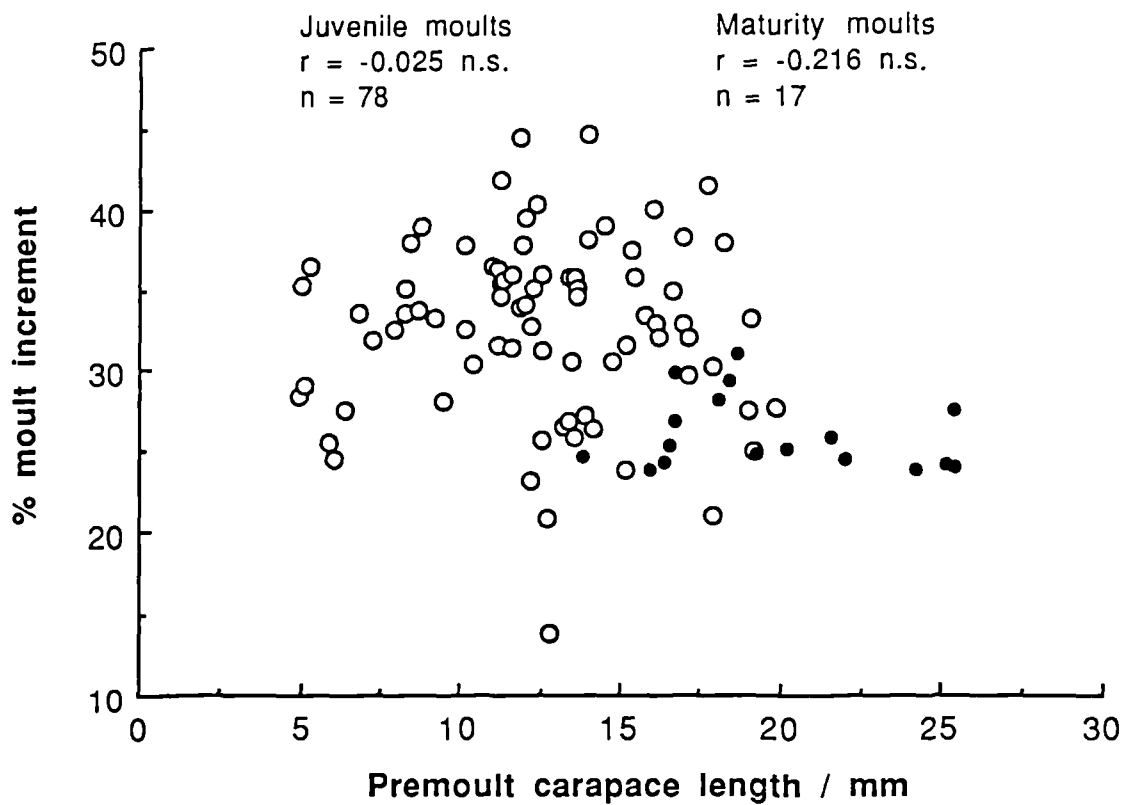


Fig. 3.3. The moult increment of female *Hyas coarctatus*. The open circles represent juvenile moults; closed circles represent moults to maturity. The correlation coefficients were calculated from angular transformed percentage data.

Juvenile moults:

$$CL_{i+1} = 0.007 + 1.33CL_i \quad \text{where } CL_{i+1} = \text{postmoult CL, mm}$$
$$CL_i = \text{pre moult CL, mm.}$$

$$r = 0.988$$

$$n = 78$$

Observed range of CL_i : 4.97 - 19.9mm.

Maturity moults:

$$CL_{\text{terminal}} = 0.555 + 1.23CL_i$$

$$r = 0.996$$

$$n = 17$$

Observed range of CL_i : 13.8 - 25.4mm.

The effect of CL and temperature upon intermoult period is shown in Fig. 3.4 and Table 3.1. From Fig. 3.4 there would appear to be little evidence for considering juvenile and penultimate instar individuals separately; the two groups follow the same basic pattern with respect to both CL and temperature. The data are therefore pooled in the regression analysis in Table 3.1. This shows that intermoult period increases with increasing CL, and decreases with increasing temperature. The fit of the linear model is highly significant and explains 46.3% of the variance in intermoult period.

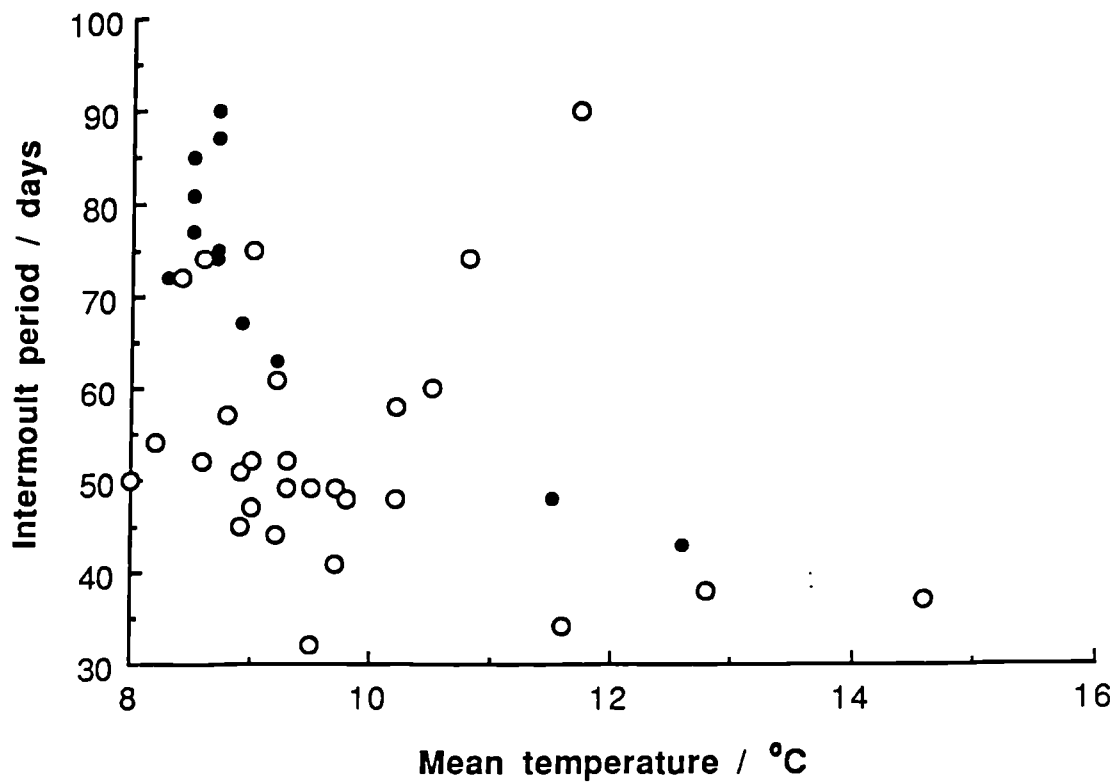
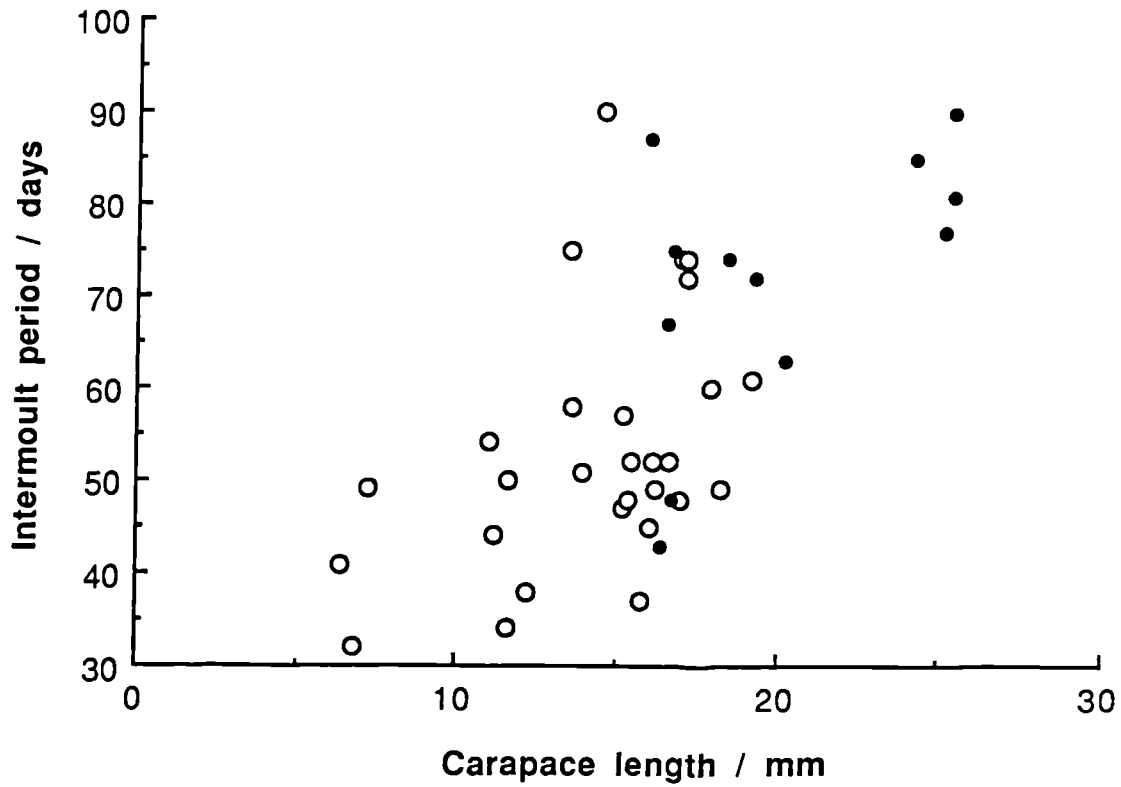


Fig. 3.4. The intermoult period of female *Hyas coarctatus*. The open circles represent juvenile non-penultimate instar individuals; closed circles represent penultimate instar individuals.

Fitted equation (by least squares regression).

$$P = 57.1 + 2.12CL - 3.34T$$

where P = intermoult period, days
 CL = carapace length, mm
 T = temperature, °C
 averaged over the intermoult

$$R^2 \text{ (adjusted)} = 46.3\%$$

Analysis of variance.

Source	d.f.	S.S.	M.S.	F	P
Regression	2	5009	2505	17.8	<0.001
Residual	37	5199	141		
Total	39	10210			

Significance of each fitted parameter.

Predictor	Parameter	S.D.	t ratio	P
Constant	57.1	16.1	3.55	<0.001
CL	2.12	0.438	4.83	<0.001
T	-3.34	1.36	-2.46	<0.05

Table 3.1. Regression of the intermoult period of *Hyas coarctatus* females on the size of the animal and mean temperature.

3.3.2. *Hyas coarctatus* males.

Adults are shown to be clearly separable from the juveniles in Fig. 3.5, on the basis of relative growth of the chelae. This discrimination is important for the analysis which follows, in which juvenile and maturity moults are compared.

The form of the relative growth is described by Fig. 3.5 and Table 3.2. In the juvenile group two straight lines were fitted, below and above 15mm CL. This was selected as the most "appropriate" point on the basis of SSR and RR. The inset graph of Fig. 3.5 shows these two statistics calculated for different CL break-points. If a break-point is assumed to exist *a priori* then its position is indicated by a minimum in the SSR line and a maximum in the RR line. In this example there is a range of CL (14-17mm) over which the transition occurs. There is a second peak in RR at 11-12mm CL, at which point there is no corresponding minimum in SSR. This transition point was rejected as spurious as it was indicated by only one statistic rather than by both. The details of the equations fitted to the juvenile subgroups are given in Table 3.2. As indicated, the two juvenile slopes differ significantly, which strengthens the evidence for this hypothesised transition point. Furthermore when only a single line was fitted to the juvenile group, the residuals were found to be large (SSR = 14.0) and non-random (RR = -3.34, $P < 0.001$).

A similar analysis was performed for the adults. No evidence of a transition point was found using both untransformed data and logarithmic data. A single line was therefore fit to this group (see Fig. 3.5 and Table 3.2).

As with the females of this species, neither juvenile nor maturity moult increments showed a significant correlation with CL (Fig. 3.6). Percentage increment of both moult types was negatively correlated with temperature however (same figure). The large scatter plot indicates that moulting in the two groups occurs over almost the full temperature range investigated, with slightly fewer moults at the higher temperatures. Again, this should not be interpreted as a tendency to moult with increasing frequency at lower temperatures, for the same reasons as described for females.

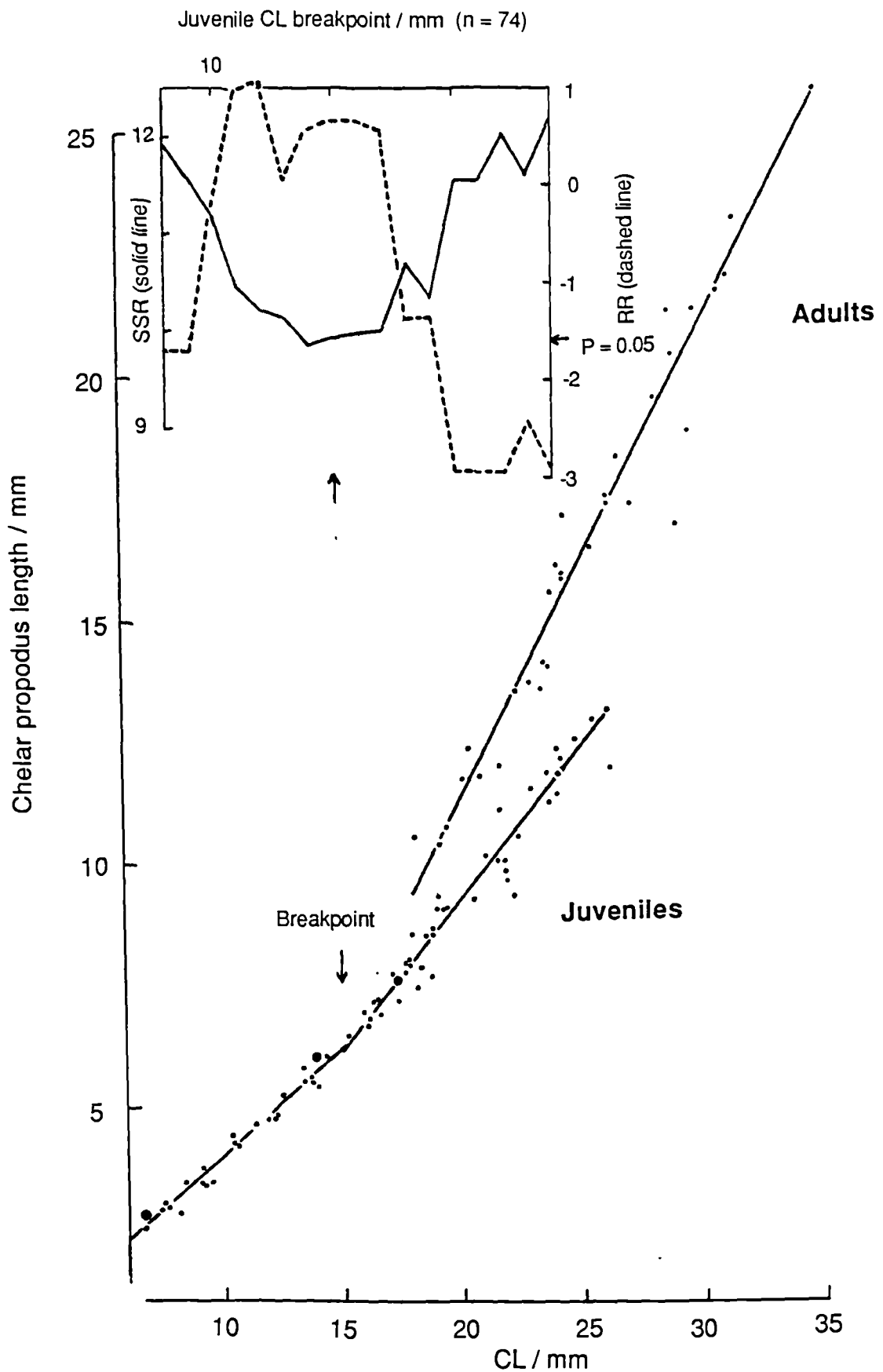


Fig. 3.5. The relative growth of *Hyas coarctatus* male chelae. Enlarged circles indicate the coincidence of two data points. The statistic SSR (sum of the squared residuals) represents the deviation of the fitted lines from the data. The statistic RR (randomness of residuals) represents a lack of systematic deviation from the fitted lines. Both statistics are from Lovett and Felder (1989).

Fitted equation (using GM regression).

$$\text{CPL} = a + b\text{CL}$$

where CPL = chelar propodus length, mm
 CL = carapace length, mm.

Parameters.

Group	n	a	b	r	Applicable CL range, mm	
					Min.	Max.
Juveniles (1)	28	-0.408	0.445	0.988	6	15
Juveniles (2)	46	-3.21	0.625	0.974	15	26
Mature	32	-8.18	0.976	0.974	18	35

Test for equality of the two juvenile slopes (Clarke 1980).

$$\begin{aligned} T &= 7.658 \\ \text{Var}(T) &= 1.056 \\ \text{d.f.} &= 37.8 \end{aligned}$$

$$P < 0.001$$

Table 3.2. Relative growth of the chelae of *Hyas coarctatus* males. Parameters of the fitted equations and a comparison of slopes for the two juvenile sub-groups.

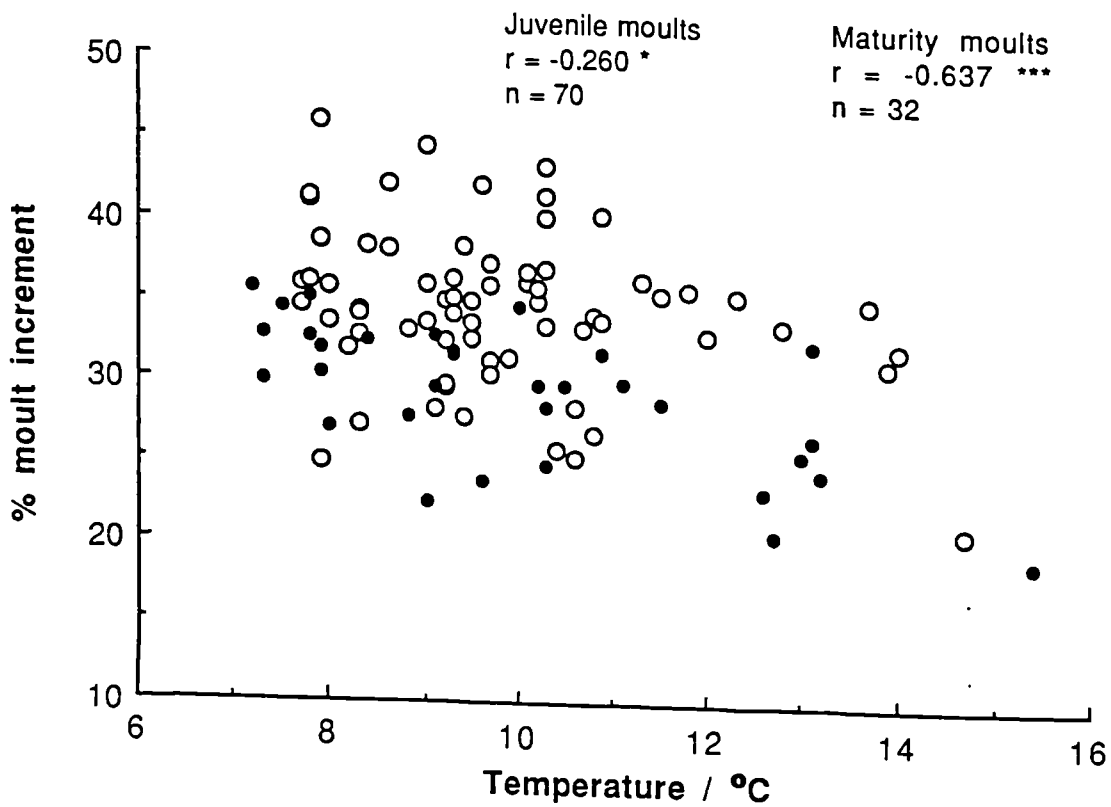
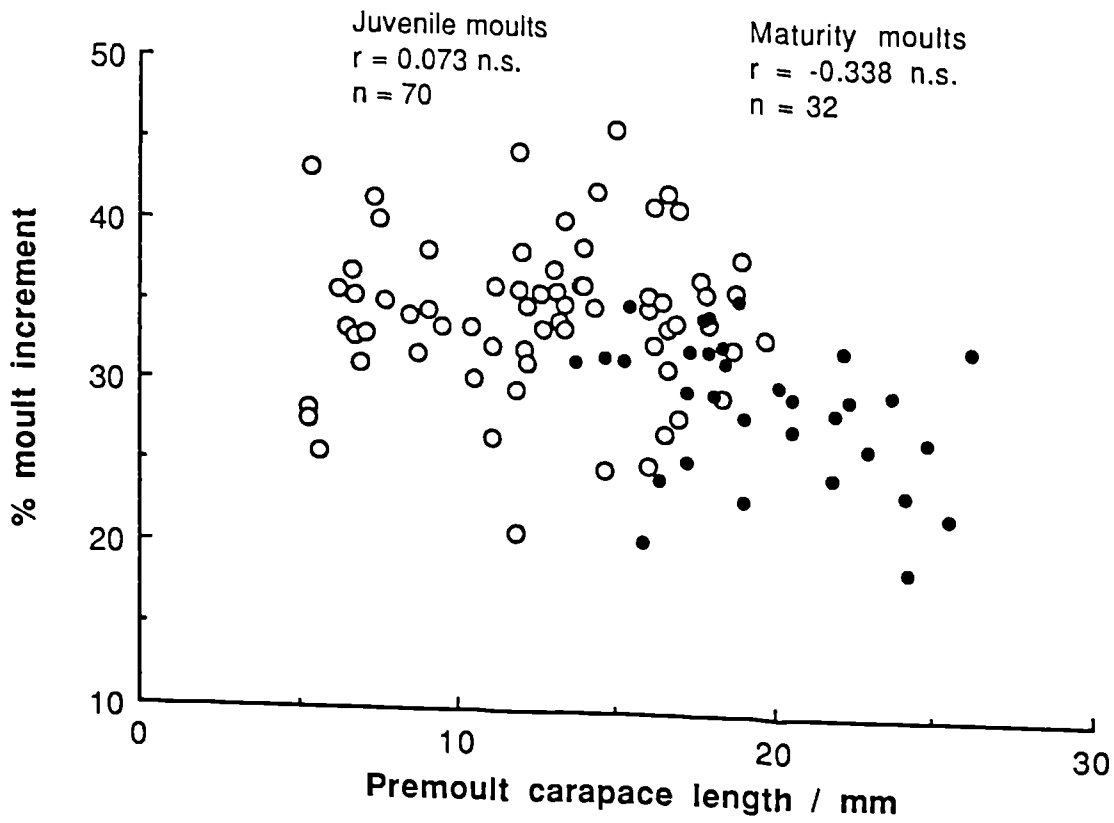


Fig. 3.6. The moult increment of male *Hyas coarctatus*. The open circles represent juvenile moults; closed circles represent moults to maturity. The correlation coefficients were calculated from angular transformed percentage data.

A comparison of percentage increment between moult types and between sexes is given in Table 3.3. In the analysis of variance the interaction between the two factors is not significant, so their effects may be considered to be independent of each other. Both sex and moult type have a significant effect upon percentage increment. The means, back-transformed to percent in Table 3.3, indicate that female moults are smaller than male moults, and that maturity moults are smaller than juvenile moults.

Intermoult period was analysed in the same way as was done for the females, treating juvenile and penultimate instar individuals as a single group (see Fig. 3.7). Linear regression using both predictor variables showed that mean temperature did not contribute significantly to the equation (t ratio = 0.09, P = 0.93). Consequently, regression using only CL as a predictor is shown in Table 3.4. This table shows that the two fitted parameters differ significantly from zero and that the equation explains 39.6% of the variance, a smaller percentage than that explained in females.

Analysis of variance.

Source	d.f.	adj. S.S.	adj. M.S.	F	P
Sex	1	0.0230	0.0230	8.04	<0.01
Moult type	1	0.142	0.142	49.5	<0.001
Interaction	1	0.00141	0.00141	0.49	n.s.
Residual	191	0.547	0.00286		
Total	194				

Means, back transformed to % (large figures), and **sample sizes** (small figures).

		Sex			
		Female		Male	
Moult type	Juvenile	32.7	78	34.5	68
	Maturity	26.1	17	29.1	32

Table 3.3. Comparison of the percentage increment between females and males, and between juvenile and maturity moults, in *Hyas coarctatus*. The comparison is an unbalanced two factor crossed ANOVA on angular transformed data.

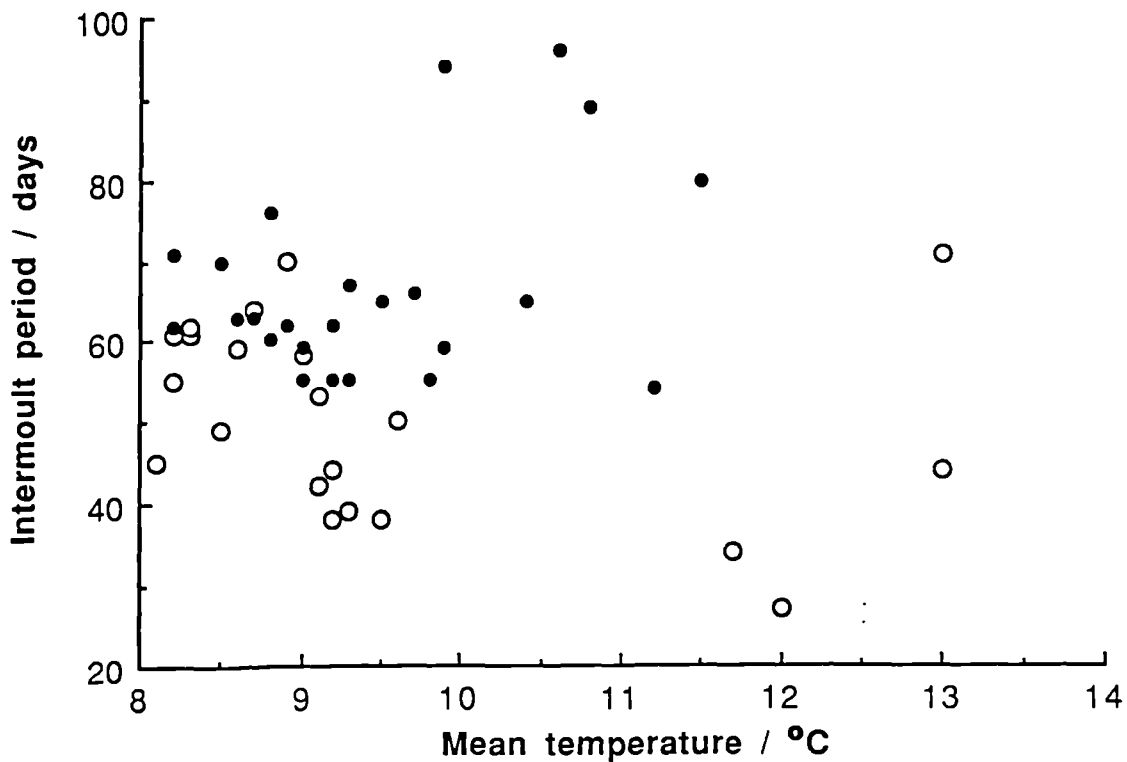
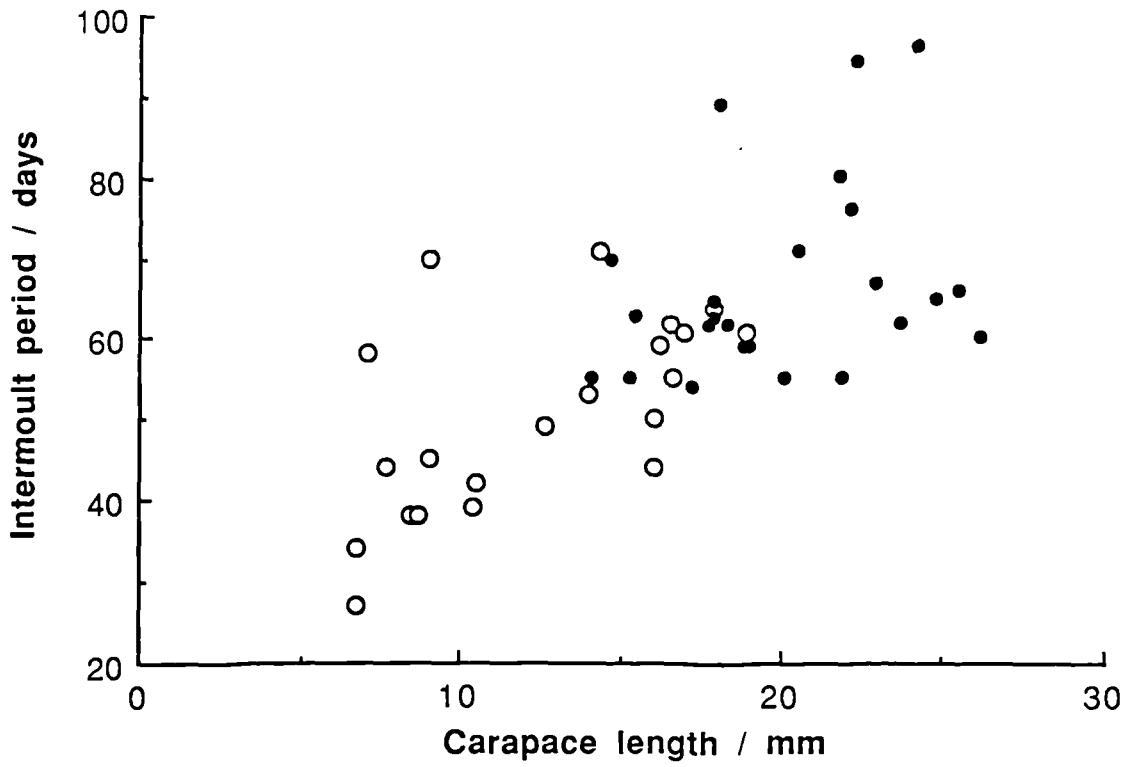


Fig. 3.7. The intermoult period of male *Hyas coarctatus*. The open circles represent juvenile non-penultimate instar individuals; closed circles represent penultimate instar individuals.

Fitted equation (by least squares regression).

$$P = 31.2 + 1.68CL$$

where P = intermoult period, days
CL = carapace length, mm.

$$R^2 \text{ (adjusted)} = 39.6\%$$

Analysis of variance.

Source	d.f.	S.S.	M.S.	F	P
Regression	1	3780	3780	29.9	<0.001
Residual	43	5440	127		
Total	44	9230			

Significance of the fitted parameters.

Predictor	Parameter	S.D.	t ratio	P
Constant	31.2	5.40	5.77	<0.001
CL	1.68	0.308	5.46	<0.001

Table 3.4. Regression of the intermoult period of *Hyas coarctatus* males on carapace length.

3.3.3. *Inachus dorsettensis* females.

Scatterplots of percentage increment are shown in Fig. 3.8. There is no significant correlation, for either juvenile or maturity moults, with either CL or temperature. Percentage increment is analysed further in Tables 3.5 and 3.6. The former indicates that juvenile moults are significantly smaller than maturity moults, the opposite of that found for *Hyas coarctatus*. Table 3.6 shows that maturity moults were undertaken at a significantly higher temperature than juvenile moults. Maturity moults were observed mainly during August and September despite individuals of penultimate instar size being in the experiment over the whole 500 day period.

Moult increment was also analysed in terms of postmoult versus premoult CL, for the same reasons as given for *Hyas coarctatus* females. The equations, fitted by GM regression, are:

Juvenile moults:

$$CL_{i+1} = 0.080 + 1.27CL_i \quad \text{where} \quad \begin{array}{l} CL_{i+1} = \text{postmoult CL, mm} \\ CL_i = \text{pre moult CL, mm.} \end{array}$$

$$r = 0.970$$

$$n = 45$$

Observed range of CL_i : 7.51 - 15.1mm.

Maturity moults:

$$CL_{\text{terminal}} = 1.68 + 1.20CL_i$$

$$r = 0.946$$

$$n = 25$$

Observed range of CL_i : 11.1 - 18.8mm.

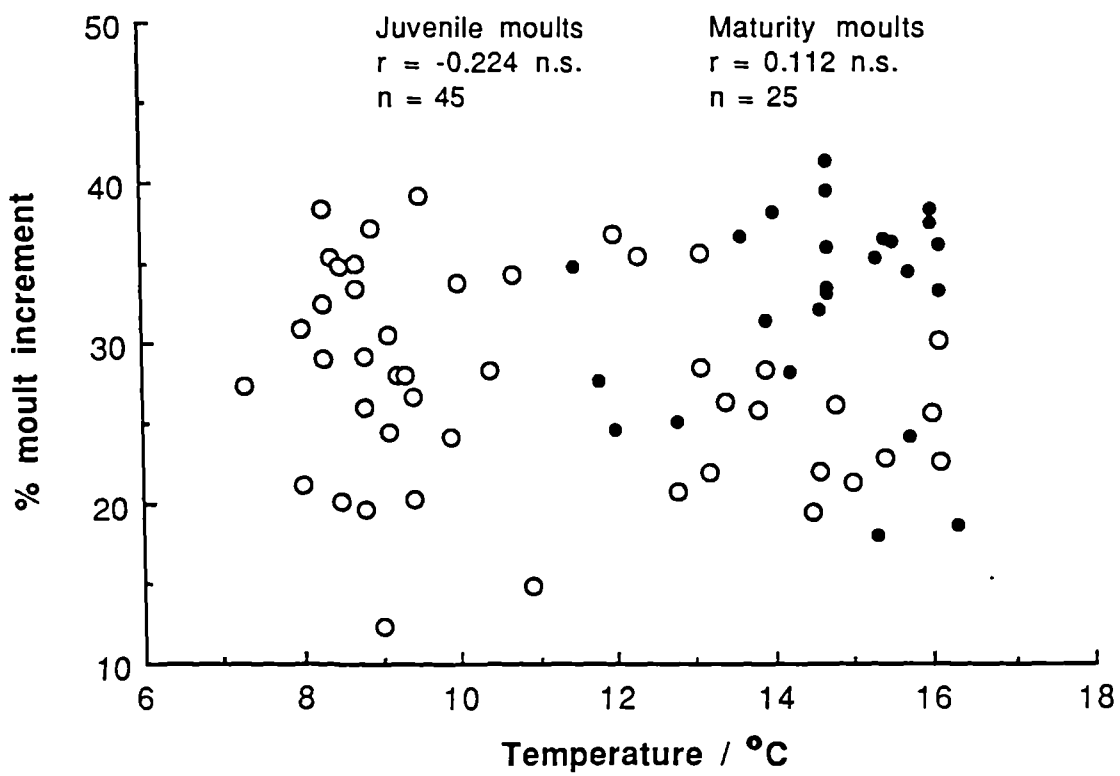
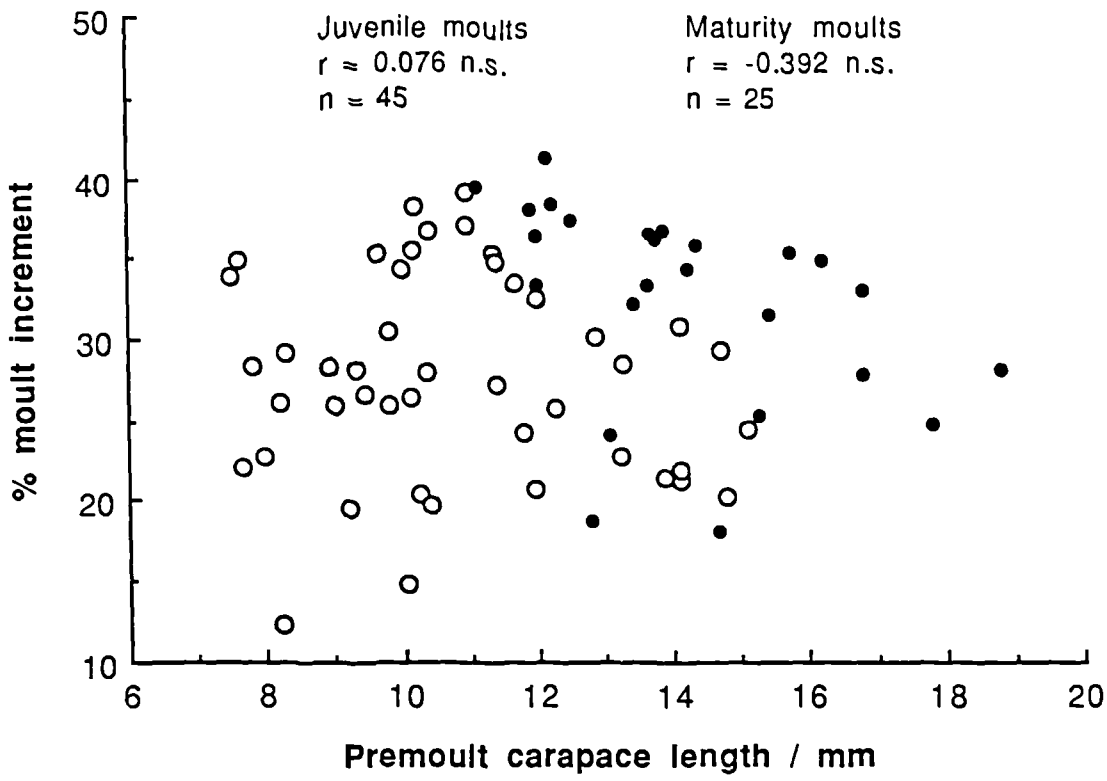


Fig. 3.8. The moult increment of female *Inachus dorsettensis*. The open circles represent juvenile moults; closed circles represent moults to maturity. The correlation coefficients were calculated from angular transformed percentage data.

Moult type	n	Mean %	Transformed data	
			Mean	S.D.
Juvenile	45	27.7	0.551	0.0728
Maturity	25	32.4	0.604	0.0690
			Pooled	0.0715

t = -2.95
d.f. = 68
P < 0.01

Table 3.5. Comparison of the percentage increment between juvenile and maturity moults in *Inachus dorsettensis* females. The statistic is Student's t calculated from angular transformed data.

Moult type	n	Mean °C	S.D.
Juvenile	45	10.9	2.71
Maturity	25	14.6	1.38

t = -7.51
d.f. = 67
P < 0.01

Table 3.6. Comparison of the temperature at which moults were undertaken, between juvenile and maturity moults, in *Inachus dorsettensis* females. The statistic is an unpooled Student's t.

Intermoult period analysis is shown in Fig. 3.9 and Table 3.7. Juvenile and penultimate instar individuals were again treated as a single group and regressed on the two predictor variables. CL was found not to contribute significantly to the equation (t ratio = -0.38, P = 0.71) and was therefore eliminated. Simple linear regression using only mean temperature (Table 3.7) accounts for 37.0% of the variance and both fitted parameters contribute significantly to the equation.

3.3.4. *Inachus dorsettensis* males.

As with *Hyas coarctatus* males, mature animals are separable from juveniles on the basis of relative growth of the chelae (Fig. 3.10). As there were only two mature individuals, no further analysis could be performed on that group. Within the juveniles however, a transition point of chelar growth is indicated at or near 18mm CL. Straight lines were fitted below and above this point, the slopes of which differed significantly from each other (see Fig. 3.10 and Table 3.8). A similar result was obtained when the data were logarithmically transformed, with the transition point being slightly lower at 15-18mm CL. The evidence for this point is not as strong as that for *H. coarctatus* juvenile males: when a single line is fit to the raw data, the pattern of the residuals is random (RR = -0.40, n.s.) although deviations from the line are considerable (SSR = 6.46).

Analysis of absolute growth was limited to juveniles as a result of the above discrimination. The percentage increment of this group (Fig. 3.11) is negatively correlated with CL but not significantly correlated with temperature. There is a paucity of data on intermoult period (Fig. 3.12). No significant correlation was found with either CL or mean temperature and consequently no regression analysis was attempted.

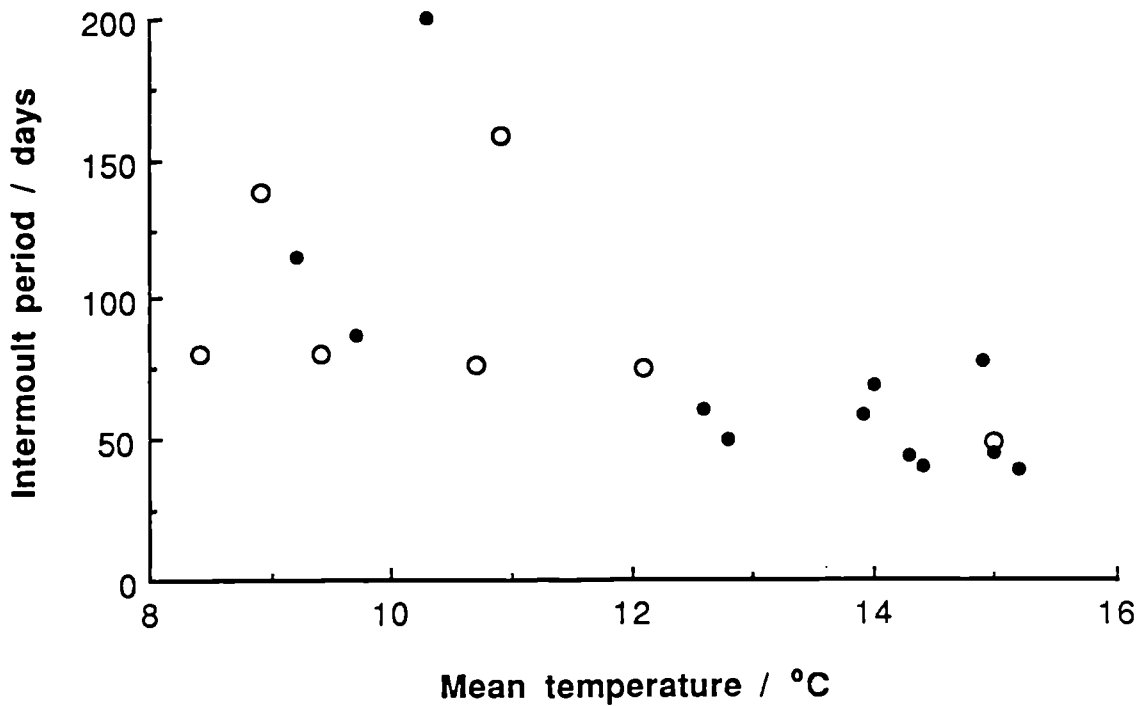
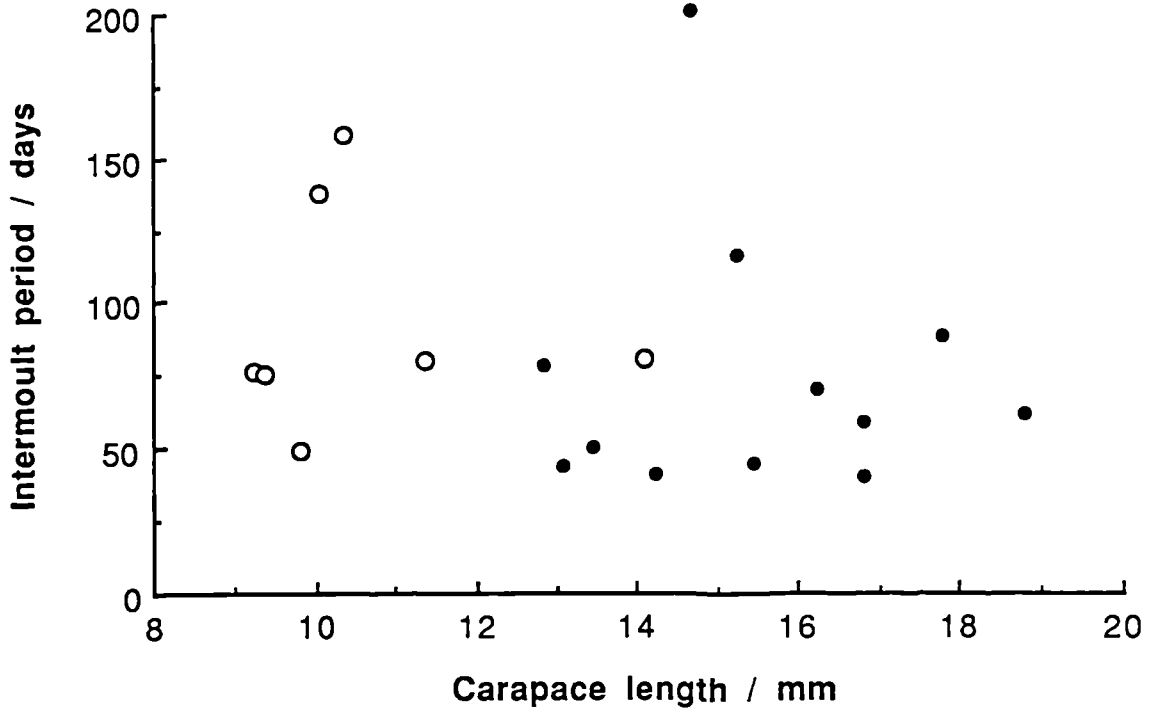


Fig. 3.9. The intermolt period of female *Inachus dorsettensis*. The open circles represent juvenile non-penultimate instar individuals; closed circles represent penultimate instar individuals.

Fitted equation (by least squares regression).

$$P = 221 - 11.4T$$

where P = intermoult period, days
T = temperature, °C,
averaged over the intermoult.

$$R^2 \text{ (adjusted)} = 37.0\%$$

Analysis of variance.

Source	d.f.	S.S.	M.S.	F	P
Regression	1	13580	13580	11.57	<0.01
Residual	17	19960	1170		
Total	18	33540			

Significance of the fitted parameters.

Predictor	Parameter	S.D.	t ratio	P
Constant	221	41.8	5.29	<0.001
T	-11.4	3.36	-3.40	<0.01

Table 3.7. Regression of the intermoult period of *Inachus dorsettensis* females on mean temperature.

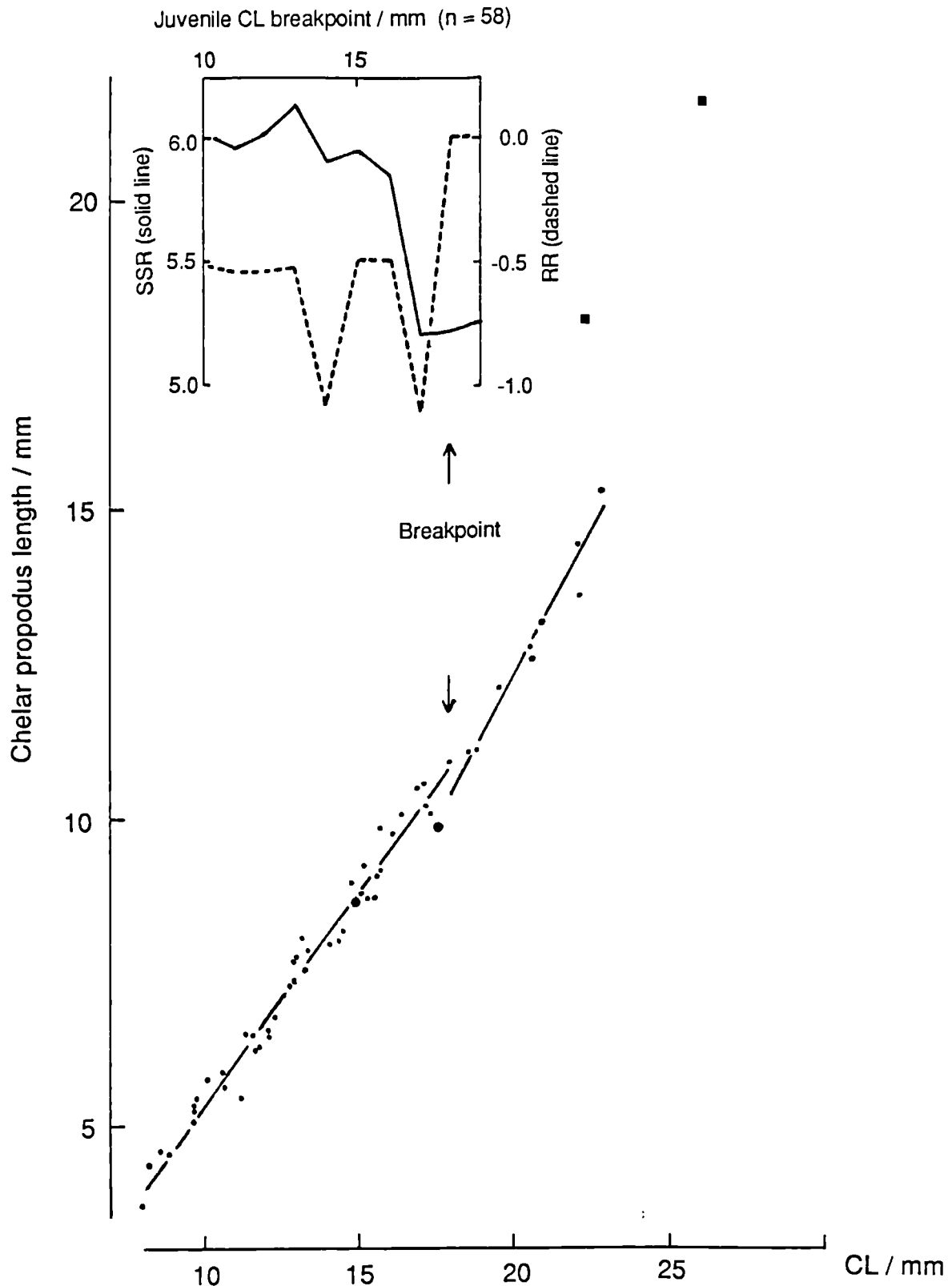


Fig. 3.10. The relative growth of *Inachus dorsettensis* male chelae. Enlarged circles indicate the coincidence of two juvenile data points. The two square symbols represent adults. The statistic SSR (sum of the squared residuals) represents the deviation of the fitted lines from the data. The statistic RR (randomness of residuals) represents a lack of systematic deviation from the fitted lines. Both statistics are from Lovett and Felder (1989).

Fitted equation (using GM regression).

$$\text{CPL} = a + b\text{CL}$$

where CPL = chelar propodus length, mm
CL = carapace length, mm.

Parameters.

Group	n	a	b	r	Applicable CL range, mm	
					Min.	Max.
Juveniles (1)	49	-1.462	0.682	0.987	8	18
Juveniles (2)	9	-6.539	0.940	0.975	18	23

Test for equality of the two juvenile slopes (Clarke 1980).

$$\begin{aligned} T &= 4.138 \\ \text{Var}(T) &= 1.284 \\ \text{d.f.} &= 9.03 \end{aligned}$$

$$P < 0.01$$

Table 3.8. Relative growth of the chelae of *Inachus dorsettensis* males. Parameters of the fitted equations and a comparison of slopes for the two juvenile sub-groups.

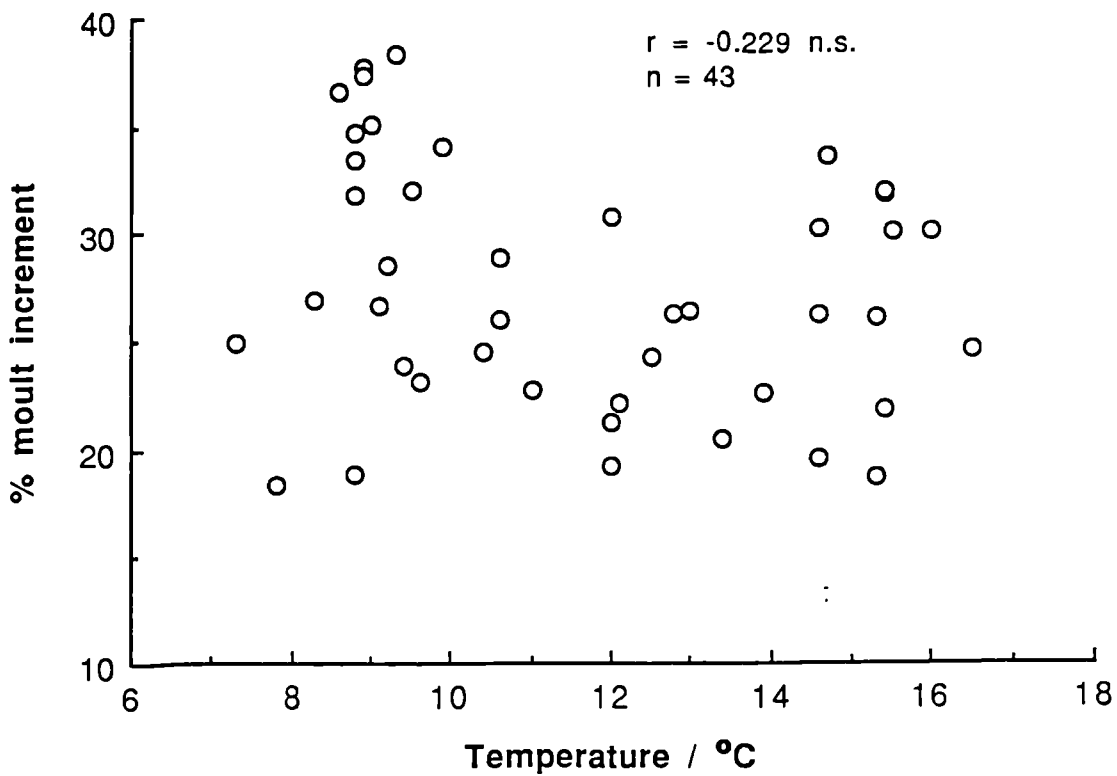
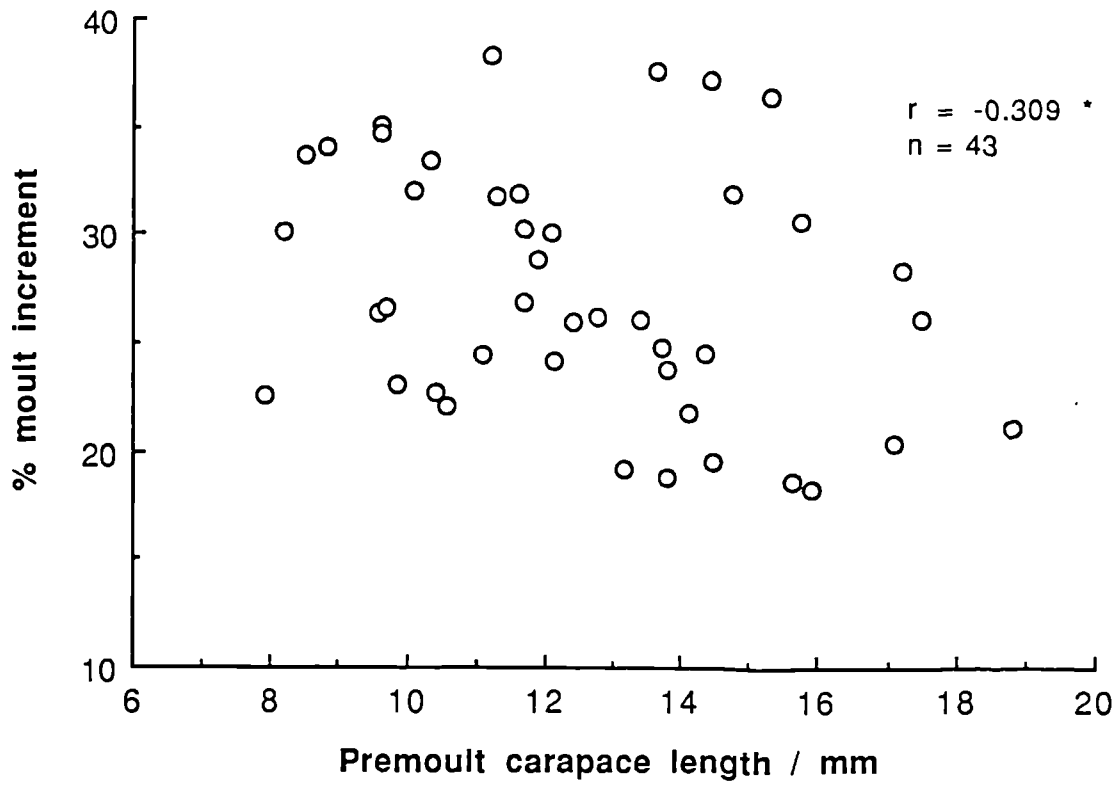


Fig. 3.11. The moult increment of male *Inachus dorsettensis*. Only juvenile moults are shown. The correlation coefficients were calculated from angular transformed percentage data.

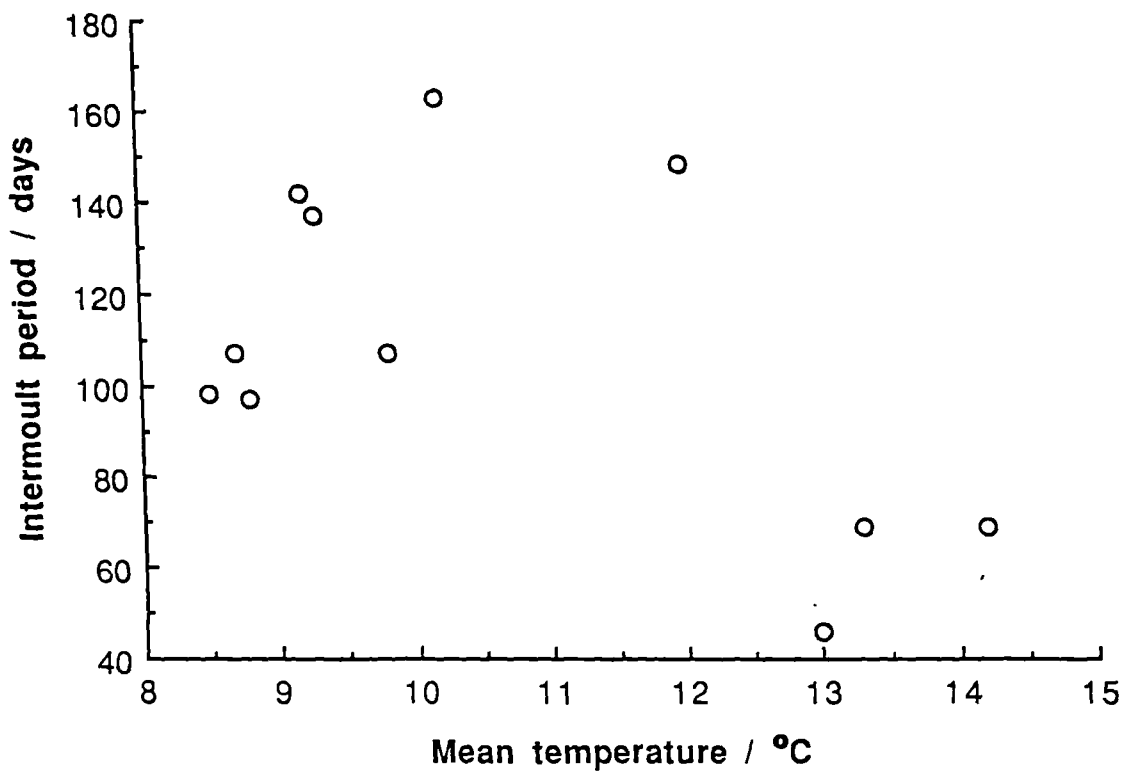
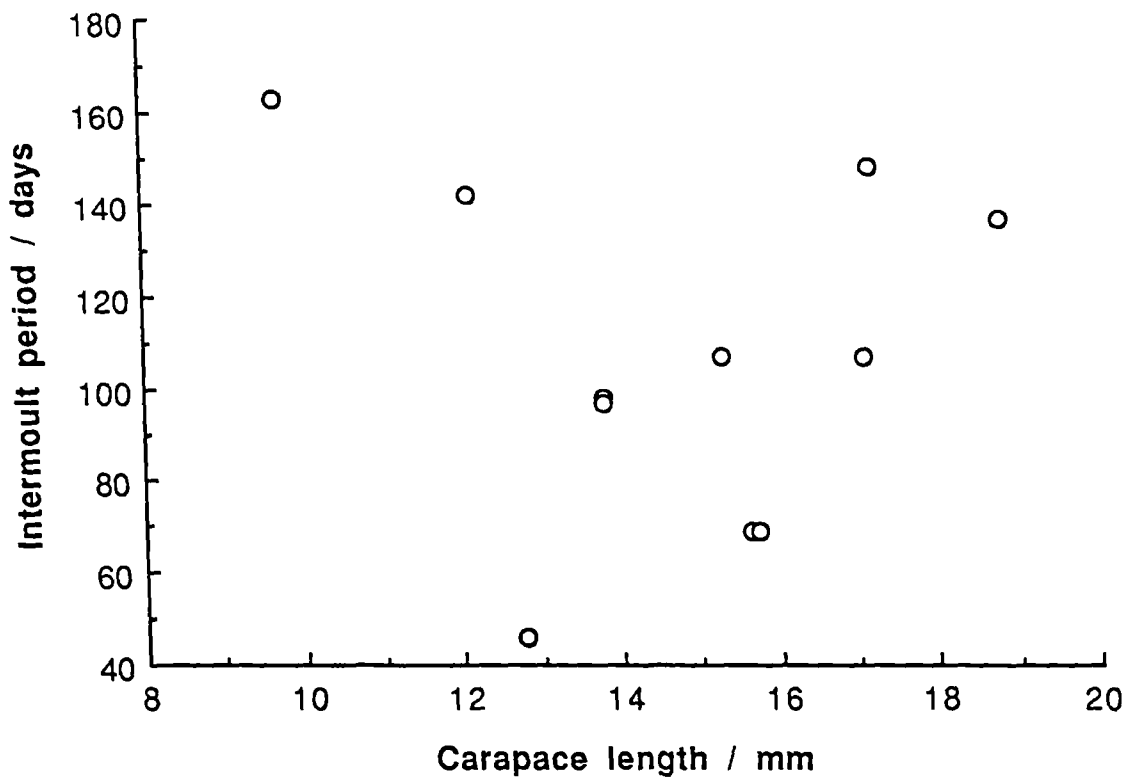


Fig. 3.12. The intermolt period of male *Inachus dorsettensis*. Only juvenile non-penultimate instar individuals are shown.

3.4. Discussion.

3.4.1. Relative growth of the chelae.

In the males of both species, mature individuals were clearly distinguishable from juveniles on the basis of chelar relative growth. This was possible by eye alone in the case of *Hyas coarctatus*, the separation being such that more sophisticated methods, such as discriminant function analysis as used for *Chionoecetes opilio* males by Conan and Comeau (1986), were unnecessary. For the discrimination of the two mature *Inachus dorsettensis* males, reference was made to Hartnoll's (1963) work on relative growth in field populations of this species in the same area. These relative growth analyses demonstrate morphometric maturity (*sensu* Conan and Comeau 1986) in males of these two species. As it has been shown that the puberty moult is the final moult in both sexes of both these species (Hartnoll 1963), it may be assumed that these morphometrically-mature individuals are in terminal anecdyasis.

Within the mature males of *Hyas coarctatus*, Hartnoll (1963) found a point of inflexion in the chelar length-carapace length relationship. The difference in slope below and above this point, with both variates logarithmically transformed, was very slight. No such point was found in the present study. This may be because the subtle change in slope was undetected because of the variance around the regression line. Alternatively, the point may be genuinely missing as an artefact of the laboratory rearing.

A break-point was found, however, within the juvenile chelar length-carapace length relationships of both species. The slope is greater above the point than below, the same as was found by Hartnoll (1963). The CL at which the point occurs is similar to that found by Hartnoll in the case of *Hyas coarctatus*, but is slightly larger in *Inachus dorsettensis*. These comparisons must be regarded rather tentatively as there are no confidence limits available for these points, in either study.

3.4.2. Absolute growth.

In general, the percentage moult increment showed only weak relationships with the two factors investigated in this study. In *Hyas coarctatus* there was a tendency for it to decrease with temperature. Only in juvenile male *Inachus dorsettensis* did it decrease significantly with CL. The relationship with CL has been investigated for many species, but temperature has received less attention. Within the Decapoda moult increment tends to show no relationship with CL in determinate species, but a negative relationship is usually observed in indeterminate species (Hartnoll 1982). In *Callinectes sapidus*, a determinate species with a single mature instar, Leffler (1972) found no consistent change in increment with size but found a decrease with temperature. *Carcinus maenas* and *C. mediterraneus*, species which have a terminal anecdysis but several mature instars, show no significant decrease in increment with size (see Hartnoll 1982). Hines (1989) found no variation in increment with size, or between samples from neighbouring populations, in *Scyra acutifrons*, a majid of similar size to the species studied here. A significant but slight decrease (from 26% to 19%) with CL was observed in the majid *Pisa tetraodon*, in both males and females (Vernet-Cornubert 1958). In the males of another majid, *Maja squinado*, the volume increase at the moult remains nearly constant through seven pre-puberty moults but is smaller at the puberty moult (Carlisle 1957). In *Chionoecetes bairdi*, however, moult increment does decrease considerably with size, from 32-37% at 10-30mm CL to 15% at 130mm CL (Donaldson *et al.* 1981). A considerable decrease is seen also in juveniles of the congeneric *C. opilio* (Miller and Watson 1976).

In a number of species of Majidae it has been shown that the puberty moult is the terminal moult. Carlisle (1957) investigated the endocrinology of terminal anecdysis in *Maja squinado* and showed that it differed fundamentally from that in *Carcinus maenas*. In male *M. squinado* the Y organ (the site of moulting hormone production) was found to degenerate in this instar, such that the animal was physiologically incapable of moulting again. Vernet-Cornubert (1960) found a similar degeneration in *Pisa tetraodon* which caused the animals to enter terminal anecdysis. Hines (1989) stated that the puberty moult is terminal in *Scyra acutifrons*. There is strong evidence for a terminal

instar in *Hyas* spp., *Inachus* spp., *Macropodia* spp. and *Eurynome* spp. (Hartnoll 1963), although it is not known whether each sex of each species undergoes the Y organ degeneration that is found in *M. squinado* and *P. tetraodon*.

It would appear from this evidence, pertaining to thirteen species in seven genera, that a single reproductive terminal instar is the general condition for the Majidae. Recently, however, exceptions to this rule have been claimed for the genus *Chionoecetes*. Two species, *C. bairdi* and *C. opilio*, are fished commercially and consequently have received much attention. It was thought that male *C. opilio* may moult after puberty in the Bering Sea (Donaldson 1988), but that it does not in Atlantic Canada (Conan and Comeau 1986; Conan *et al.* 1988). There has been considerable debate about this because males, not females, are fished because of their large size. In the short history of Alaskan *Chionoecetes* fisheries management it has been assumed, rather strangely, that growth continues after puberty, and this growth format has been regarded as 'conventional wisdom' (Donaldson 1988, Conan *et al.* 1990). The Y organ, which produces a moulting hormone in Crustacea, does degenerate in both sexes of post-puberty *C. opilio*, but is never totally absent (see Jamieson *et al.* 1988). Post-puberty moulting may be possible in these species therefore, but direct evidence for this is lacking. The literature since 1986 suggests that neither sex of *Chionoecetes* spp. moult again following the puberty moult (Conan *et al.* 1990).

Decreasing increment with increasing temperature, which was found in *Hyas coarctatus* but not in *Inachus dorsettensis*, has been observed in a number of other species (Hartnoll 1982). Anger (1984) found a temperature, 9 °C, at which CL was maximised when rearing the first few crab instars of *H. coarctatus*. Size-in-instar decreased consistently with higher experimental temperature, indicating that the same effect as shown in this study is found in the smallest post-larval individuals.

The change in moult increment at the puberty moult, a decrease relative to juvenile moult increments, is similar for both sexes of *Hyas coarctatus*. A decreased puberty increment is also found in male *M. squinado* (Carlisle 1957), as mentioned earlier, and in *C. opilio* of both sexes (Miller and Watson 1979; Moriyasu *et al.* 1987). In female *H. coarctatus* the cause of

this may be the early diversion of resources to reproduction: it is known that the ovaries develop before the puberty moult in this species (Hartnoll 1963). That the same decrease should be shown in the males is rather difficult to explain, as the testes mature only after the puberty moult (Hartnoll 1963). Both male and female *C. opilio* undergo pre-puberty moult gonad development (Watson 1970) so a decreased increment at this moult is not unexpected in both sexes of this species.

Interestingly, *Inachus dorsettensis* females show an increased increment at puberty relative to the juvenile moults. In this species ovarian development occurs only after the puberty moult (Hartnoll 1963). This pattern of growth may be tentatively interpreted as a tactic for maximising body size in the terminal instar, subsequently enabling maximal egg production.

A final comment on moult increment may be made by comparing my results for *Hyas coarctatus* to those of Anger (1984). That author represented growth in the early post-larval instars not as percentage increment but as a 'Hiatt' or 'Gray-Newcombe' (Botsford 1985) diagram. The result is similar to that given in section 3.3.1 (juvenile moults), but his slope is slightly smaller and intercept slightly greater. Apart from the obvious differences in rearing conditions and populations sampled, part of this difference is caused by my use of reduced major axis (GM) rather than least squares regression. The former is more appropriate for data of this type (Ricker 1973, Sokal and Rohlf 1981 and numerous others), although the difference between techniques is minimal when the variance is small. A further possible reason why the results differ is the range over which data were taken; Anger examined growth up to the fourth post-larval instar whereas the present study considered from the third or fourth instar (estimated) through to maturity.

On intermoult period, fewer studies are available for comparison. This reflects the logistical problems involved in obtaining reliable data on this component of growth (Mauchline 1977, Hartnoll 1982, Botsford 1985). Direct observation, and therefore accurate determination, is possible only in laboratory studies. The difference between this accurately-determined

period and that in the field remains uncertain however. The problem is confounded by the great variability within species due to intrinsic and extrinsic factors (Hartnoll 1982). In the present study animals were kept for just two moults, specifically to minimise the time of laboratory observation per individual. The experimental conditions will inevitably have had some affect on intermoult period and, to a lesser extent, moult increment. The absolute extent to which the measurements are affected cannot be determined unfortunately.

Notwithstanding this doubt, some interesting trends can be extracted from these data. In *Hyas coarctatus* intermoult period increases with CL and, in the females, decreases with temperature. Both of these relationships have been observed in many species of Crustacea (Hartnoll 1982). The effect of temperature is apparent even in species in which moulting has not been investigated in the laboratory, as a distinct moulting season is often observed in the field. This is an extreme effect, probably wholly due to temperature, where moulting is suppressed in the winter season.

The conclusions for *Inachus dorsettensis* are more tentative as fewer data are available. The following pertains only to the females as the paucity of data for the males precludes further discussion. Intermoult period is negatively related to temperature in the females, but is unrelated to CL. A lack of relationship with size has been observed before only in a cirripede and several copepods, and in the special case of some larger species in which the moult is entrained annually (Hartnoll 1982). It is somewhat surprising that this should be observed in a decapod which is subject to only slight moulting seasonality (Hartnoll 1963).

A synthesis of the moult increment and intermoult period results is shown in Fig. 3.13. Due to the doubt raised earlier, some caution must be exercised in extrapolating from this laboratory study to growth in the field. The predictions shown in Fig. 3.13 are based on means for which considerable variance exists and are to some extent biased.

Initially the lag between the earliest and the latest *Hyas coarctatus* recruits is an estimated 42 days. In the females this is predicted to vary

subsequently, between 27 and 41 days, due to the effect of annual temperature variation upon intermoult period. This variation does not occur in male *H. coarctatus* as temperature does not affect intermoult period. Nevertheless the difference between the growth overall of the two sexes is small. In *Inachus dorsettensis* females the time lag between individuals settling at different times of the year will be variable as it is predicted that intermoult period is controlled by temperature alone.

These combined growth estimates enable prediction of the time and number of moults taken to reach maturity. To moult to adult size within the range observed in the field (Chapter two and Hartnoll 1963) a *Hyas coarctatus* female would be in its 5-9th juvenile instar. A male *H. coarctatus* would be in its 6-10th juvenile instar. For the female, a moult to maturity after the 8th or 9th instar would be possible within the puberty moult season after one year of juvenile growth. Similarly, a male's penultimate instar would be its 6-9th juvenile instar in the first puberty moult season. The overall prediction is that the full size range of adults is the result of just one year of juvenile growth. The range of sizes observed may be caused by the timing of metamorphosis, an individual's growth rate (affected by genetic and environmental factors) and the timing of the puberty moult. The prediction contrasts to that of Hartnoll (1963), who estimated that the smallest mature individuals had undergone one year of juvenile growth whereas the largest had undergone two years. This was based on size frequency analysis of field samples and a roughly-estimated 25% moult increment. Anger (1984), by extrapolation but taking into account the variance in growth, estimated that between five and fourteen moults would precede maturity in *H. coarctatus*.

Inachus dorsettensis is predicted to grow through 8-11 juvenile instars before moulting to a mature size within the range observed in the field (Chapter two and Hartnoll 1963). This would take between two and almost three years. In this species, Hartnoll (1963) was not able to estimate juvenile lifespan from field samples due to aseasonal recruitment, so comparison is not possible. The range in adult size, which is smaller than that of *Hyas coarctatus*, may be due to individual and environmental differences, and the timing of recruitment.

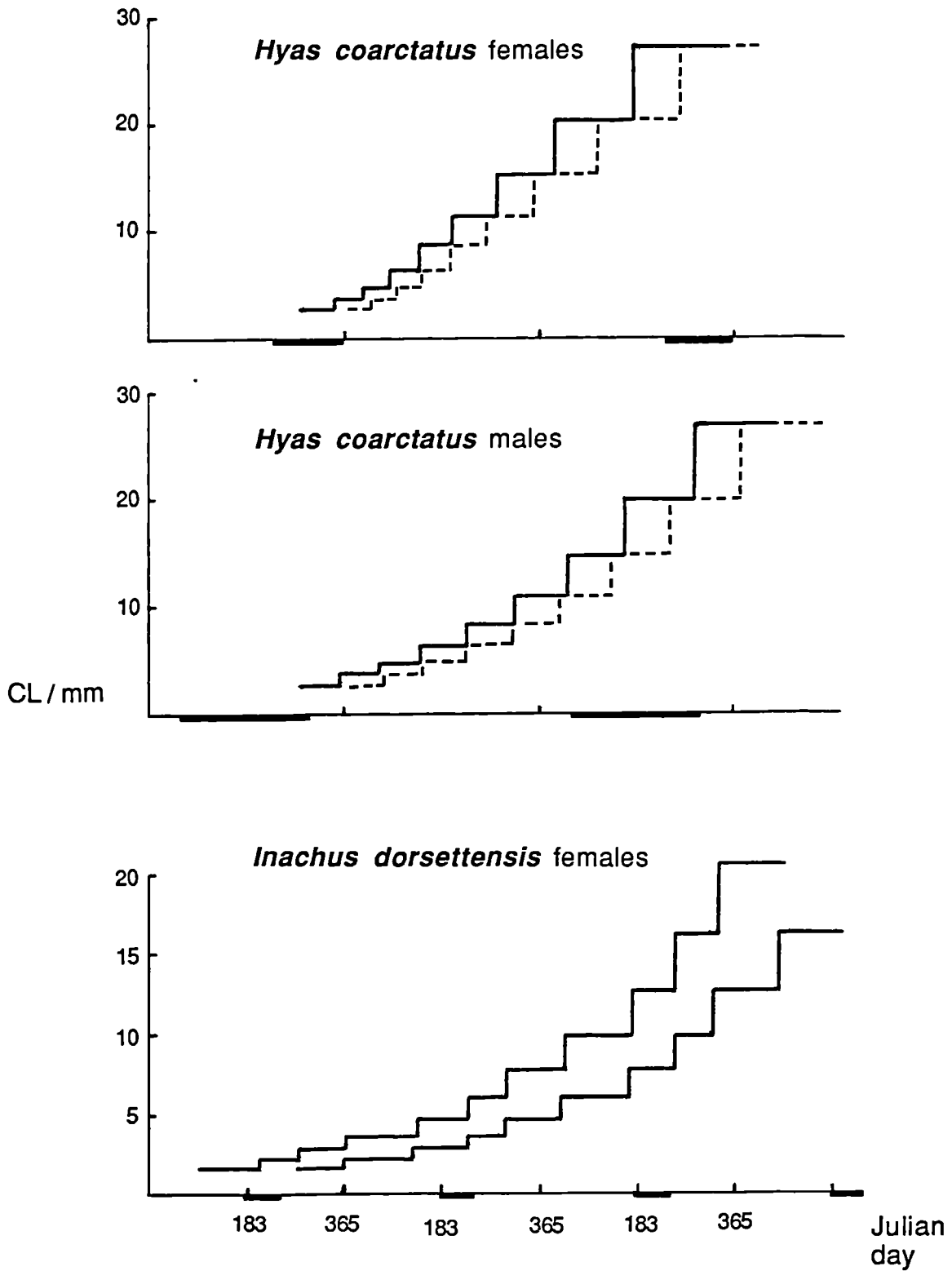


Fig. 3.13. Growth in body length over time. The two lines shown for *Hyas coarctatus* are derived from earliest and latest settlement to instar 1 (estimated in Chapter five). The two lines shown for *Inachus dorsettensis* females are derived from two possible dates of settlement. *H. coarctatus* first instar CL from Anger (1984). *I. dorsettensis* first instar CL from measurement of preserved samples. Bars on the abscissae indicate observed timing of maturity moults (Hartnoll 1963). The calculation of intermoult period under a constantly changing temperature regime is explained in section 5.2.3.

Chapter 4.

**Reproductive investment in mature female
Hyas coarctatus and *Inachus dorsettensis*.**

4.1. Introduction.

Reproduction and growth have traditionally been regarded as competing processes, with each requiring resources from the finite pool acquired by an organism (Sibly and Calow 1986, Clarke 1987). 'Trade-offs', negative relationships between variables, play a central role in life history theory (Stearns 1989). In iteroparous organisms, the trade-off between reproduction and growth prompts questions about the optimal timing of first reproduction and the number of broods (eg. Calow 1978, 1981). Another important trade-off is that between the size and number of gametes produced by an organism (Calow 1981). A very prominent life history trade-off (Stearns 1989) involves the cost of reproduction. Reproduction at one instant in time is generally assumed to be associated with costs of either or both of reduced survival probability (Stearns 1989) and reduced future reproductive performance (Calow 1979). These ideas on life history patterns, as observed and predicted for marine invertebrates, have been reviewed by Grahame and Branch (1985).

A first step towards understanding these life history trade-offs is the observation of variables of reproductive effort in natural populations. This chapter considers fecundity, egg size and energetic investment in reproduction in female *Hyas coarctatus* and *Inachus dorsettensis*. The latter variable was measured as reproductive output (weight-specific reproductive production), from which reproductive effort (reproductive output per unit time) was inferred. These variables represent the component tactics of the reproductive strategy of these species (see also sections 1 and 5.1, and Southwood 1988). They are studied here as being of interest in their own right and, in the case of fecundity at least, because of the relevance to the model of Chapter five.

The phenology of these species' life cycles is summarised in Fig. 4.1. *Hyas coarctatus* females undergo their terminal moult to maturity, the puberty moult, mostly in May to July with a few as late as September. The ovaries mature before this moult and mating then egg laying follow almost immediately afterwards. A long diapause follows the gastrula stage of egg development (Wear 1974) and it is not until March to April that the eggs hatch. In those animals which survive, a second batch of eggs is laid during

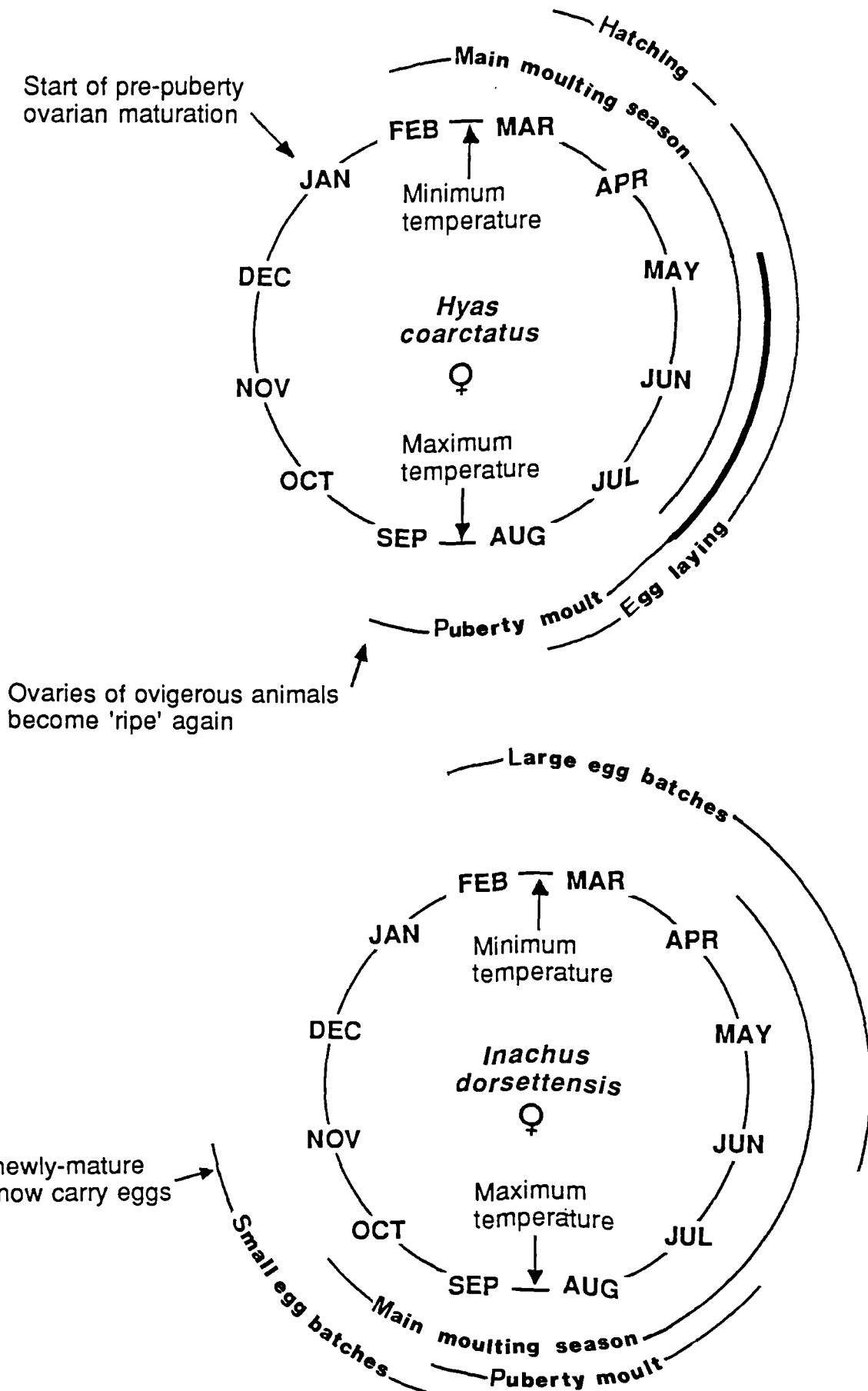


Fig. 4.1. The phenology of the life cycles of *Hyas coarctatus* and *Inachus dorsettensis* females. Data from Hartnoll (1963) and from Chapters two and three.

the period April to August. Egg development is synchronised with the seasons in this species.

Inachus dorsettensis females mature their ovaries only after the terminal moult, which occurs between July and September. After a short delay for ovarian maturation the first egg batch is laid in the autumn. These females are termed primiparous whereas those producing subsequent batches are termed multiparous (Paul and Fuji 1989). There is no diapause in this species (Wear 1974) and a second egg batch is laid in the spring. Hartnoll (1963) observed mostly small egg batches during September to November, presumably belonging to primiparous females. During February to June, females were observed carrying larger egg batches. Those early observations are quantified in this chapter. Egg development of *I. dorsettensis* is not synchronised with the seasons - all stages of development may be found in all seasons.

Hines (1982) has considered variables of reproductive effort in 20 species of brachyuran crab, including 6 majid species, from the east and west coasts of North America. Those data present, therefore, an ideal context in which to discuss the present results. Comparisons are made also with the reproductive ecology of the much-studied *Chionoecetes* species (Haynes *et al.* 1976, Foyle *et al.* 1989, Paul and Fuji 1989, Thompson and Hawryluk 1990).

4.2. Methods.

4.2.1. Fecundity.

At the beginning of this work the possibility of counting and sizing eggs using a Coulter Multisizer was considered. The principle of this technique is that particles, suspended in an aqueous medium, pass through an aperture and alter the conductance of the medium as they do so. The volume of a particle can be calculated from this alteration of conductance. The number of particles passing through the aperture per unit time is recorded and this gives an estimate of the number of particles in the suspension. The technique has been used successfully for barnacle eggs (Burrows 1988), which are of similar number (1000-7000) to the spider crab egg numbers but are smaller (less than half of the diameter).

It is necessary to separate eggs from each other prior to suspension in order to use a technique such as Coulter counting. Brachyuran eggs have a trichromatic polysaccharide membrane, the middle layer of which is chitin (Cheung 1966, Hartnoll in press). The outer layer of this membrane attaches to the setae of the endopods of the mother, becoming twisted and drawn out into strong threads to form the funiculus, the stalk of attachment. Cheung (1966) tried unsuccessfully to degrade the egg membrane of *Carcinus maenas* using amylase, pepsin, trypsin and chitinase. Barnes and Barnes (1968) separated barnacle egg masses by soaking them in Gilson's fluid (Bagenal 1966) followed by gentle agitation. Burrows (1988, pers. comm.) used a protease, Pronase E, to separate barnacle eggs.

Preliminary separation experiments were conducted with *Hyas coarctatus* and *Inachus dorsettensis* eggs, using a general protease in phosphate-buffered seawater, Gilson's fluid and a seawater control. These attempts were largely unsuccessful; the eggs were never completely separated and were therefore unsuitable for Coulter counting. Furthermore, significant size increases were noted in eggs subjected to these treatments. Eggs treated with Gilson's fluid became fragile and were difficult to handle without breakage. Due to the

inadequacy of separation in these experiments, counting and size analysis by the Coulter method was abandoned.

Diaz *et al.* (1983) described a volumetric method for estimating fecundity in decapods. This was tried, briefly and unsuccessfully, for the two spider crab species. Their method is appropriate where the egg mass has a total volume of approximately 1ml or more. The volume of *Hyas coarctatus* and *Inachus dorsettensis* egg masses was found to be too small to be measured accurately by this method.

A new method was developed for these two species, using fresh volume and dry weight. Firstly, fresh volume and dry weight per egg was estimated for each species and each early development stage 1-3 (Hartnoll 1963). A minimum and maximum diameter was measured for 10 eggs in seawater from each of 5 individuals using a binocular microscope, with minimum delay between removal of the eggs from the (live) animal and measurement. The figure of 10 was used after investigating the number required (up to 50) in order to estimate a population mean with a particular precision (Zar 1984). A sub-sample of 100 (in *Inachus dorsettensis*) or 200 (in *Hyas coarctatus*) eggs was removed from each of the 5 individuals and dried at 60°C for 48 hours. These small (4-9 mg) sub-samples were weighed using a Cahn electrobalance. From these measurements the 'density' of an average egg was calculated (Table 4.1). For each subsequent individual for which fecundity was to be estimated 10 eggs were measured (in the same way as before) and the dry weight of the whole egg batch was ascertained. The animals were killed (45 mins. in freshwater) before removal of the whole egg batch. Care was taken to exclude any endopodite material and to avoid breaking the eggs. The total number of eggs was estimated from mean egg volume, total dry weight and the appropriate 'density' following Table 4.1.

Egg number was regressed upon body size using a Model II technique (GM regression, Ricker 1973). A runs test (Lovett and Felder 1989) was used to test for randomness of residuals and comparisons between regression lines were made using Clarke's (1980) test. Where egg volumes are presented in the Results section, each replicate represents 10 eggs, measured as described above.

Table 4.1. Egg measurements of *Hyas coarctatus* and *Inachus dorsettensis*: fresh volumes and 'density' in dry weight per unit fresh volume.

Species	Egg dev. stage	Mean egg volume/mm ³ *	S.D. egg volume	Density mg mm ⁻³ **	S.D. density
<i>H. coarctatus</i>	1	0.067	0.004	0.569	0.035
	2/3	0.082	0.005	0.472	0.031
<i>I. dorsettensis</i>	1	0.103	0.007	0.472	0.031
	2	0.107	0.009	0.440	0.013
	3	0.171	0.014	0.264	0.025

* $\frac{4}{3} \pi r^3$ using $r=(d_1+d_2)/4$ where d_1 and d_2 are minimum and maximum measured egg diameters. The quoted numbers are means of the mean of 10 eggs per individual, 5 individuals.

** Mean of densities calculated for eggs of the 5 individuals.

4.2.2. Calorimetry and respirometry.

Terminal instar females were starved for 2 days, killed (freshwater for 45 mins.), dissected and dried at 60°C for 48 hours. Grinding of samples for calorimetry was done using a pestle and mortar or, in the case of some including exoskeleton, a purpose-built ball mill. Ash weight was measured, using material which was not required for calorimetry, after burning at 550°C for 4 hours. Calorimetric analysis was performed on the dried samples using a Gentry Instruments Phillipson microbomb calorimeter (Phillipson 1964). Calibration against benzoic acid was performed during the first day and, on each subsequent day that the machine was used, a single benzoic acid firing was performed. Determinations were made in triplicate for two replicate

specimens of each species at each egg development stage for soma, ovaries and eggs. Samples of *Inachus dorsettensis* were available for the 3 early stages, but for *Hyas coarctatus* stages 1, 2/3 and 4 (hatching) were used due to difficulty in obtaining samples. The few remaining unhatched eggs carried by the stage 4 specimens were not used in the analysis.

Closed-cell respirometry experiments were carried out at different times of the year at the ambient temperature of the sea on each occasion. Conditions were standardised as far as possible between these experiments. Jar size (353 ml for *Hyas coarctatus*, 1190 ml for *Inachus dorsettensis*) and experimental duration (8 hours) were determined after pilot experiments to establish typical oxygen consumption rates. Eight ovigerous females of each species, or slightly fewer when insufficient numbers were available, were used for each experiment. They were transferred from holding tanks to a tank of aerated, filtered seawater in a room at the temperature to be used in the experiment. An unfed 24 hour acclimation period followed before being transferred, individually, to jars held in another tank of aerated, filtered seawater. The jars were closed underwater, times were recorded and the tank was covered for the experimental period. In each experiment there were two control jars for each jar size. The light level was a semi-darkness which was consistent between experiments. Dissolved oxygen levels at the beginning and end of the experiment were measured using the Winkler titration (Parsons *et al.* 1984).

Summer and winter multiple temperature respirometry experiments were performed and followed the same basic procedure. Due to the difficulty in obtaining sufficient numbers of animals, the same specimens were used for each of the 3 temperatures tested. In September 1989 (14°C offshore bottom temperature) an 8 hour experiment was conducted at 14°C, preceded by a 24 hour unfed acclimation period. The animals were then allowed to feed on scallop (*Chlamys opercularis*) muscle over a 15 hour period whilst the temperature was reduced gradually to 10.5°C. Acclimation and experiment followed, as before, but at the lower temperature. Finally the temperature was reduced to 7°C over another 15 hour fed period, followed by acclimation and experiment as before. In early May 1990 (delayed due to unavailability of samples, 8°C offshore bottom temperature) an identical experiment was

carried out, but with the temperature sequence reversed. For this winter experiment the results are presented for only 6 replicate individuals, due to the difficulty in obtaining specimens of *Hyas coarctatus*.

Data analysis was done using Minitab (Release 7.2, Minitab Inc. 1989) and Genstat (Version 4.04b, Alvey *et al.* 1982, 1983, Weekes 1986). The multiple temperature respirometry experiments were treated as 3 factor ANOVA designs, with species, individual and temperature as factors. There is a mixture of nesting and crossing: individuals are nested within species, both of which are crossed with temperature. Species and temperature are fixed effect factors, individuals are random. Analysed in this way, the design has no replication.

4.3. Results.

4.3.1. Fecundity.

The egg number results for both species are shown in Fig. 4.2. For *Hyas coarctatus* GM regression of log egg number on log CL gave a slope of 3.45, indicating that egg number (E) varied very nearly as the cube of CL. Accordingly, E was regressed upon CL^3 to give the line which is shown on the graph:

$$E = -118 + 0.236CL^3$$

Units: CL is in mm

$$r = 0.919$$

$$n = 38$$

Residuals are random

(runs test, $P > 0.40$)

For *Inachus dorsettensis*, autumn (October - November) and spring (April - May) samples were analysed separately. A large proportion of the former sample represented females laying their first batch of eggs (primiparous), whereas the latter represented subsequently laid egg batches (multiparous - see Fig. 4.1.). In both cases, double logarithmic regression indicated that egg number was related to a power of CL greater than 3. As with *Hyas coarctatus*, CL^3 was used as the predictor variable for the lines shown on the graph. The equations are:

Autumn: $E = -443 + 0.106CL^3$

$$r = 0.639$$

$$n = 39$$

Residuals are random

(runs test, $P > 0.40$)

Spring: $E = -1380 + 0.438CL^3$

$$r = 0.809$$

$$n = 20$$

Residuals are random

(runs test, $P = 0.13$)

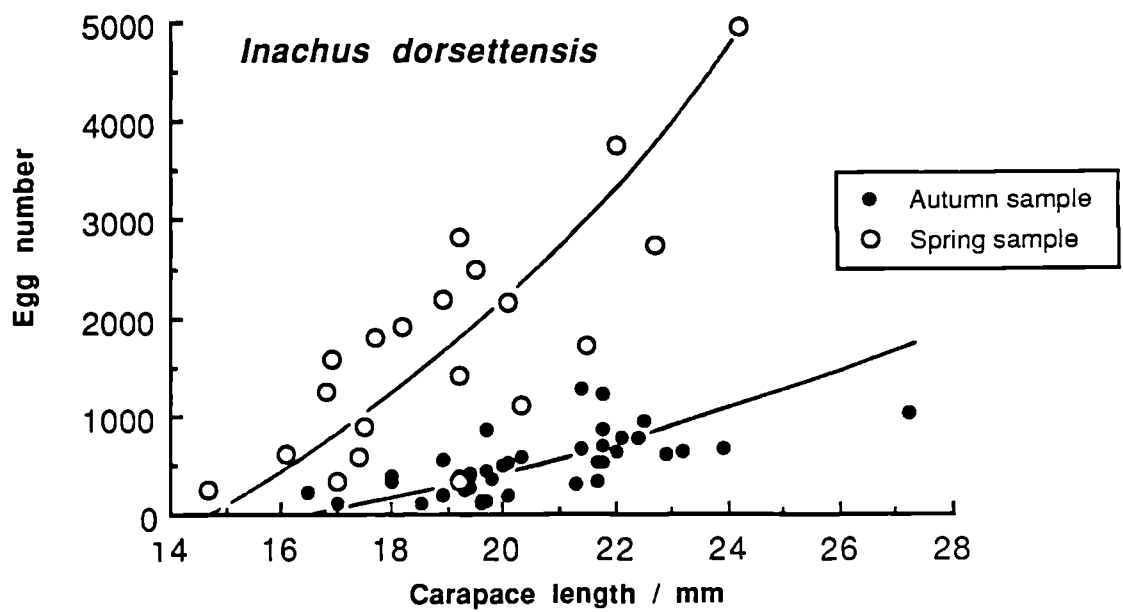
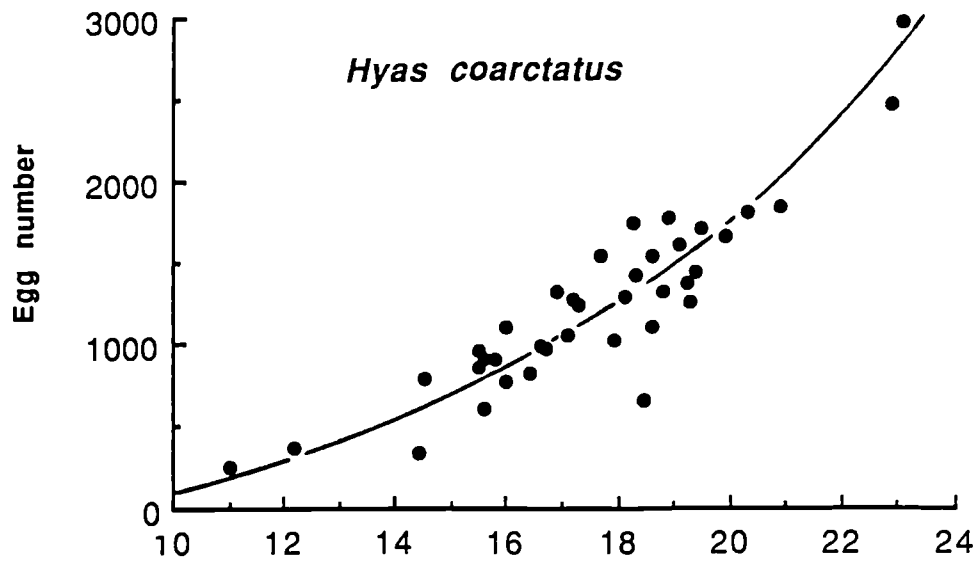


Fig. 4.2. The fecundity relationships of *Hyas coarctatus* and *Inachus dorsettensis* females. See text for details of the fitted lines.

The difference in slope between these two curves is highly significant ($T = 7.87$, $\text{Var}(T) = 1.078$, $\text{d.f.} = 27.6$, $P < 0.0005$).

There are problems in the use of the *Inachus dorsettensis* equations, as an egg number of zero is predicted for carapace lengths of 14.7 mm (spring) and 16.1 mm (autumn). Mature females, carrying eggs, have been observed which are smaller than these sizes. The slope of a GM regression is greater than that of least squares and this produces in turn a relatively low, in this case highly negative, intercept. Least squares solutions are as follows:

$$\text{Hyas coarctatus:} \quad E = -8.01 + 0.217\text{CL}^3$$

$$I. \text{ dorsettensis, autumn:} \quad E = -99.7 + 0.068\text{CL}^3$$

$$I. \text{ dorsettensis, spring:} \quad E = -790 + 0.355\text{CL}^3$$

The least squares equations are used in the Model chapter of this thesis (section 5.2.3.) as there is the need to calculate likely fecundities for a wide range of mature female sizes.

Egg size results are shown in Tables 4.2 and 4.3. Egg volume, at stage 1 of development, was found to be uncorrelated with both egg number and the size of the mother (Table 4.2). Stage 1 egg volumes were found to differ significantly between species (Table 4.3). In *Inachus dorsettensis* there was an 81% increase in volume between stages 1 and 3. In the latter stage the mean volume was 0.178 mm^3 (S.D. = 0.047, $n=18$). Wear (1974) found an 85% volume increase between extrusion and hatching in this species. Table 4.1 shows a slight decrease in the 'density' term in early development, and a marked decrease between stages 2 and 3 in *I. dorsettensis*. It is likely that increased water content with development causes this change. Holland (1978) found a similar dry weight for early *Hyas araneus* eggs, of which 0.8% was carbohydrate, 21.9% lipid and 56.5% protein. Lipid and protein are important yolk reserves in decapods and other benthic marine invertebrates, with up to 60% utilisation occurring before hatching of the eggs (Holland 1978, Amsler and George 1984).

Table 4.2. Stage 1 egg volume correlations in *Hyas coarctatus* and *Inachus dorsettensis*. The spring sample of *I. dorsettensis* was used in this analysis. None of the correlation coefficients is significant at the 5% level.

Species	Correlation with	r	n
<i>H. coarctatus</i>	Egg number	-0.251	35
	Mother's CL	-0.146	35
<i>I. dorsettensis</i>	Egg number	-0.191	15
	Mother's CL	-0.395	15

Table 4.3. Comparison of stage 1 egg volumes between *Hyas coarctatus* and *Inachus dorsettensis*. All available samples, from all seasons, were used. The statistic is Student's t, with pooled variances.

Species	Mean volume/mm ³	S.D./mm ³	n
<i>H. coarctatus</i>	0.0702	0.0073	35
<i>I. dorsettensis</i>	0.0983	0.0075	23
Pooled :		0.0074	

t = 14.15
d.f. = 56
P < 0.001

4.3.2. Calorimetry and Respirometry.

Energy per unit weight results are shown in Table 4.4. These figures, from the direct calorimetry, were used to calculate energy allocation between the body components in a larger sample of individuals, for which dry weight of the body components was measured. The energy allocation results are given in Figs. 4.3 and 4.4.

Table 4.4. Energy content of somatic tissue, ovaries and eggs for different stages of egg development in *Hyas coarctatus* and *Inachus dorsettensis*. Standard deviations are calculated from all 6 determinations and therefore represent variation due to individuals and due to calorimetric technique. All figures are in J mg⁻¹ dry weight. Conversion factor: 1 J ≈ 0.239 cal. (Brafeld and Llewellyn 1982).

Species	Stage	Soma		Ovaries		Eggs	
		Mean	S.D.	Mean	S.D.	Mean	S.D.
<i>H. coarctatus</i>	1	6.14	0.367	23.7	0.456	25.4	1.81
	2/3	6.89	0.780	23.5	1.93	24.8	1.46
	4	7.31	0.210	24.3	1.05	-	-
<i>I. dorsettensis</i>	1	6.76	0.389	22.4	0.911	23.3	0.474
	2	7.60	0.716	21.3	1.84	23.2	0.729
	3	6.96	0.327	22.9	1.45	20.2	1.40

Table 4.4 shows that somatic tissue (including exoskeleton) had a very low energy content, and that the differences between tissues were similar for the two species. No formal comparisons were made however. Various patterns

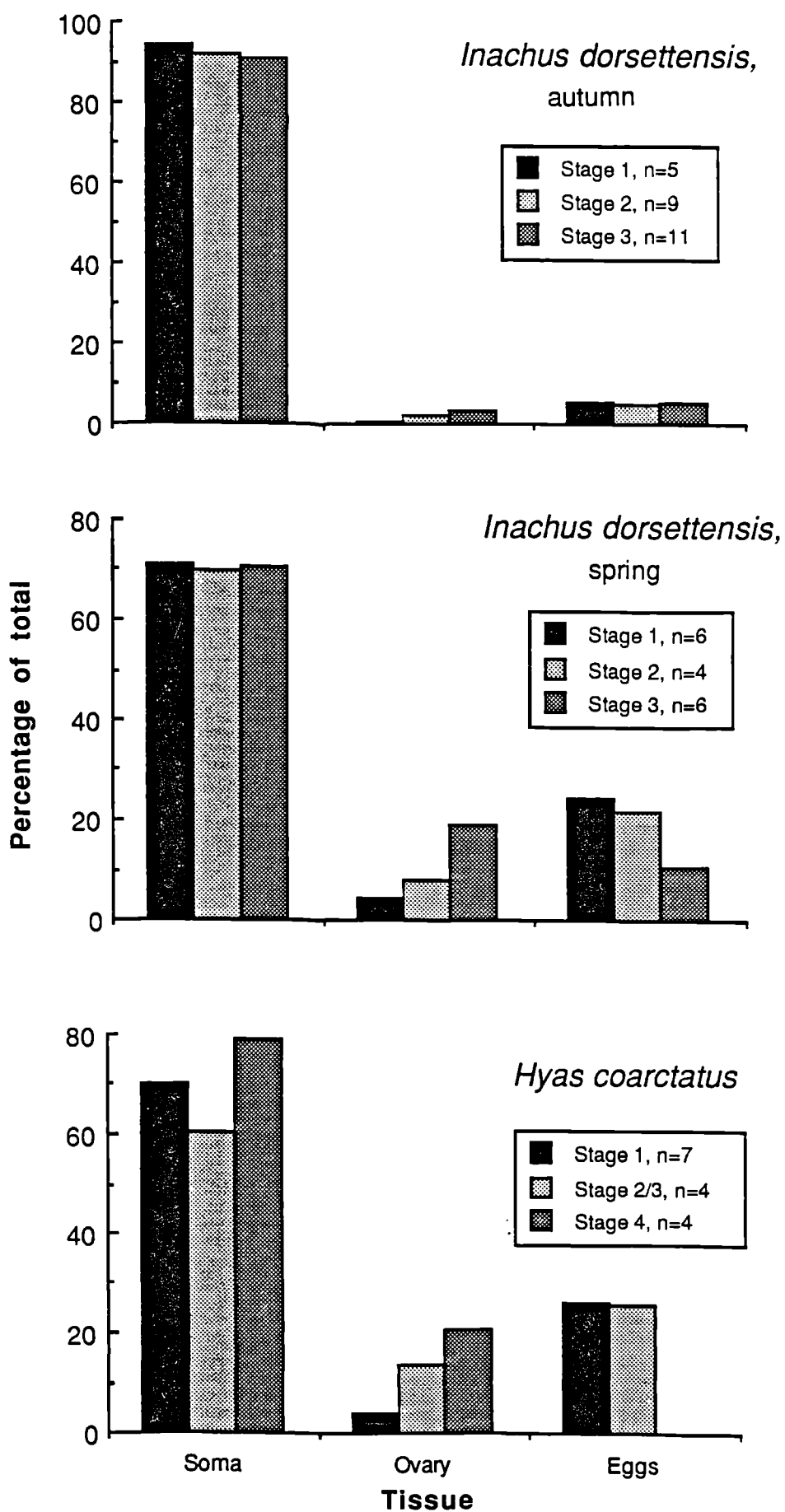


Fig. 4.3. Female energy allocation between tissues as a percentage of total allocation in autumn and spring *Inachus dorsettensis*, and *Hyas coarctatus*.

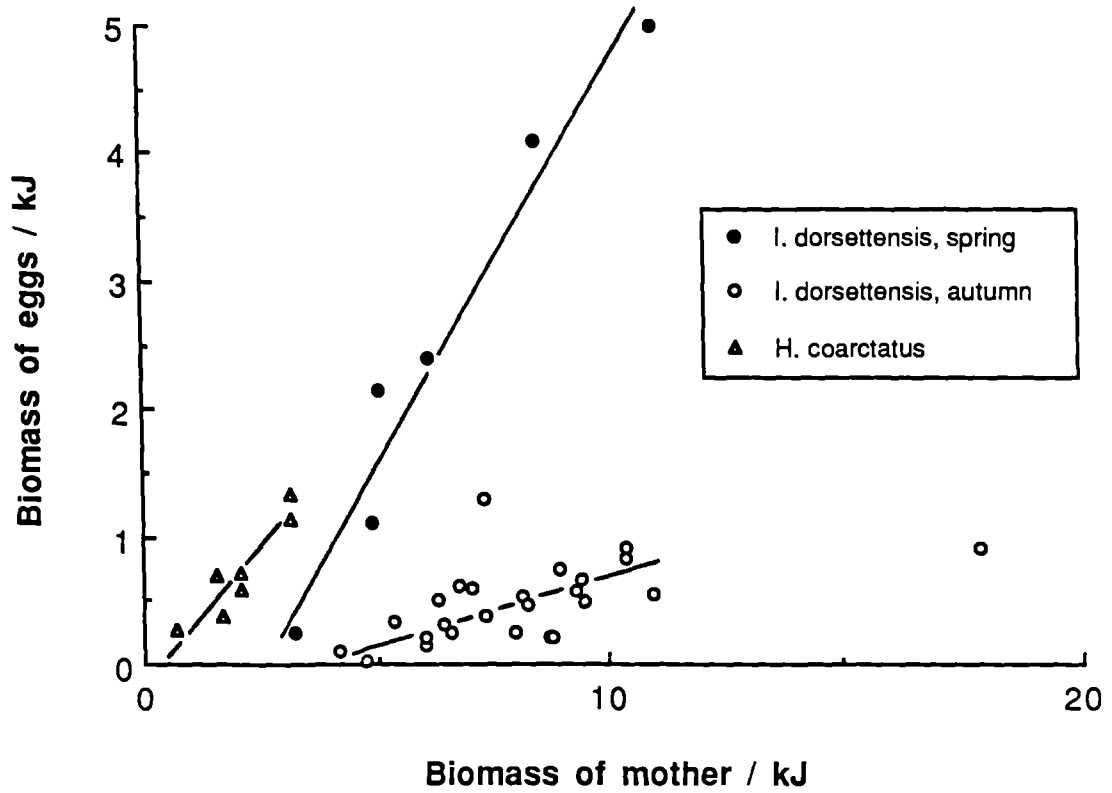


Fig. 4.4. Energy allocation in *Hyas coarctatus* and *Inachus dorsettensis* females. See text for details of the fitted lines.

can be seen in the energy allocation results. In autumn *Inachus dorsettensis* investment in eggs was very low (Fig. 4.3), as would be expected from the egg number results (Fig. 4.2). Unexpected, however, is the very low allocation to ovaries in this group. In *Hyas coarctatus* and multiparous (spring) *I. dorsettensis* the energy invested in ovarian tissue increased with egg development to a maximum of around 20% of total body resources at stages 4 and 3 respectively (Fig. 4.3). Eggs, at stage 1 of development, accounted for over 20% of total body resources in these two groups. In the multiparous *I. dorsettensis* group, the energy invested in eggs appears to decrease with development, possibly reflecting gradual egg loss from the female.

Although the percentage investment in eggs at stage 1 was similar in *Hyas coarctatus* and multiparous *Inachus dorsettensis* (Fig. 4.3) differences in allocation are shown in Fig. 4.4. The equations for the GM regression lines shown in Fig. 4.4 are:

$$H. coarctatus: \quad y = 0.432 x - 0.153 \quad (\text{stage 1 eggs})$$

$$I. dorsettensis, \text{ spring:} \quad y = 0.628 x - 1.59 \quad (\text{stage 1 eggs})$$

$$I. dorsettensis, \text{ autumn:} \quad y = 0.110 x - 0.412$$

The slope of the spring *I. dorsettensis* relationship is significantly greater than that of the *H. coarctatus* relationship ($T = 2.30$, $\text{Var}(T) = 1.32$, $\text{d.f.} = 8.3$, $P < 0.05$). The biomass of eggs thus increased with body biomass at a greater rate in multiparous *I. dorsettensis* relative to *H. coarctatus*. There is very little overlap between these two regression lines: *I. dorsettensis* is the larger of the two species.

Initial analyses of the respirometry results considered the relationship between oxygen consumption rate and body weight. Correlations were strongly positive ($r > 0.89$, $n = 6$, $P < 0.0025$) and, for *Hyas coarctatus*, the intercepts of fitted regression lines were very near to zero. Further analysis considered weight-specific oxygen consumption rate. The results for all experiments are summarised in Table 4.5. The results of the September multiple temperature experiment are given in Fig. 4.5.

Table 4.5. Results of the respirometry experiments. All figures are in $\mu\text{l O}_2 \text{ hr}^{-1} \text{ g}^{-1}$ dry weight. Sample size $n=8$ except where stated, in brackets.

Date	Temperature °C	<i>Hyas coarctatus</i>		<i>Inachus dorsettensis</i>	
		Mean	S.D.(n)	Mean	S.D.(n)
1988					
17 Aug.	15.3	98.1	15.9(6)	183.8	39.2(6)
1 Oct.	13.5	68.9	16.4	100.9	22.0
2 Dec.	10.3	102.2	12.9	97.2	31.7
1989					
16 Mar.	7.5	106.5	17.8	90.6	9.41
13 Jun.	10.2	115.1	11.4	169.5	26.2(7)
Sept.	14.0	88.3	13.9	114.9	9.2(7)
	10.5	72.4	16.2	84.2	9.3
	7.0	56.5	18.0	47.1	3.9
12 Dec.	10.5	61.8	15.6(4)	89.0	14.7
1990					
May	7.0	104.2	15.8(6)	86.6	21.9(6)
	10.5	149.2	34.6(6)	132.5	25.5(6)
	14.0	178.7	55.2(6)	142.5	26.1(6)

There are some anomalous results in Table 4.5. The lowest standard deviations, in general, were obtained in the September multiple temperature experiment. Analysis of variance of this experiment showed significant differences due to species ($F_{1,14}=5.01$, $P<0.05$) and to temperature ($F_{2,28}=63.6$, $P<0.001$), but the interaction between these two factors was also significant ($F_{2,28}=10.6$, $P<0.001$). The reason for the significant interaction is clear from Fig. 4.5. *Inachus dorsettensis* was affected by temperature to a greater extent than *Hyas coarctatus*. *I. dorsettensis* respired at a considerably higher rate than *H. coarctatus* at 14°C but the difference was smaller at 10.5°C, just exceeding the 5% L.S.D. ($11.7\mu\text{l hr}^{-1}\text{ g}^{-1}$). At 7°C Fig. 4.5 indicates a reversal of the difference between species, but this is not significant at the 5% level. Results comparable to this September experiment, with similarly low standard deviations, were obtained in October at 13.5°C and December (1989) at 10.5°C (Table 4.5).

There are difficulties in interpreting the results of the other four single temperature experiments (Table 4.5). In general the consumption rates were very high and those of *Inachus dorsettensis* were very variable in August, December (1988) and June. There is not always the difference between *Hyas coarctatus* and *I. dorsettensis* which was found in the above described experiments. Indeed, the mean consumption rate of *H. coarctatus* actually exceeded that of *I. dorsettensis* in December 1988 and March. Similarly, there are difficulties in interpreting the results of the May multiple temperature experiment. The consumption rates were very high and very variable (Table 4.5). Analysis of variance showed a significant increase in consumption rate with temperature ($F_{2,20}=31.8$, $P<0.001$) but no significant difference due to species ($F_{1,10}=2.16$, $P=0.172$) and no significant interaction between these two factors ($F_{2,20}=0.865$, $P=0.436$).

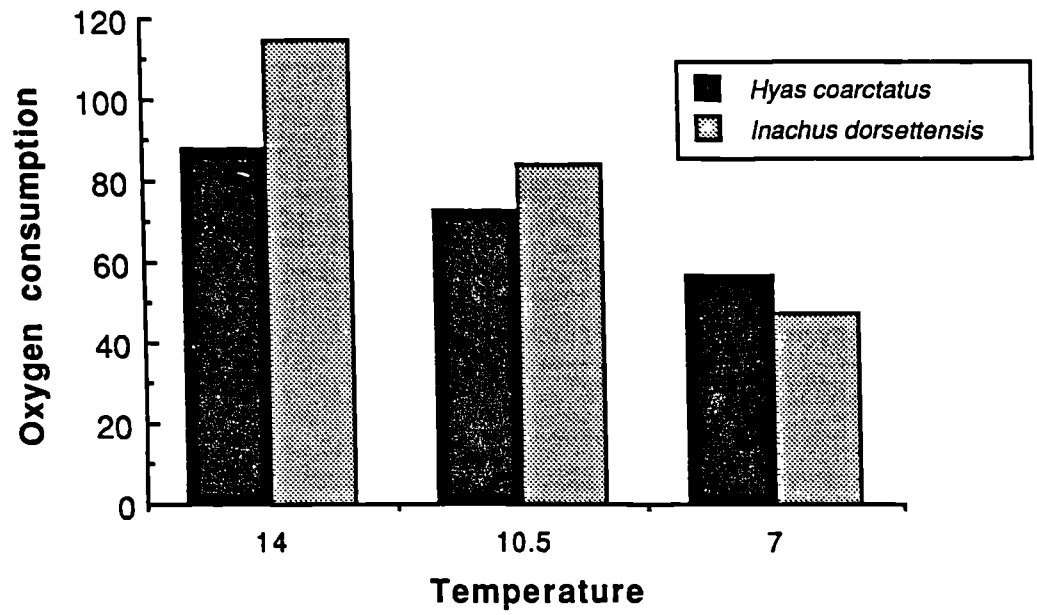


Fig. 4.5. Oxygen consumption (in $\mu\text{l O}_2 \text{ hr}^{-1} \text{ g}^{-1}$ dry weight) of *Hyas coarctatus* and *Inachus dorsettensis* females during the September multiple temperature experiment.

4.4. Discussion.

4.4.1. Fecundity.

The fecundity results may be compared with those of Hines (1982), which pertain to North American brachyurans. That author found that the 6 species of spider crab investigated had larger, fewer eggs in general than species from other families. After statistically controlling for variation in body size (using ANCOVA) and comparing against the grand means for all 20 species studied, the Majidae had significantly fewer eggs per batch, larger eggs and approximately average brood weight. The Majidae which he studied fall into two discrete groups on the basis of body size and egg number. The small body size group (0.06-2.3 g maximum observed range of body dry weight of ovigerous females) comprised *Scyra acutifrons*, *Mimulus foliatus* and *Pugettia richii*, and produced approximately 1000-6500 eggs per batch. The large body size group (14-69 g range) comprised *Pugettia producta*, *Libinia emarginata* and *Loxorhynchus crispatus*, and produced tens to hundreds of thousands of eggs per batch. In all brachyuran species investigated, egg number was strongly related to body weight (logarithmic allometric equations fitted, $r \geq 0.715$, $n \geq 6$).

The present results show *Hyas coarctatus* and *Inachus dorsettensis* females to be within the former majid group in terms of both body size and egg number. *H. coarctatus* females fall to the smaller, less fecund end of this group and multiparous *I. dorsettensis* females fall to the opposite end. Both species have mean egg volumes (at development stage 1) which are slightly larger than those of the other three species of the group. The significant difference which was found in egg volume between *H. coarctatus* and *I. dorsettensis* is small relative to the range found by Hines (1982) for the 6 Majidae and the 20 brachyurans generally.

Egg number was strongly related to body size in *Hyas coarctatus* and *Inachus dorsettensis*, as was shown in all species studied by Hines (1982) and as is almost universally the case for the Crustacea (reviewed by Hartnoll 1985). The variance around the egg number regression lines may in fact be an

overestimate of the true variance in egg number, as eggs of all early development stages (1-3) were used in the derivation of these relationships. The extra possible source of error relates not to changes in egg volume or density with development, as these are taken into account, but to loss of eggs during development. This is suggested in Fig. 4.3 for multiparous *I. dorsettensis* but not for *H. coarctatus*. This phenomenon has been observed in the female *Chionoecetes bairdi* (Hilsinger 1976), which lost 21% of its egg number during development. Such egg loss may be the reason for the greater variance of the *I. dorsettensis* egg number relationships relative to that of the *H. coarctatus* relationship.

Another methodological problem with the egg number relationships is the type of regression used for analysis. The model II technique, specifically reduced major axis or geometric mean regression, is preferable (eg. Ricker 1973, Laws and Archie 1981, Sokal and Rohlf 1981, Lovett and Felder 1989) as statistical error is to be expected in both variates. Hence this is the analysis which is presented in full detail in the Results section and used in the plotting of Fig. 4.2. It represents the most meaningful functional relationship between the two variates. In a predictive context, however, it is rather limited by unfeasibly low, indeed negative, egg numbers at the smaller body sizes. It is for this reason that the least squares equations are used in the model of Chapter five, despite the theoretical problems with the model I technique.

Hartnoll's (1963) observation that the first egg batch of *Inachus dorsettensis* females is smaller than those laid subsequently is confirmed by the present study. It is most likely that this difference is the consequence of low reproductive investment due to the energetic cost of the preceding moult. An alternative, less likely, explanation is that success of attachment may be lower for the first batch laid (cf. Haynes *et al.* 1976). Both sexes of *I. dorsettensis* undergo a terminal moult of large percentage increment relative to that of the juvenile moults (Chapter three). The ovaries of the female develop only after this moult (Hartnoll 1963), necessitating the delay between moult and egg extrusion (Fig. 4.1). Low investment in the first egg batch may be due to high energetic cost of the large terminal moult, such that resources are scarce during the period of post-moult ovarian development.

Hyas coarctatus females develop their ovaries fully before the terminal moult (Hartnoll 1963), which is of smaller percentage increment than the juvenile moults (Chapter three). There was no evidence of a primiparity/multiparity egg number difference in this species. Although it was not possible to classify ovigerous *H. coarctatus* into first or subsequent year groups, it is likely that some of the 38 individuals were carrying their second egg batch (see also Hartnoll 1963). As the development of the ovaries for the first time takes place during the penultimate instar one might expect this development to be compromised, by lack of body cavity space, relative to a second (terminal instar) development. However, the low variance around the regression line, and the lack of highly fecund outliers, suggest that terminal instar body size is the sole determinant of egg number.

Differences in egg number between primiparous and multiparous females have been noted in *Chionoecetes bairdi* (Somerton and Meyers 1983) and possibly exist also in the congeneric *C. opilio* (Haynes *et al.* 1976). These are large, fecund majid species, which fall into the second group proposed earlier on the basis of the Majidae studied by Hines (1982). *C. bairdi* females develop the ovaries to some extent before the puberty moult, then extrude their first egg batch immediately after the moult. Somerton and Meyers (1983) found a difference in intercept (but not slope) of the logarithmic egg number - body size relationships, predicting that primiparous females carry 70% of the egg number of multiparous females. The difference was more extreme in *Inachus dorsettensis*; autumn egg numbers were 15-22% (at 18mm and 24mm CL respectively) of those recorded in spring.

The lack of correlation of egg volume with egg number and with size of the mother, although relying upon implicit acceptance of a null hypothesis rather than rejection, is an important observation. Hines (1982) found significant interspecific relationships of egg volume with number (negative, $r=-0.846$, $n=279$) and with body weight (positive, $r=0.490$, $n=20$). In *Hyas coarctatus* and *Inachus dorsettensis* there is no trade-off representing extremes of many small or fewer larger offspring. Additionally, egg volume appears to be constant with respect to body size of the mother. Thus lifetime egg production, as used in the model of Chapter five, is likely to be a reasonable

index of lifetime reproductive success. The seasonal timing of hatching, which will differ considerably between the two species, is one factor which may complicate this simplistic assumption.

4.4.2. Calorimetry and Respirometry

The energy per unit weight results (Table 4.4) for eggs are comparable with figures for the eggs of other brachyurans and decapods. Paul and Fuji (1989) found a mean energy content of 26.8 kJ g^{-1} for *Chionoecetes bairdi* eggs, which was lower than a figure quoted for a palinurid lobster but slightly higher than figures quoted for two species of caridean shrimp. The mean energy content of *Inachus dorsettensis* stage 1 eggs (25.4 J mg^{-1}) is approximately 5% lower than that of *C. bairdi* whilst that of *Hyas coarctatus* (23.3 J mg^{-1}), approximately 13% lower, is comparable to those of the caridean shrimps.

The energy contents of somatic tissue are lower than those published for other species. Both *Hyas coarctatus* and *Inachus dorsettensis* females contained approximately 55% ash in the terminal instar. Using this figure, the somatic energy contents per unit ash-free dry weight, averaged over development stages, are 15.1 J mg^{-1} for *H. coarctatus* and 15.8 J mg^{-1} for *I. dorsettensis*. Griffiths (1977) reviewed caloric content with particular reference to the Crustacea, as a re-examination of Slobodkin and Richman's (1961) hypothesis. The earlier authors proposed that selection favours high fecundity with consequently low body caloric content per unit weight in most species, but that in a few species energy is accumulated as fat in response to unpredictability of the environment. They rejected two other hypotheses, that of an optimal biochemical composition for all organisms, and that of large differences between taxonomic groups. In the Crustacea, Griffiths (1977) found a bimodal distribution of caloric content. Benthic species had lower body caloric contents ($18\text{-}21 \text{ kJ g}^{-1}$ ash-free dry weight) than pelagic species ($21\text{-}31.5 \text{ kJ g}^{-1}$). This difference was attributed to the stability of the benthic habitat relative to the pelagic. The earlier hypothesis was thus supported, in a limited sense, by Griffiths' review: benthic organisms had a lower body energy content, which would be expected on the basis of the predictability of food supply.

Figures which are higher than both the present results and the results for the benthic species reviewed by Griffiths (1977) have been found for *Carcinus maenas* (23.7 J mg⁻¹, Klein Breteler 1975d) and *Chionoecetes bairdi* (22.2 kJ g⁻¹, Paul and Fuji 1989). Both of the latter two studies considered animals immediately following the moult, during calcification of the new shell, such that ash contents were 25% and <30% respectively. This method was adopted in order to avoid bias due to endothermy associated with high ash contents (Paine 1966, Crisp 1984), and the possibility of incomplete combustion (Klein Breteler 1975d). Somatic energy contents will have been underestimated slightly by the use of direct calorimetry on fully calcified specimens in the present study. Furthermore, it is likely also that the ash content will have been underestimated due to the high calcium carbonate content of the samples (Dennell 1960, Crisp 1984). Thus the caloric content per unit ash-free dry weight will have been more seriously underestimated than that per unit dry weight. The differences between the present results and those of the other studies will be due partly to methodological differences rather than true differences between species.

Paine (1966) suggested an empirically-derived correction factor for endothermy in bomb calorimetry of 3-4% over observed values for ash contents of 50%. The error associated with calorimetry is thus small, and will not have too great an effect upon the reproductive investment results.

The low energy investment in eggs in autumn-sampled *Inachus dorsettensis* (approximately 5% of total) is unsurprising and merely reflects the low egg number result. That the ovarian investment is low also (<5%) is difficult to explain. One would expect ovarian development, in preparation for the laying of the second batch, to be similar to that of the spring-sampled *I. dorsettensis*.

Hines (1982) found brachyuran brood weight to be constrained to 'about 10%' of body weight. Equivalent figures for stage 1 *Hyas coarctatus* and multiparous *Inachus dorsettensis* are 8.9% and 9.6% respectively. The two species studied thus appear to be similar to other brachyurans in this respect. In terms of energy, however, the two species invest 35.1% and 31.6%

respectively. It is likely that figures for other brachyurans would be similar, due to their similar investment by weight (Hines 1982) and broadly similar somatic ash contents. These comparisons must be regarded rather tentatively, however, as doubts have been expressed regarding the usefulness of reproductive output as a comparative measure, in the absence of information on reproductive effort, especially when organisms from different temperatures and latitudes are involved (Clarke 1987).

The regressions of brood biomass upon body biomass (Fig. 4.4) indicate small differences between *Hyas coarctatus* and multiparous *Inachus dorsettensis*. *H. coarctatus* females invest the shown amount of energy in eggs once per year (Fig. 4.1), whereas *I. dorsettensis* females produce the first then several subsequent egg batches per year. Hartnoll (1963) estimated that 3 batches of eggs could be carried in the first year of maturity. The equations of section 5.2.3 indicate that as many as 5 batches may be carried per year. Clearly, then, reproductive effort is greater in *I. dorsettensis* than in *H. coarctatus*.

Comparisons may be made between the oxygen consumption results and results for other species. Klein Breteler (1975c,d) found two patterns of consumption within individuals of *Carcinus maenas*, an irregularly fluctuating high level and a constant low level. There was as much as an order of magnitude difference in consumption rate between these levels. The high level was considered to be routine level respiration and the low level was attributed to ceased gill ventilation. Large, fed juveniles (200 mg ash-free dry weight, \approx 400 mg dry weight, \approx 18 mm CW) had a weight-specific consumption rate of $587 \mu\text{l hr}^{-1} \text{g}^{-1}$ dry weight at 20°C . This exceeds considerably the results obtained for unfed *Hyas coarctatus* and *Inachus dorsettensis* at the higher temperatures ($<20^\circ\text{C}$).

For the west Atlantic spider crab *Libinia emarginata*, Aldrich (1974) found a consumption rate of $38 \mu\text{l hr}^{-1} \text{g}^{-1}$ live weight ($\approx 115 \mu\text{l hr}^{-1} \text{g}^{-1}$ dry weight) for mid-sized (123 g) specimens at summer temperatures ($20\text{-}22^\circ\text{C}$). The spider crab species of the present study showed very similar rates at the higher temperatures. The same author (Aldrich 1975) found strong diel cycles in oxygen consumption for *Cancer pagurus* and *Maia squinado*. Feeding altered

the amplitude of these cycles, giving a 3-5 fold increased scope for activity over the starved state. The latter study casts doubt upon the routine/active classification of other studies when in fact diel variation, often unmeasured, is likely to have a strong effect.

A rather different comparison may be made with the large, cold water spider crab *Chionoecetes bairdi*. An oxygen consumption rate of $12 \mu\text{l hr}^{-1} \text{g}^{-1}$ live weight ($\approx 36 \mu\text{l hr}^{-1} \text{g}^{-1}$ dry weight) was found by Paul and Fuji (1989) in large (750 g live weight) unfed specimens at 5°C , which is similar to the rates measured in the congeneric *C. opilio* (McLeese and Watson 1968, Foyle *et al.* 1989). Those low rates were considered to be typical of cold water decapods and were lower than those of similar species inhabiting warmer environments. Feeding caused an immediate 46% increase in oxygen consumption rate, declining over several days dependent on the size of the ration.

In performing the respirometry experiments at ambient temperature through the seasons and at various temperatures on two occasions, it was hoped that the difference between seasonal acclimatisation and short-term acclimation could be assessed. Klein Breteler (1975d) considered that for energy budget work the measurements should be made during the appropriate seasons. Various authors (eg. Vernberg 1959, Dalla Via 1985) have found a lower metabolic rate in specimens acclimatised to a particular temperature than in those exposed to the test temperature for only a short acclimation period. Leffler (1972) found various degrees of acclimation in *Callinectes sapidus* after four weeks of exposure to a test temperature. Demeusy (1957) found that metabolic differences between groups were retained after 7-8 weeks in *Uca pugilator*, although in that study different latitudinal populations were considered, which may have represented two sub-species. In *Carcinus maenas* Klein Breteler (1975c) found a 1.5-2.2 times increased rate in spring compared to summer and autumn.

There are problems, however, in comparing the results of the experiments reported here. Although attempts were made to standardise conditions between experiments, variation of factors other than temperature appear to have had a significant effect. This is a problem which is to some extent

inherent in the design. The use of inferential statistics is dubious when factors other than those being investigated may have a confounding effect although, arguably, if the effect of those factors is known to be negligible then such comparisons may be valid.

There is an additional problem, in the multiple temperature experiments, of non-independence between temperature treatments. Nevertheless one would expect, in the absence of confounding factors as discussed above, comparable results between experiments. The consumption rate at 14°C was expected to be lower in the summer experiment than in the winter experiment and likewise that at 7°C in winter relative to summer. The latter was not found, and there was a large residual variance, in addition to generally high rates, in the winter experiment.

As mentioned above, small differences between experiments in factors other than temperature could have caused these anomalous results. One factor, handling of the animals immediately prior to the period during which measurements were made, may have stressed some animals more than others, thus contributing to the unexplained variance. In retrospect, more detailed observations of the effect of these factors, using flow-through respirometry, should have been conducted in order to reliably determine oxygen consumption in these species.

Chapter 5.

Simulation modelling of life history tactics.

5.1. Introduction.

This chapter describes a simulation model of crab life history patterns. The model is developed from that of Hartnoll and Gould (1988). As described in that initial publication, the model predicts an optimal life history for female *Carcinus maenas* under given survival conditions. *C. maenas* females have several mature, or ovigerous, instars and grow 'determinately', that is they have a definite terminal anecdyosis (Hartnoll 1985). That species is considered here, and the model is used to investigate the effect of different survival patterns upon optimal life history. As proposed by the authors the model is applied, with appropriate modifications, to other species. *Cancer pagurus* is considered as this is a species for which life history data exist in the literature, due to its commercial importance. *C. pagurus* grows indeterminately (Hartnoll 1982), but all other aspects of its life history are qualitatively the same as those of *Carcinus maenas*. Thus the model required little modification in application to this species. The model is applied also to the life histories of the spider crabs *Hyas coarctatus* and *Inachus dorsettensis*, using data from other chapters of this thesis. As spider crab females have a single ovigerous, terminal instar (Hartnoll 1963), some simplification was required in applying the model to these species.

The impetus for the development of this model was the observation of diversity of life history patterns within the Brachyura, the true crabs, and the decapod Crustacea generally (Hartnoll 1982, 1985). The Brachyura, a group with restricted body form and mostly benthic habit, show the full range of crustacean reproductive patterns (Hartnoll 1982). Iteroparity is represented in the species with several mature instars and near-semelparity is represented in some of the species possessing only a single mature instar. In the latter group, however, some species lay many batches of eggs, sequentially, in that instar. The restriction of egg laying to a single terminal instar has arisen independently on several occasions in the Brachyura and may represent the avoidance of moult-related mortality once reproductive size has been attained (Hartnoll 1982).

Life history strategies have been the subject of much theoretical and empirical investigation (Stearns 1976, Southwood 1977, 1988, Begon *et al.* 1990). The

strategy, as referred to in the literature, is a genotypic property of the organism. A strategy comprises combinations of traits ('tactics') which are assumed to be generated by particular environments and habitats (Southwood 1988). There is some inconsistency in the use of these terms (Stearns 1976, Wootton 1984) but in general 'tactics' refers to the behavioural and physiological traits which together form the 'strategy'.

The model developed here predicts which tactics may be favoured, in response to survival rate, within a given species-strategy. As noted above, the species which are considered differ in life history strategy, particularly the spider crabs relative to the other two species. The predictions of the model refer to the tactics employed by the species rather than to their strategies. More specifically, the postlarval instar number at which the female should moult to maturity and at which she should moult terminally, in order to maximise lifetime egg production, is predicted. Thus the model represents a specific investigation within the general topic of optimal age-distribution of reproductive effort (Stearns 1976). The variation of the optimal tactic with differing survival regimes is investigated. Mortality is considered at the moult and during the intermoult period. The former will be due almost exclusively to predation and the latter will be due to various causes.

The literature on life history patterns in marine invertebrates has been reviewed by Grahame and Branch (1985). Attention has focussed upon the cost of reproduction (Calow 1979), the timing of reproduction, semelparity versus iteroparity and the risk associated with reproduction. Much of the literature concentrates on one particular life history question at strategy level - why have planktonic larvae? (Grahame and Branch 1985). Vance (1973a,b) described a model to predict evolutionary stable forms of larval development, following on from Thorson's early (1950) ideas. The mode of development in marine invertebrates has remained a topic of active discussion (eg. Underwood 1974, Vance 1974a,b, Christiansen and Fenchel 1979, Strathmann 1985, Hines 1986, Havenhand and Todd 1989, Roughgarden 1989, Grant 1990, Todd and Havenhand 1990 and Willows 1990). Thus, there has been considerable emphasis at strategy level. This study differs in concentrating on the tactics employed by particular closely-related species of benthic marine invertebrates.

5.2. Methods.

The formulation which follows is due in part to P. Gould (unpublished) and was outlined non-mathematically by Hartnoll and Gould (1988) for *Carcinus maenas*. The parameter values, and to some extent the nature of the equations, are based upon experimental data (Shen 1935, Bückman and Adelung 1964, Adelung 1971, Wear 1974, Klein Breteler 1975a,b, Mohamedeen 1984, Mohamedeen and Hartnoll 1989). In the formulation the subscript r refers to postlarval instar number. The first ovigerous instar is denoted by p and the penultimate instar, that which precedes terminal anecdysis, is denoted by n (see Fig. 5.1). It is assumed that one or more batches of eggs is laid during instars p to n inclusive, and that several batches are laid in the terminal instar.

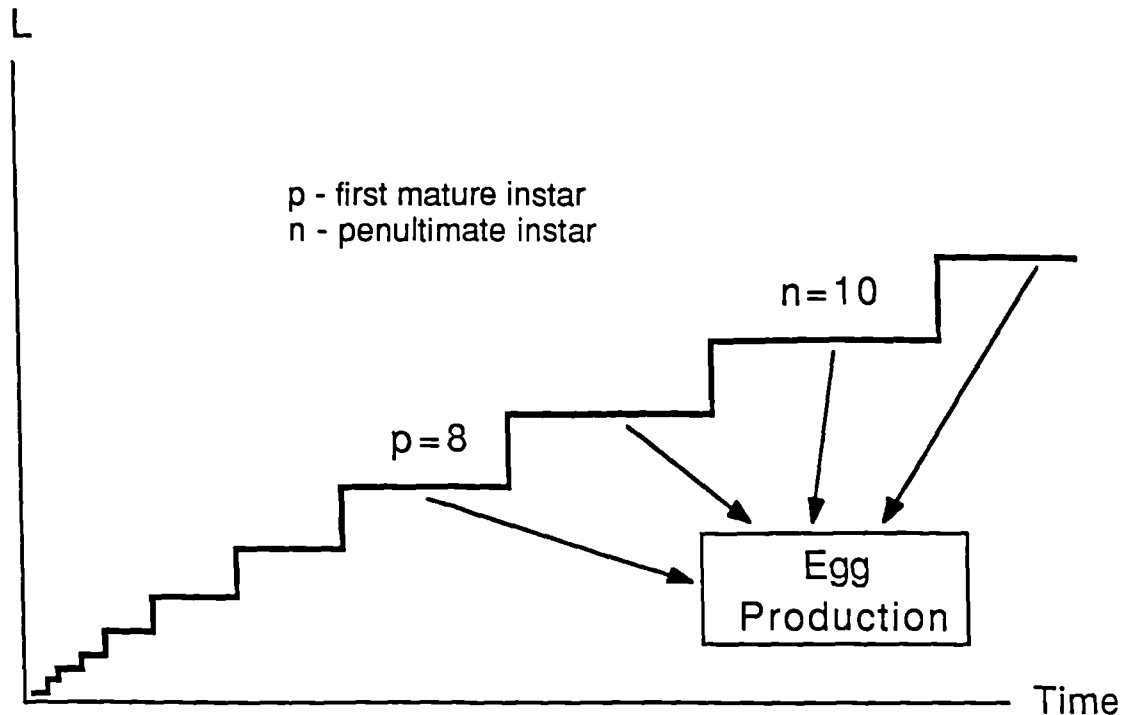


Fig. 5.1. The growth and reproduction of female *Carcinus maenas*.

Further developments were necessary to apply the model to *Cancer pagurus* and the two majid species. These developments are described relative to the *Carcinus maenas* formulation.

5.2.1. *Carcinus maenas* formulation.

Moult increment, mm:

$$L_{r+1} = L_r [1 + \mu e^{-L_r/\lambda}] \quad (1)$$

From Klein Breteler (1975b) and
Mohamedeen and Hartnoll (1989)

L = size of animal, CW, mm

$L_{\text{instar 1}} = 2\text{mm}$ (Shen 1935)

$\mu = 0.5$

$\lambda = 91 \text{ mm}$

Intermoult period, days:

$$\tau_r = aL_r + b + cK_r \quad (2)$$

From Bückman and Adelung (1964)

$a = 0.75 \text{ days / mm}$

$b = 12 \text{ days}$

$c = 30 \text{ days, incubation period}$

(Wear 1974)

Number of egg batches laid:

$K_r = 0, 1 \leq r \leq p-1$

$K_r = 1, 2 \text{ or } 3, p \leq r \leq n$

Duration of terminal anecdysis:

$$\tau_{n+1} = c(K_{n+1} + 0.5) \quad (3)$$

$K_{n+1} = 6$

$$\text{Lifetime} = \sum_{r=1}^{n+1} \tau_r$$

$$= a \sum_{r=1}^n L_r + n b + c \sum_{r=p}^n K_r + \tau_{n+1} \quad (4)$$

Survival:

$$X_{r+1} = X_r \omega_r e^{-\tau_r/v_r} \quad r \leq n \quad (5)$$

X_r = population density at
start of instar r

$X_{\text{instar } 1}$ = 1 crab / unit area

$e^{-\tau_r/v_r}$ = survival probability
during instar r

ω_r = survival probability of the
moult at end of instar r

Egg production:

Number of eggs per batch carried by an individual female

$$= d L_r^3 \quad p \leq r \leq n+1 \quad (6)$$

$d = 1 \text{ egg mm}^{-3}$

(constant of proportionality)

From Hartnoll and Gould (1988). In many brachyuran species fecundity is linearly related to body volume (Hines 1982). The cube of CW is assumed to be related approximately to body volume.

Therefore, number of eggs hatched,

$$E_r = L_r^3 X_r e^{-c/v_r} \quad K_r=1, \quad p \leq r \leq n+1 \quad (7)$$

Generalising with respect to K_r ,

$$E_r = L_r^3 X_r [e^{-c/v_r} + e^{-2c/v_r} + \dots + e^{-K_r c/v_r}] \quad (8)$$

During anecdysis,

$$E_{n+1} = L_{n+1}^3 X_{n+1} A(c/v_{n+1}) \quad (9)$$

$A(c/v)$ is an arbitrary survival function for terminal anecdysis, where $v_{n+1} = v_r$ during anecdysis

For $K_{n+1} = 6$,

$$A(c/v) = e^{-c/v} + e^{-2c/v} + e^{-3c/v} [20/7 - 2(c/v)]$$

(Arbitrary function derived by P. Gould, pers. comm. It describes an exponential decrease in survival during the time in which the first 3 egg batches are laid, that is, an identical regime to that of any other instar. During the remaining time of anecdysis (3.5c days) the function decreases quadratically to zero.)

Hence, lifetime egg production,

$$H(p,n) = \sum_{r=p}^n E_r + E_{n+1} \quad (10)$$

From this formulation, and from Fig. 5.2, it may be seen that variation of p and n will give different lifespans and lifetime egg productions, $H(p,n)$. An optimum, H_{opt} may be found within the range of $H(p,n)$. The values of p and n of this optimal tactic are denoted by p_{opt} and n_{opt} respectively.

In equation (5), moult and intermoult survival are expressed separately. They can, therefore, be varied independently (Fig. 5.2), allowing investigation of the effect that both parameters have upon predicted tactics. Furthermore, as both parameters are instar-dependent in the general formulation above, they may be made size-dependent. In the absence of hard data on survival rates, the two parameters were set initially to a constant level with respect to r : $\omega = 0.9$, $\nu = 1000$. The values of ω and ν were then varied incrementally and the resultant variations in H_{opt} , P_{opt} , n_{opt} and the lifetime of the optimal tactic were observed. Thus the results are presented in two sections: variation of H with p and n given fixed survival rates, then the variation of the optima with changing ω and ν .

The calculations made for these two sections of the results are outlined in Fig. 5.2. A FORTRAN 77/GINO/GLIB implementation of this algorithm is given in Appendix 3. The computation in this program is quite involved: evidence of testing, explanation of data structures and pseudocode explanations are not presented but are available upon request. In addition to routine testing, the program was tested against a FORTRAN program by P. Gould which had in turn been tested against hand calculations. With both programs using double precision arithmetic, there was complete agreement in their results.

5.2.2. *Cancer pagurus* formulation.

The following modifications were required to adapt the model to the life history of *C. pagurus*. This species grows indeterminately (Hartnoll 1985): the final instar is not special, on morphological or endocrinological grounds, and is therefore not equivalent to the terminal anecdyosis of determinate species. The concept of a penultimate instar (n) was retained, however, in the *C. pagurus* formulation. The final instar ($n+1$) is considered to be identical to earlier instars in terms of survival and egg production. As a result of this, survival will not actually reach zero by the end of instar ($n+1$) for each $[p,n]$ life schedule. Some care must be exercised, therefore, in the interpretation of the calculated lifespan for this species.

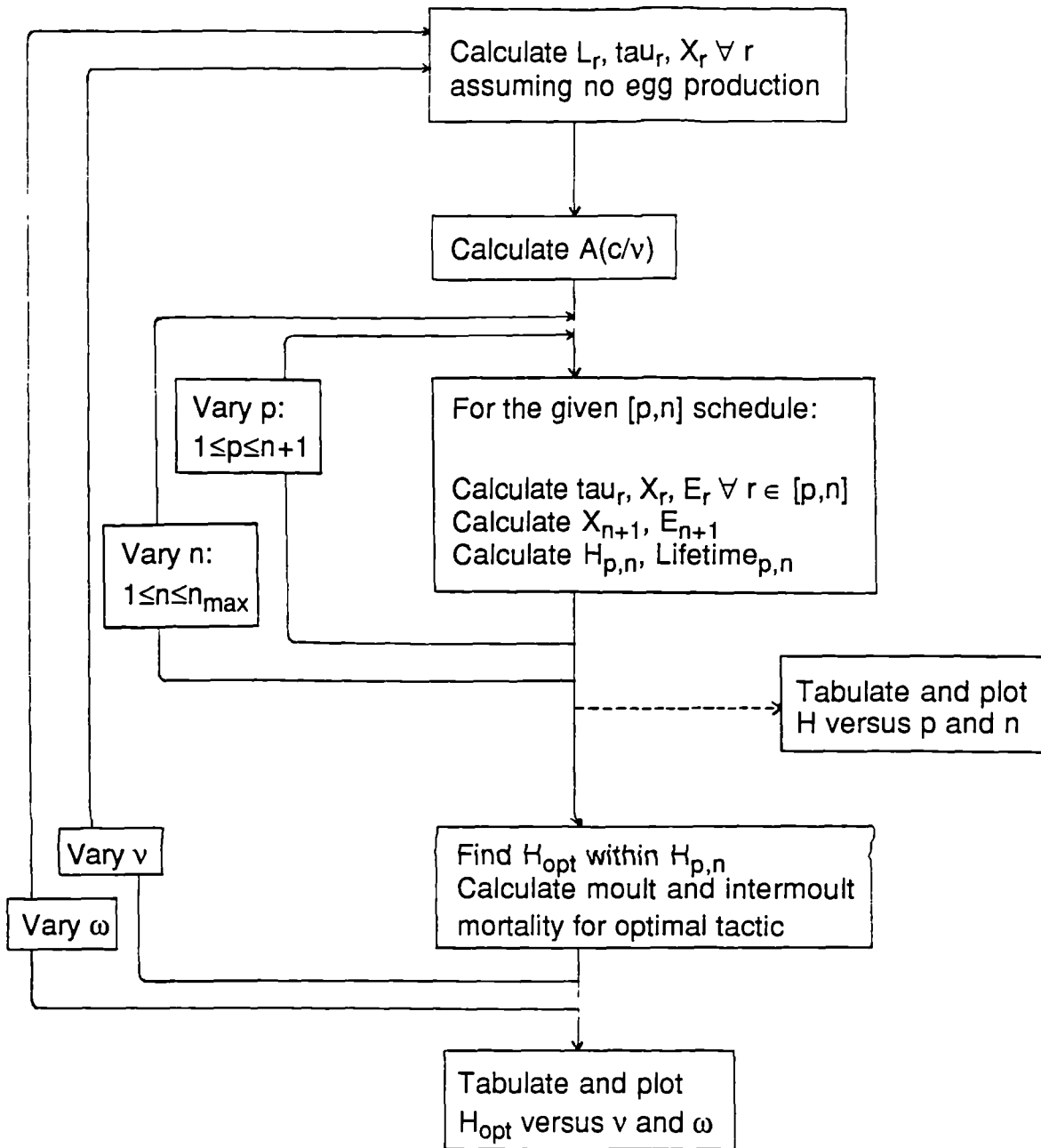


Fig. 5.2. The basic steps involved in running the *Carcinus maenas* model. In this scheme the survival parameters v and ω are assumed to be constant with respect to r and thus appear without their subscripts.

Moult increment, mm:

$$L_{r+1} = \alpha + \beta L_r \quad (11)$$

$$\alpha = 0.445\text{mm}$$

$$\beta = 1.18$$

(from GM regression of combined field and laboratory data of Edwards (1965); correlation coefficient = 0.996, number of observations = 65)

Explicit solution:

$$L_r = \alpha (\beta^{r-1} - 1) / (\beta - 1) + \beta^{r-1} L_1 \quad \text{for } \beta \neq 1 \quad (12)$$

Intermoult period, days:

$$\tau_r = aL_r + cK_r \quad (13)$$

$$a = 3.43 \text{ days mm}^{-1}$$

(see Appendix 4)

$$c = 365 \text{ days batch}^{-1}$$

(from Edwards 1965)

$$K_r = 1, 2 \text{ or } 3 \quad \forall r \in [p, n+1]$$

Survival:

$$X_{r+1} = X_r \omega_r e^{-\tau_r/v_r} \quad r \leq n \quad (14)$$

Egg production:

Number of eggs per batch taken to be L_r^3 , as for *Carcinus maenas*. GM regression of log egg number on log L gave a slope of 2.81, using the data of Edwards (1967). Egg number is therefore very nearly proportional to the cube of L.

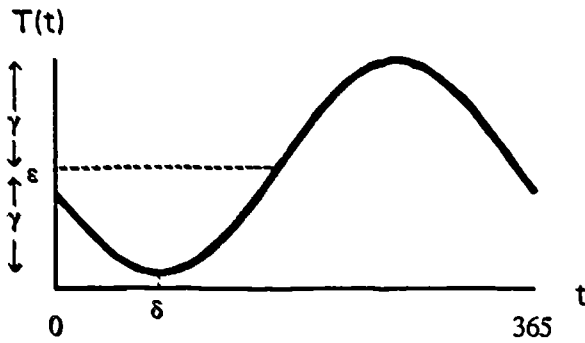
A separate FORTRAN 77 program was written to run the model for this species. This was based upon the *Carcinus maenas* program. Essentially, it follows the algorithm of Fig. 5.2, with the final instar treated as described above. As the program is very similar to that described for *C. maenas*, it is not given here.

5.2.3. *Hyas coarctatus* and *Inachus dorsettensis* formulations.

Growth is determinate in these two species, and eggs are laid only in the female's terminal instar. After a number of juvenile instars (estimated in Chapter three) the female enters terminal anecdyis, in which several egg batches may be laid. In adapting the model, therefore, the constraint $p=n+1$ was applied. The terminal instar was treated as an ordinary instar with respect to survival rate, and egg laying was allowed to continue until a predetermined low level of survival was reached. The calculated lifetime for a particular life schedule depends upon this arbitrarily-defined end-point.

A further modification was required to incorporate temperature dependence. This was not incorporated in the earlier models, as there were insufficient data available. Chapter three shows for the spider crab species the extent to which the mean temperature during the intermoult period affects the length of that period. To incorporate temperature, one needs an equation to relate it to the day of the year. The bottom water temperature data of Slinn and Eastham (1984) and Slinn (unpublished) for the 'Cypris' station, offshore from Port Erin with a depth of 37m below chart datum, were used to fit the following equation:

$$T(t) = \varepsilon - \gamma \cos [\eta (t - \delta)] \quad (15)$$



$T(t)$ = temperature, °C
 t = Julian day
 $\eta = 2\pi/365$ (non-leap year)
 (see also Halberg *et al.* 1987)

The ten years of 1980-89 were considered individually. The number of roughly equally spaced observations varied between 17 and 29 per year. Firstly the time lag δ was found by eye, from a curve drawn through the plotted data points for each individual year. The other two parameters, ε and γ , were then found by least squares linear regression. The mean values for these parameters for the ten year period are given below with corresponding standard deviations in smaller type:

$$\begin{aligned} \varepsilon &= 10.2 \quad 0.404 \text{ } ^\circ\text{C} \\ \gamma &= 3.20 \quad 0.174 \text{ } ^\circ\text{C} \\ \delta &= 78.0 \quad 5.00 \text{ days} \end{aligned}$$

Equation (15) was used in the calculation of intermoult period of both species in the following way. The basic problem is to calculate the mean temperature T_r of the days of the year between the beginning and end of instar r , that is between days t_r and $(t_r + \tau_r)$ respectively:

$$\begin{aligned} T_r &= [1 / \tau_r] \int_{t_r}^{t_r + \tau_r} T(t) dt \quad (16) \\ &= \varepsilon - [\gamma / \tau_r] \int_{t_r}^{t_r + \tau_r} \cos [\eta (t - \delta)] dt \end{aligned}$$

$$\begin{aligned}
&= \varepsilon - [\gamma / \tau_r] \left[\frac{\sin[\eta(t - \delta)]}{\eta} \right]_{t_r}^{t_r + \tau_r} \\
&= \varepsilon - [\gamma / \eta \tau_r] \left[\sin[\eta(t_r - \delta + \tau_r)] - \sin[\eta(t_r - \delta)] \right] \quad (17)
\end{aligned}$$

Moult increment, mm:

$$L_{r+1} = \alpha + \beta L_r \quad \forall r \in [1, n-1] \quad (18)$$

L represents carapace length in these two species.

Explicit solution:

$$L_r = \alpha (\beta^{r-1} - 1) / (\beta - 1) + \beta^{r-1} L_1 \quad \text{for } \beta \neq 1 \quad (19)$$

$$L_p = \alpha_f + \beta_f L_n \quad (20)$$

For *H. coarctatus* $\alpha = 0.007$, $\beta = 1.33$
 $\alpha_f = 0.555$, $\beta_f = 1.23$
 (Chapter three)
 $L_{\text{instar } 1} = 2.74\text{mm}$
 (Anger 1984)

For *I. dorsettensis* $\alpha = 0.080$, $\beta = 1.27$
 $\alpha_f = 1.68$, $\beta_f = 1.20$
 (Chapter three)
 $L_{\text{instar } 1} = 1.61\text{mm}$
 (preserved samples
 supplied by P. Clark of
 BM(NH)).

Intermoult period, days:

$$\tau_r = a + bL_r - cT_r \quad (21)$$

For *H. coarctatus* $a = 57.1$ days

$b = 2.12$ mm⁻¹

$c = 3.34$ °C⁻¹

For *I. dorsettensis* $a = 221$ days

$b = 0.0$ mm⁻¹

$c = 11.4$ °C⁻¹

(Chapter three)

Incorporating the mean temperature equation :

$$\tau_r = a + bL_r - c\varepsilon - c\gamma/\eta\tau_r \sin [\eta (t_r - \delta)] + c\gamma/\eta\tau_r \sin [\eta (t_r - \delta + \tau_r)] \quad (22)$$

Removing terms which are independent of τ_r :

$$\tau_r = P - Q/\tau_r + R/\tau_r \sin [\eta (t_r - \delta + \tau_r)] \quad (23)$$

$$P = a + bL_r - c\varepsilon$$

$$R = c\gamma / \eta$$

$$Q = R \sin [\eta (t_r - \delta)]$$

ie. $\tau_r^2 - P\tau_r + Q = R \sin [\eta (t_r - \delta + \tau_r)] \quad (24)$

This transcendental equation was solved using the Newton Raphson iteration method to give τ_r . Once τ_r has been found the equation is applied to the next instar (r+1), the beginning of which is given by $t_r + \tau_r$, and so on.

Survival:

$$X_{r+1} = X_r \omega_r e^{-\tau_r/u_r} \quad r \leq n \quad (25)$$

Egg production:

$$\text{Number of eggs per batch, } E_b = f L_r^3 - g \quad (26)$$

$$\begin{aligned} \text{For } H. \text{ coarctatus} \quad f &= 0.217 \text{ mm}^{-3} \\ g &= 8.01 \text{ eggs} \end{aligned}$$

For *I. dorsettensis*

$$\begin{aligned} \text{first egg batch :} \quad f &= 0.068 \text{ mm}^{-3} \\ g &= 99.7 \text{ eggs} \end{aligned}$$

subsequent batches :

$$\begin{aligned} f &= 0.355 \text{ mm}^{-3} \\ g &= 790 \text{ eggs} \end{aligned}$$

(Chapter four)

Seasonality :

The phenology of these two species is outlined in Fig. 4.1. *Hyas coarctatus* females undergo the terminal moult from May to July, then lay a batch of eggs almost immediately, which hatches the following March to April. The larval life was estimated from the laboratory data of Anger (1984) and the mean temperature equation (17). Anger (1984) derived an equation from constant temperature work :

$$D = a T^{-m} \quad (27)$$

D = duration, days
T = temperature, °C
a = 926
m = 1.197

Substituting equation (17), applied to D rather than to τ_r (t appears without the subscript r which it had in equation (17) and it represents the hatching day of the eggs) :

$$D = a \left[\varepsilon + \gamma/\eta D \sin [\eta (t - \delta)] - \gamma/\eta D \sin [\eta (t - \delta + D)] \right]^{-m}$$

$$= a \left[\varepsilon + Q/D - R/D \sin [\eta (t - \delta + D)] \right]^{-m} \quad (28)$$

$$R = \gamma / \eta$$

$$Q = R \sin [\eta (t - \delta)]$$

This equation was solved for D in the same way that equation (24) was solved for τ_r . On this basis, the earliest and latest hatching eggs would result in settlement to postlarval instar one on Julian days 143 and 185 respectively. An individual egg hatching at the mid-point of the observed time range would settle on day 164, mid-June. This was taken to be the start day of instar one in the model. The duration of the egg laying cycle was taken to be one year (365 days). No constraint was applied to the timing of the terminal moult in this early version of the *Hyas coarctatus* model. The females were assumed to continue laying egg batches in the terminal instar until a pre-determined low level of survival was reached.

Inachus dorsettensis undergoes its terminal moult in July to September and, after a short delay, lays its first egg batch. The delay between moulting and egg extrusion was assumed to be 60 days in the model. As can be seen from the *I. dorsettensis* parameters for equation (26), this first batch is smaller than the subsequent batches. After the first batch of eggs, laying and hatching is aseasonal; thus it was not possible to estimate a starting day for instar one. For this reason, the model was run for various starting days.

Egg incubation period for *Inachus dorsettensis* was calculated from the laboratory data of Wear (1974) and the mean temperature equation (17):

$$I = W_a (T - W_d)^{-W_b} \quad (29)$$

I = period, days
 T = temperature, °C
 $W_a = 25,000$
 $W_b = -2.3$
 $W_d = -3.5^\circ\text{C}$
 (Wear 1974)

Substituting equation (17), applied to I rather than to τ_r (t appears without the subscript r which it had in equation (17) and it represents the starting day of the incubation period) :

$$\begin{aligned}
 I &= W_a \left[\varepsilon + \gamma/\eta I \sin [\eta (t - \delta)] - \gamma/\eta I \sin [\eta (t - \delta + I)] - W_d \right]^{-W_b} \\
 &= W_a \left[P + Q/I - R/I \sin [\eta (t - \delta + I)] \right]^{-W_b} \quad (30)
 \end{aligned}$$

$P = \varepsilon - W_d$
 $R = \gamma / \eta$
 $Q = R \sin [\eta (t - \delta)]$

This equation was solved for I in the same way that equations (24) and (28) were solved.

As with *Hyas coarctatus*, it was assumed that egg batches are laid until a pre-determined low level of survival is reached.

Separate FORTRAN 77/GINO/GLIB programs were written for the *Hyas coarctatus* and *Inachus dorsettensis* models. These are substantially different from that for *Carcinus maenas* but quite similar to each other. The program for the *H. coarctatus* model is given in Appendix five.

5.3. Results.

5.3.1. *Carcinus maenas*.

5.3.1.1. Fixed survival parameters.

The variation of H with p and n is shown in the form of a surface plot in Fig. 5.3. The same data are displayed as contour plots in Fig. 5.4. The former figure shows the result very graphically, but the latter is a more accurate representation. In the contour plot the response surface is viewed from above, so there is no possibility of distorting the result, as there is with an isometric projection surface plot.

The figures show a maximum value of H at $[p=12, n=25]$ when $K_r=1$. Beyond $n=25$ H decreases very slightly, indicating that very few individuals are surviving to reproduce in these later instars. The reason for the decrease (as opposed to a simple lack of further increase) is that the terminal instar, potentially representing 6 batches of eggs, is being pushed into the region where successively fewer individuals survive. The setting of $K_{n+1}=6$ is based on assumption rather than observation.

Despite the doubt over the accuracy of the K_{n+1} assumption, it is clear that an individual gains little or nothing from living ever longer. For all values of n greater than 20 (holding p constant at 12) the resulting values of H are within 5% of H_{opt} .

There is a steady decrease in H when the value of p becomes smaller or larger than p_{opt} . If the female becomes mature very early she produces only very small egg batches, and incurs greater early intermoult mortality than non-ovigerous females due to the extra time taken in incubating eggs. Thus few individuals will survive to the later instars and lifetime egg production will be low. If the value of p approaches that of $(n+1)$ then few egg batches may be laid; H will be low irrespective of the size of the female in the later instars in which the eggs are laid.

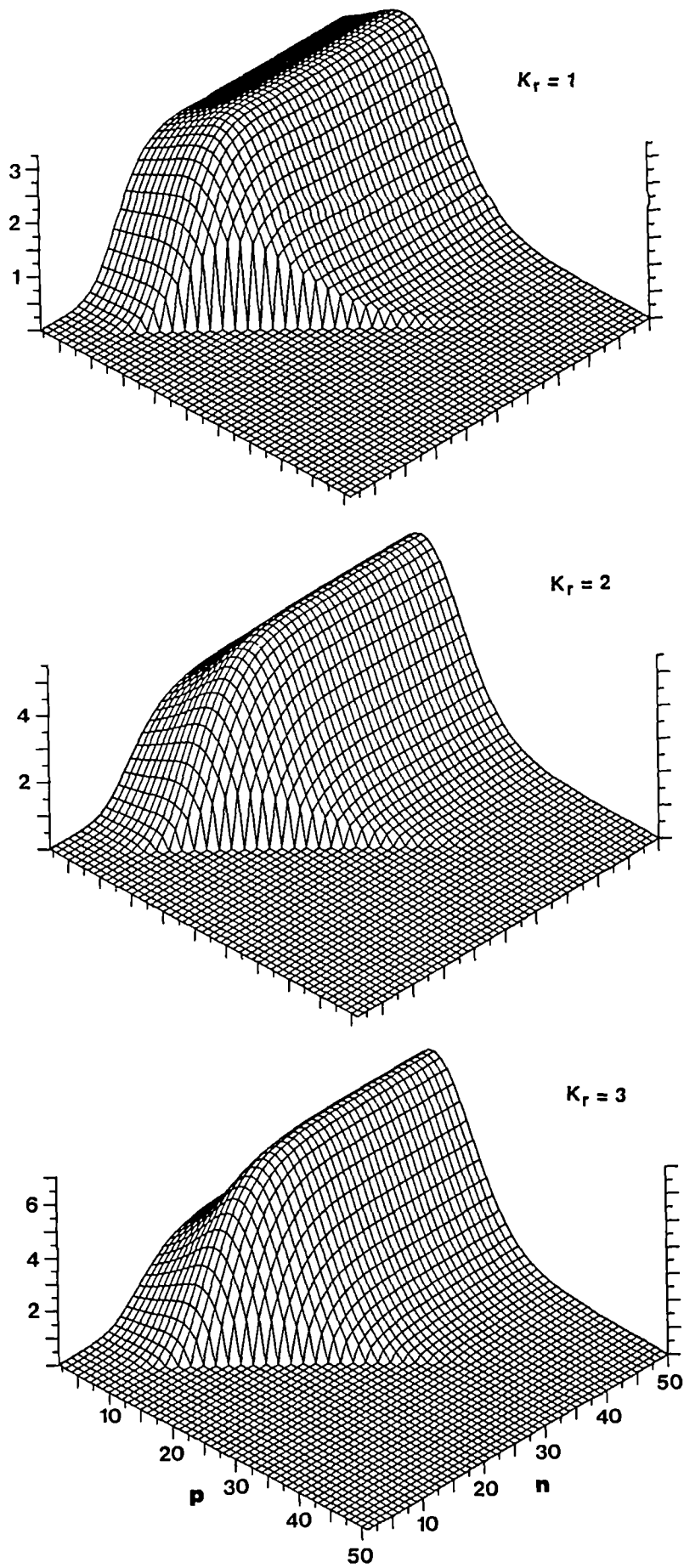


Fig. 5.3. Variation of lifetime egg production (vertical axes = $H \times 10^{-6}$) with p (first mature instar) and n (penultimate instar) in *Carcinus maenas*.

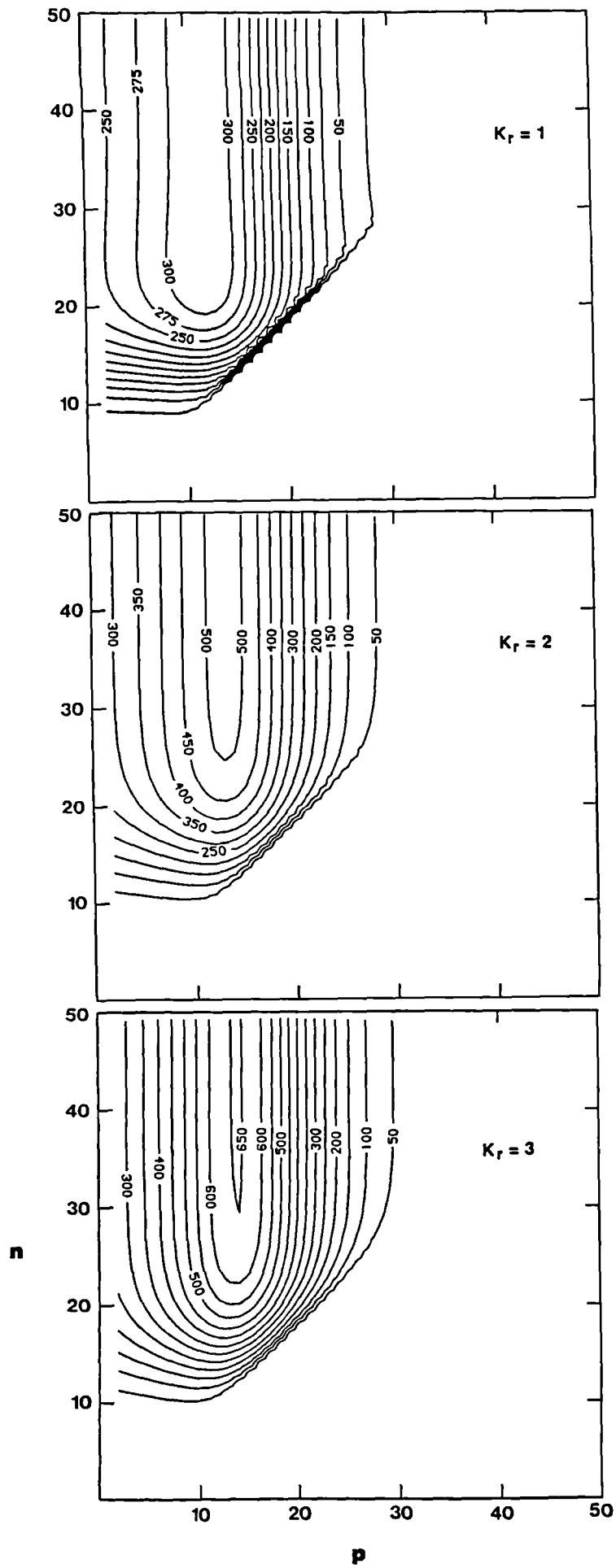


Fig. 5.4. Variation of lifetime egg production (contour heights = $H \times 10^{-4}$) with p (first mature instar) and n (penultimate instar) in *Carcinus maenas*.

The sizes at which the females are predicted to become mature and enter terminal anecdyasis are relatively large: $L_{12}=81.0\text{mm}$, $L_{20}=199\text{mm}$ and $L_{25}=248\text{mm}$. This is discussed further in the section 5.4.

Increasing K_r to 2 and then 3 (for all instars within and including p and n) appears to have a fairly small effect: H_{opt} increases, n_{opt} increases slightly and p_{opt} increases minimally. The slope of the response surface ($H(p,n)$) changes little; as K_r increases, the optimum becomes more sharply defined with respect to p.

5.3.1.2. Variable survival parameters.

Contour plots of H_{opt} , p_{opt} , n_{opt} , $p_{\text{opt}}/(n_{\text{opt}}+1)$ and lifetime of the optimal tactic, assuming K_r to be 1, are given in Fig. 5.5. The same plots, for the optimal tactics with $K_r=2$ and 3, are shown in Figs. 5.6 and 5.7 respectively.

Considering Fig. 5.5 firstly, H_{opt} is observed to increase sharply at the higher survival rates. It is more sensitive to changes in moult survival, ω , than in intermoult survival, v . At the highest survival rates, n_{opt} reaches unrealistically high values; this is treated in more detail below. The variation in lifetime of the optimal tactic follows that of n_{opt} and is affected little by the small changes in p_{opt} . The latter is remarkably stable, increasing only steadily (unlike n_{opt}) with moult survival, ω . Intermoult survival has a negligible effect upon p_{opt} . As n_{opt} increases with both intermoult and moult survival, the almost static value of p_{opt} with increasing intermoult survival represents an increasingly precocious tactic. This is demonstrated in the plot of $p_{\text{opt}}/(n_{\text{opt}}+1)$. This ratio gives some indication of the lateness of reproduction: a value of 1.0 indicates egg laying in only the terminal instar, and the value steps towards zero as p_{opt} is reduced relative to n_{opt} .

At the very highest survival rates ($\omega>9.1$, $v>1500$ when $K_r=1$) n_{opt} reaches a value of 50, a limit imposed by the program given in Appendix 3. This figure is very high and thus represents an arbitrary, computational limit rather than a realistic limit. When the survival conditions allow n_{opt} to reach this limit, all results must be regarded suspiciously; it is likely that even higher values

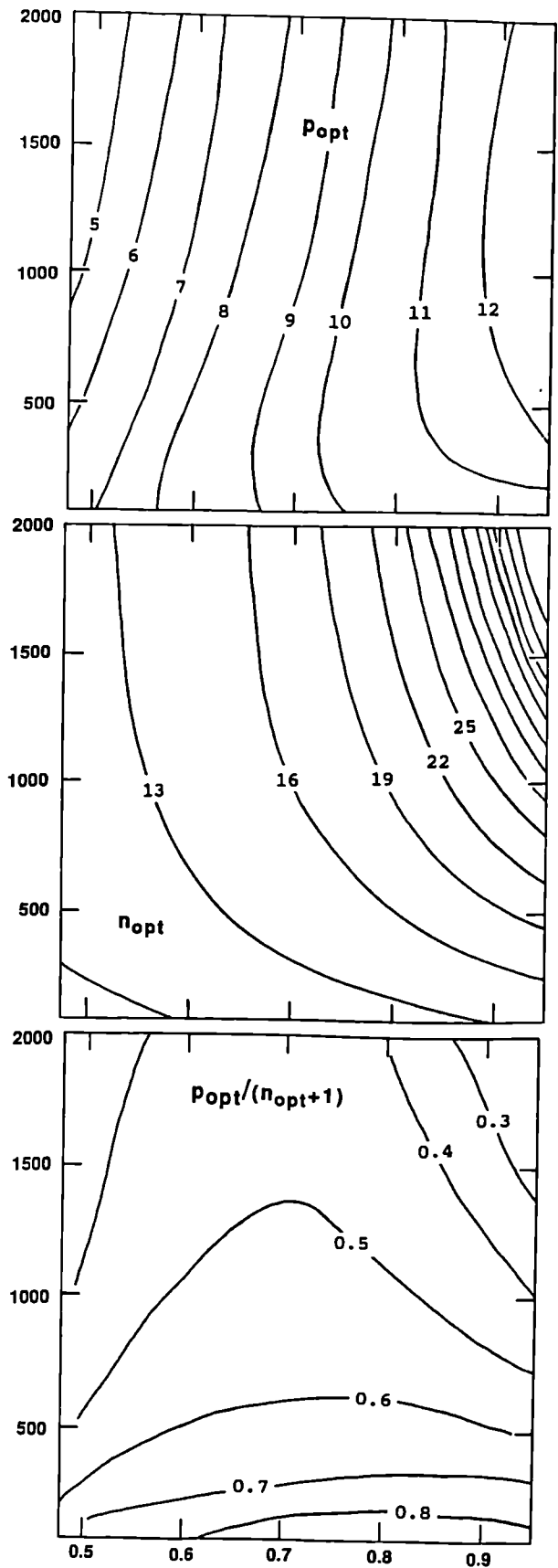
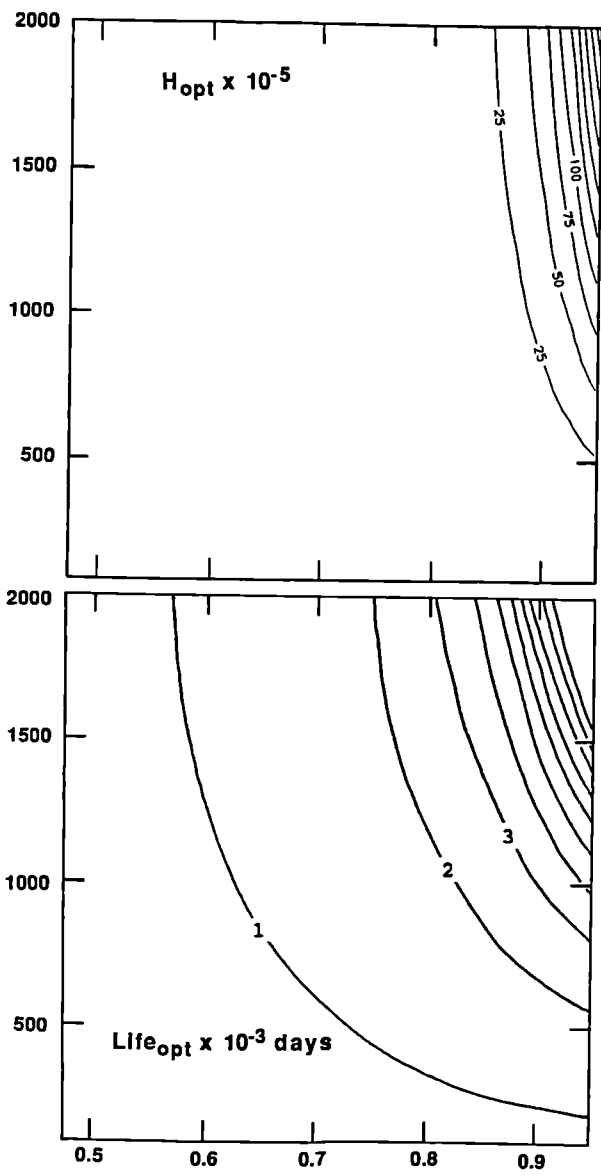


Fig. 5.5. Variation in *Carcinus maenas* optimal tactics with moult survival ω (abscissae) and intermoult survival ν (ordinates). $K_r = 1$. The range of possible tactics, $[p, n]$, was calculated for various combinations of the survival parameters (resolution = 20×20). From within each range the optimum was found and the statistics, as described in the text, are plotted.

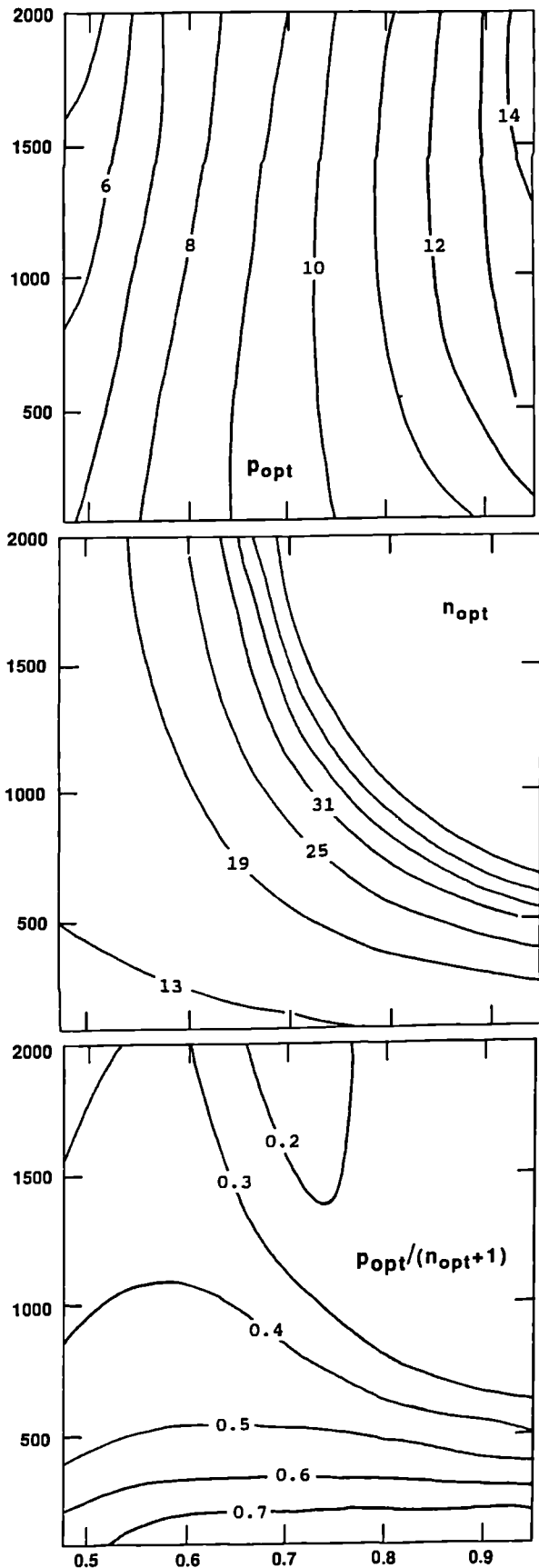
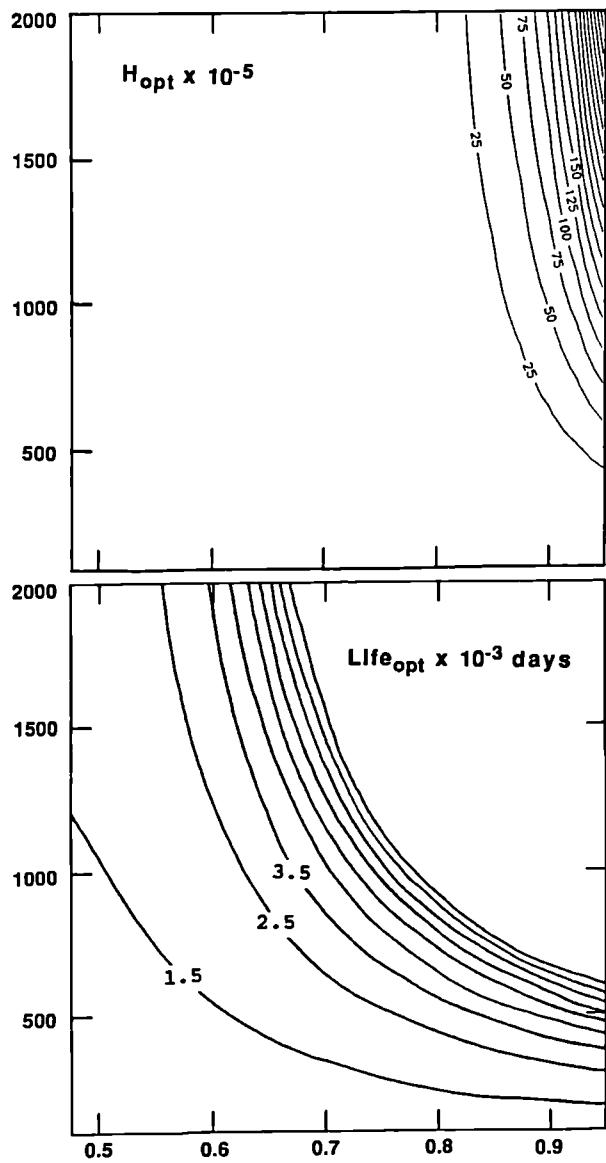


Fig. 5.6. Variation in *Carcinus maenas* optimal tactics with moult survival ω (abscissae) and intermoult survival v (ordinates). $K_r = 2$. The statistics, as described in the text, were calculated as described in Fig. 5.5.

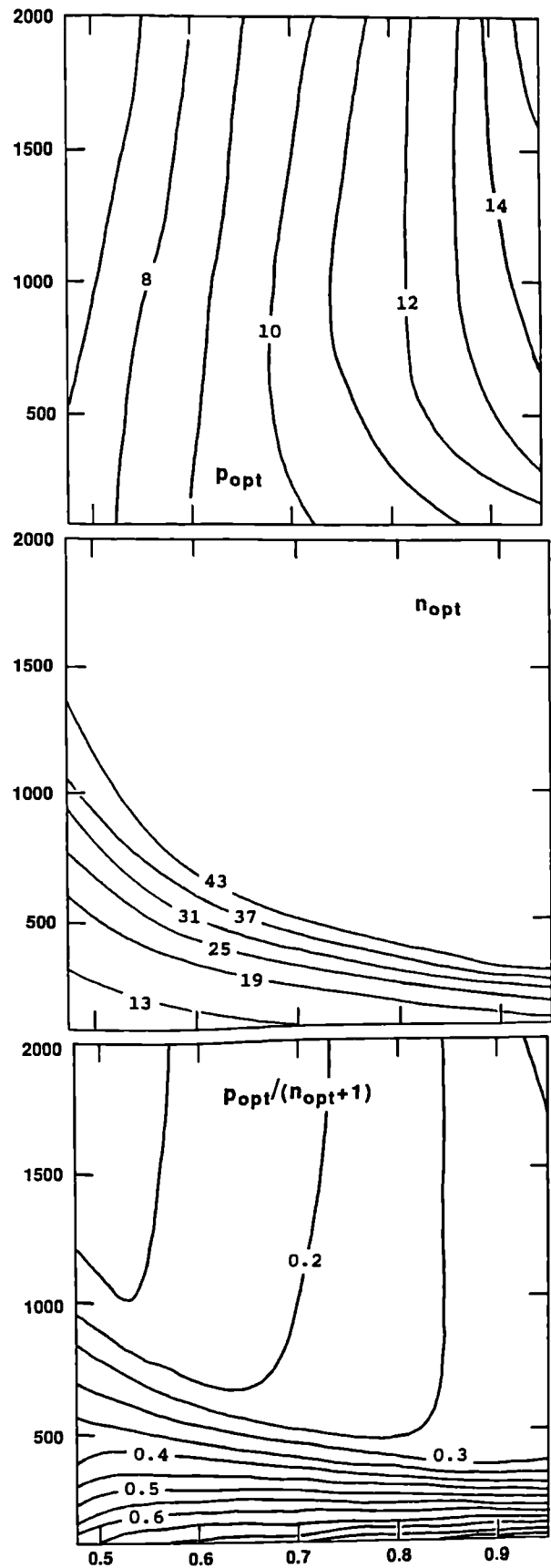
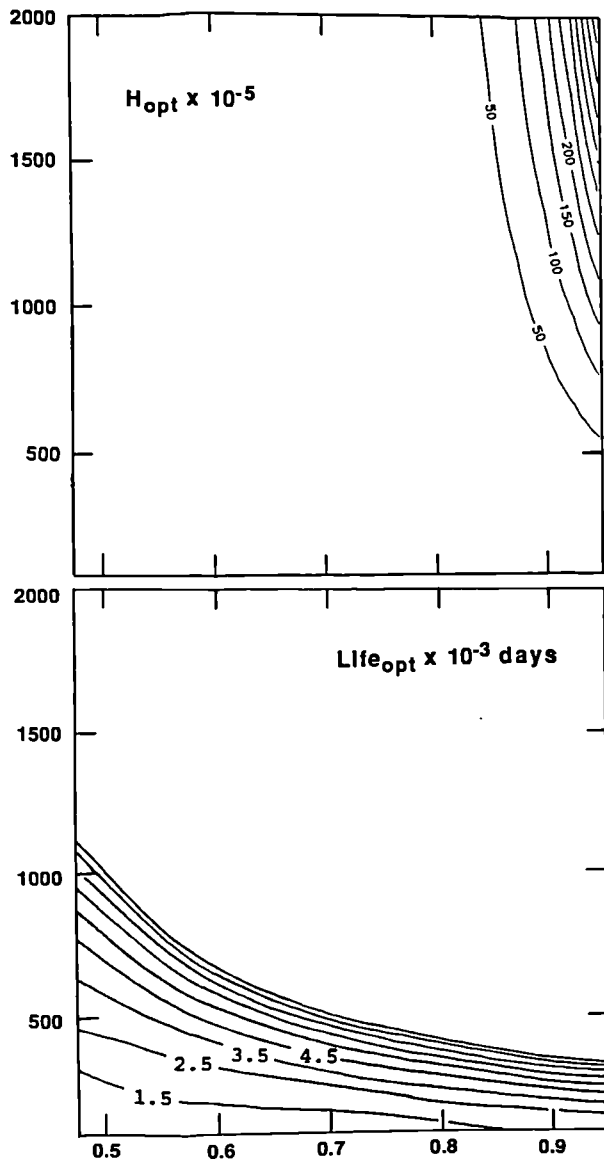


Fig. 5.7. Variation in *Carcinus maenas* optimal tactics with moult survival ω (abscissae) and intermolt survival v (ordinates). $K_r = 3$. The statistics, as described in the text, were calculated as described in Fig. 5.5.

of n_{opt} would be predicted in the absence of this limit. In Fig. 5.5 ($K_r=1$) this is not a major problem as it occurs only at extremely high survival rates. It is a significant problem however when K_r is set to 2 or 3. Under these conditions, unrealistically long life schedules are predicted at the survival rates which were thought likely at the beginning of this work (Hartnoll and Gould 1988).

5.3.2. *Cancer pagurus*.

5.3.2.1. Fixed survival parameters.

The variation of H with p and n (Figs. 5.8 and 5.9) is very similar to that predicted for *Carcinus maenas*. The number of batches of eggs laid per instar has a smaller effect in this species however: it has virtually no effect upon the optimal tactic [p_{opt} , n_{opt}] and the lifetime egg production increases only slightly with more batches per instar.

The predicted optimum tactic, with $K_r=1$, is [$p_{opt}=19$, $n_{opt}=36$]. As with *C. maenas*, a value of H which is very close to H_{opt} is reached at lower values of n : with $p=19$, all values of n greater than 24 give a value of H which is within 1% of H_{opt} . The corresponding carapace widths are $L_{19}=99.1\text{mm}$ and $L_{24}=233\text{mm}$.

5.3.2.2. Variable survival parameters.

Contour plots of the optima versus moult and intermoult survival are shown, for $K_r=1$, 2 and 3, in Figs. 5.10, 5.11 and 5.12 respectively. As with *Carcinus maenas*, H_{opt} increases sharply only at the higher survival rates and is more sensitive to moult survival than to intermoult survival.

Curiously, n_{opt} appears to be far more strongly affected by intermoult survival than by moult survival. The pattern predicted for n_{opt} differs from that predicted for *C. maenas*. In that species n_{opt} accelerated towards and reached the arbitrary maximum at the higher survival rates. In *Cancer*

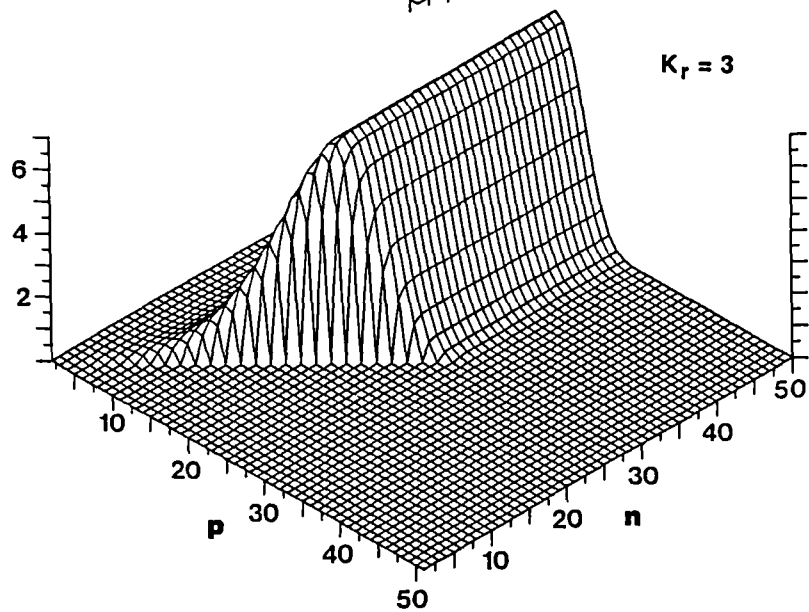
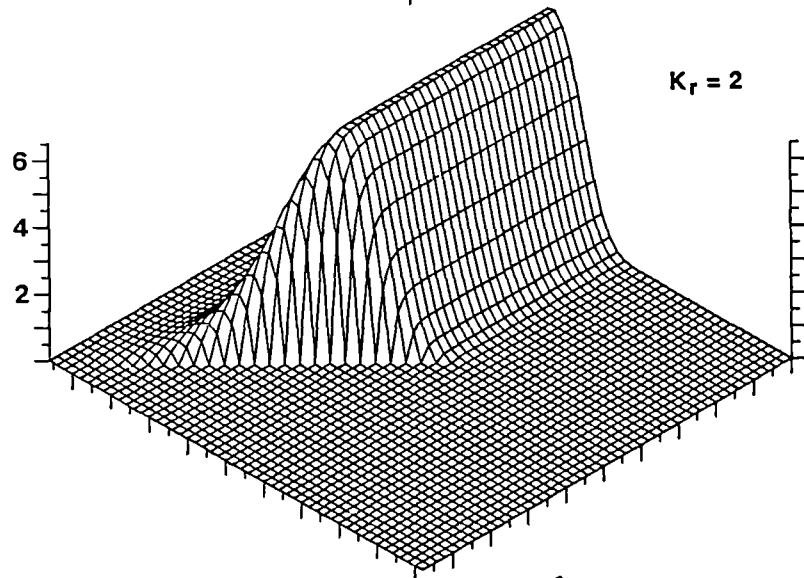
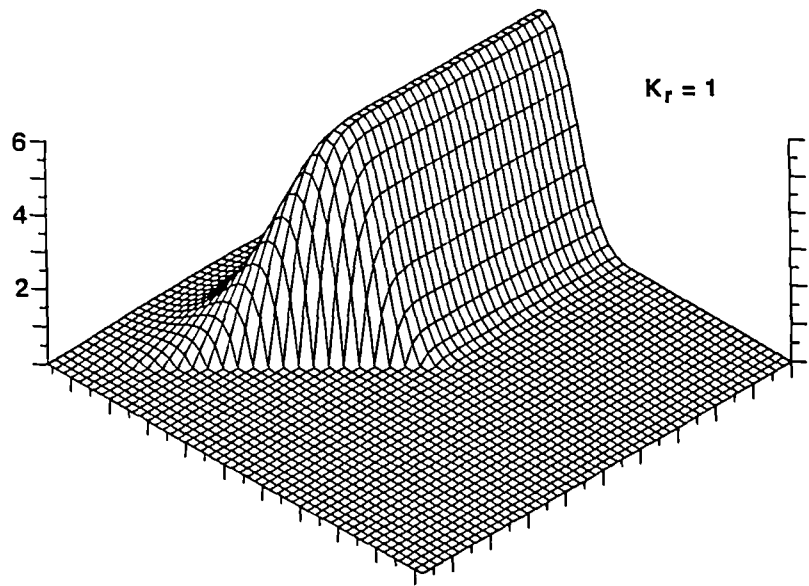


Fig. 5.8. Variation of lifetime egg production (vertical axes = $H \times 10^{-4}$) with p (first mature instar) and n (penultimate instar) in *Cancer pagurus*.

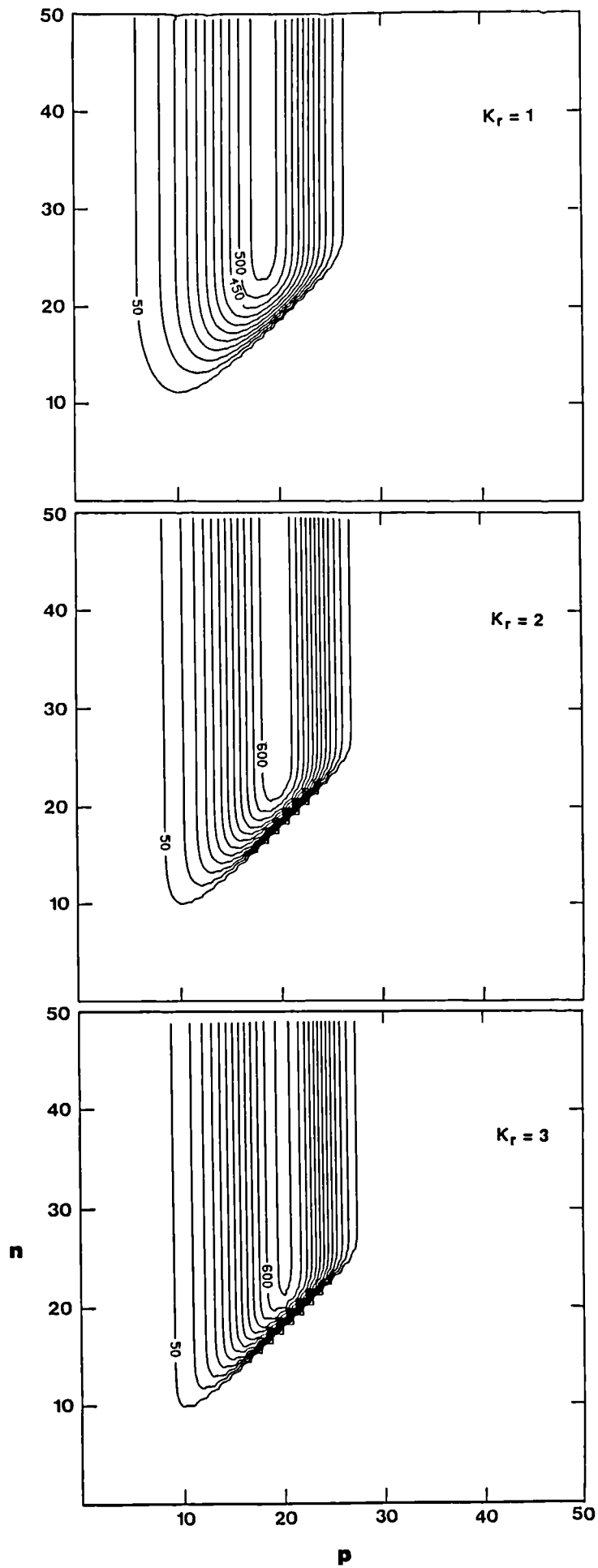


Fig. 5.9. Variation of lifetime egg production (contour heights = $H \times 10^{-2}$) with p (first mature instar) and n (penultimate instar) in *Cancer pagurus*.

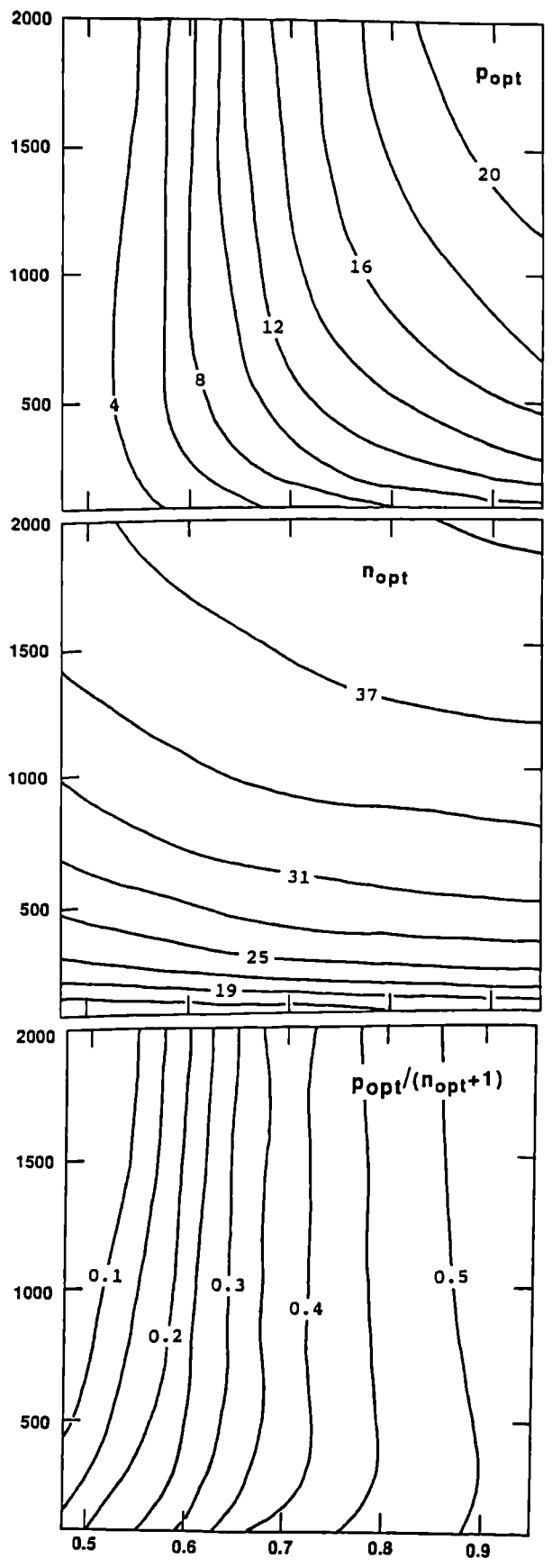
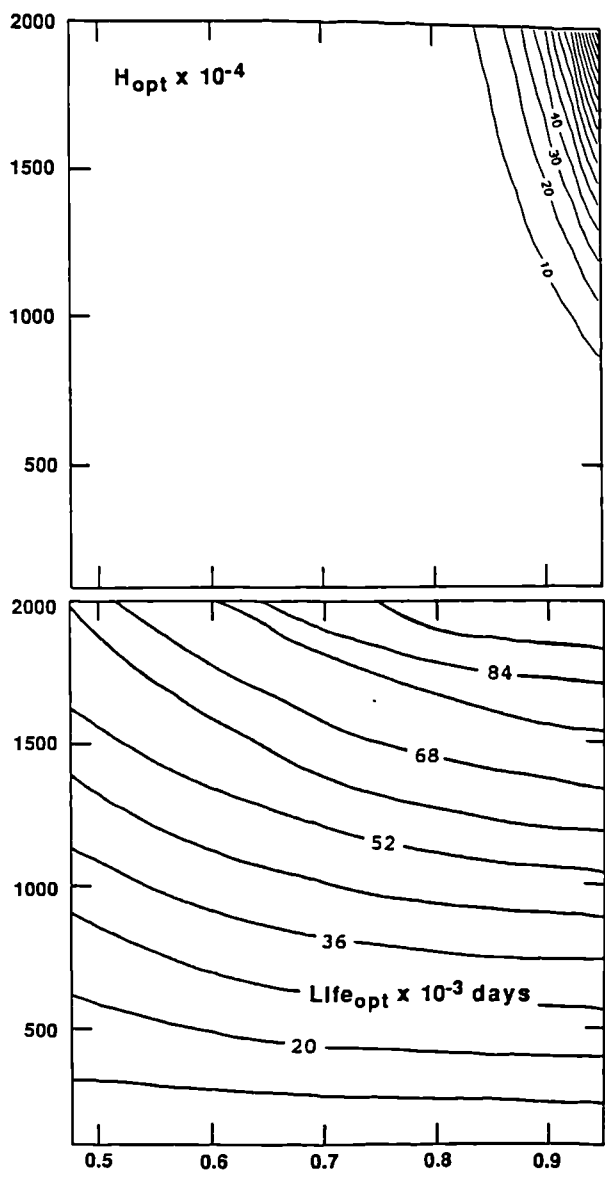


Fig. 5.10. Variation in *Cancer pagurus* optimal tactics with moult survival ω (abscissae) and intermoult survival v (ordinates). $K_r = 1$. The statistics, as described in the text, were calculated as described in Fig. 5.5.

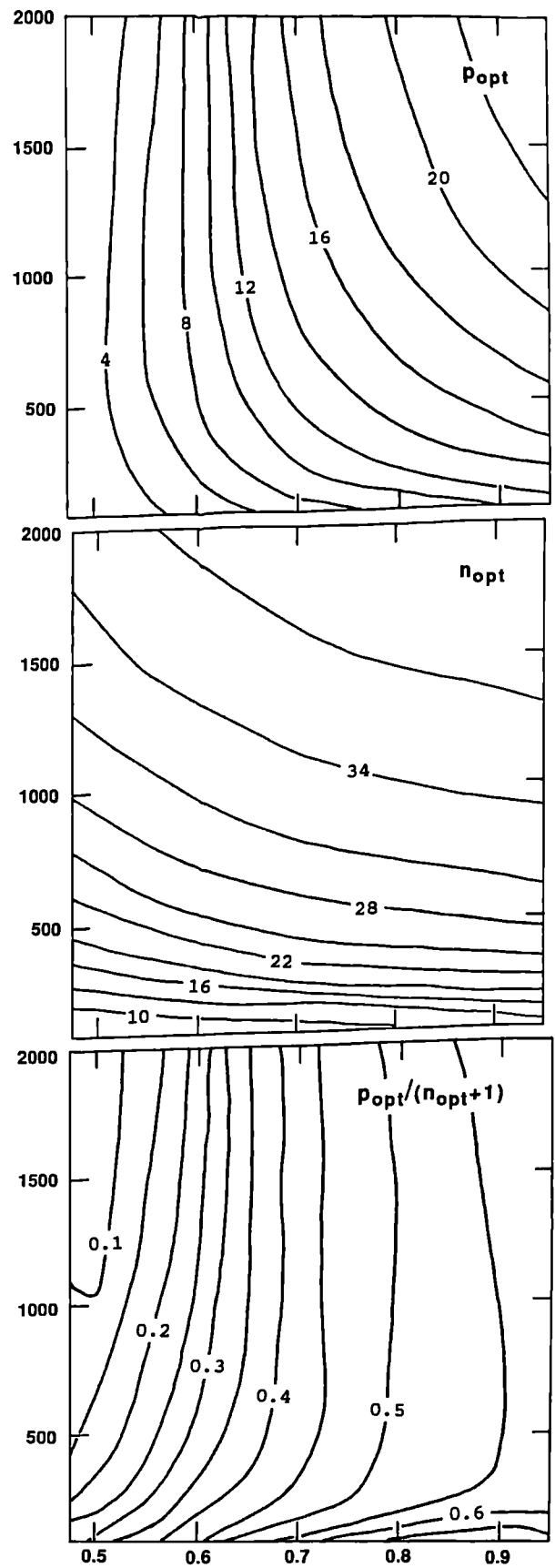
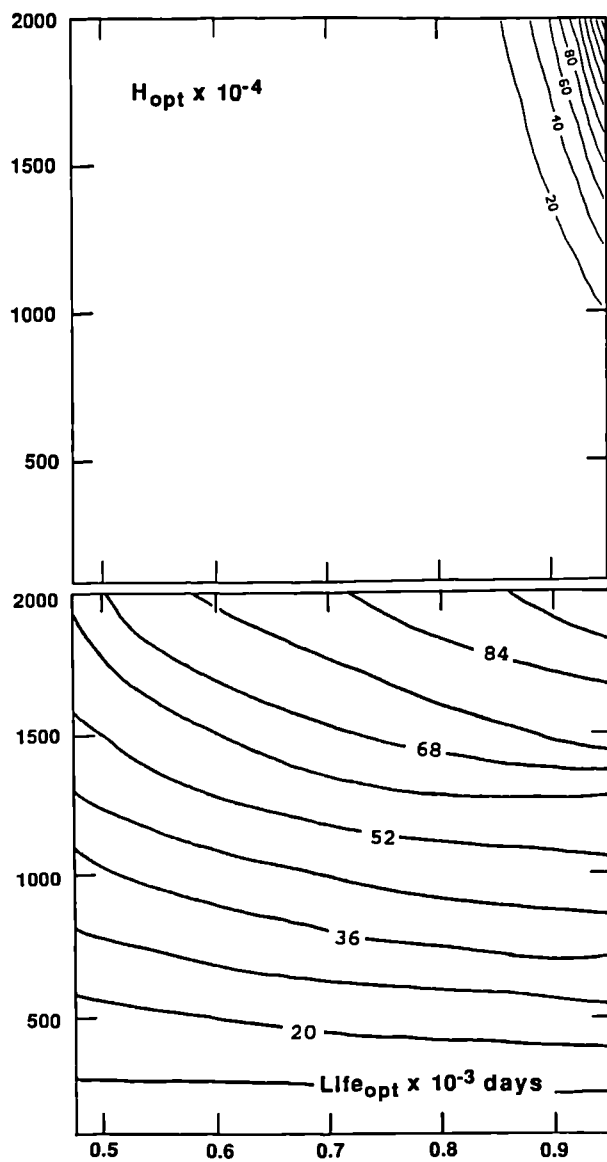


Fig. 5.11. Variation in *Cancer pagurus* optimal tactics with moult survival ω (abscissae) and intermoult survival v (ordinates). $K_r = 2$. The statistics, as described in the text, were calculated as described in Fig. 5.5.

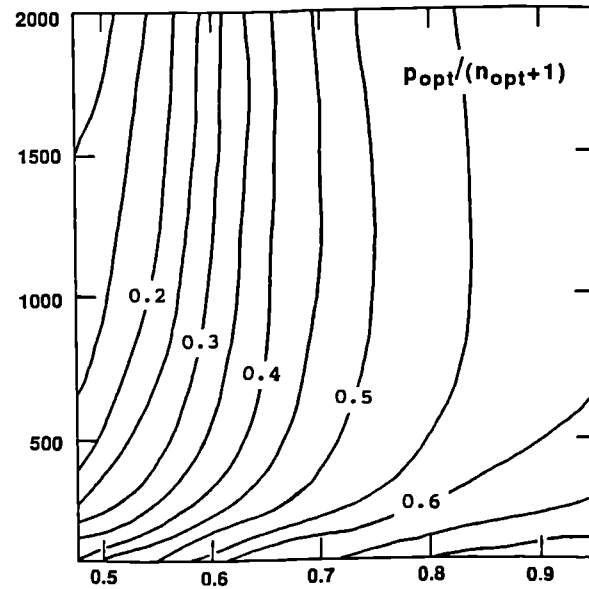
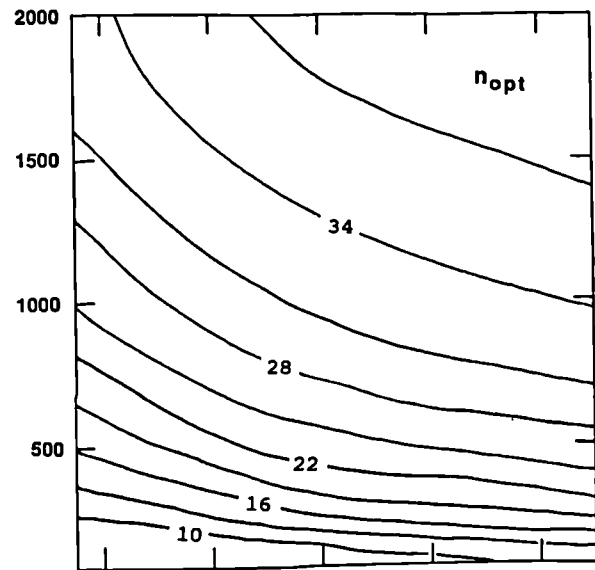
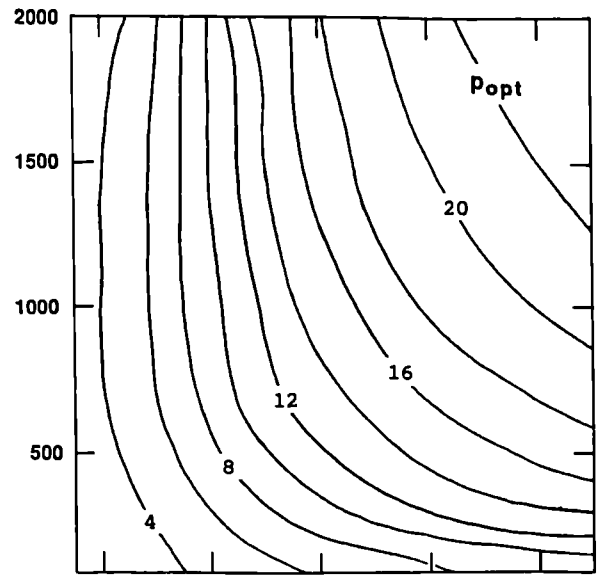
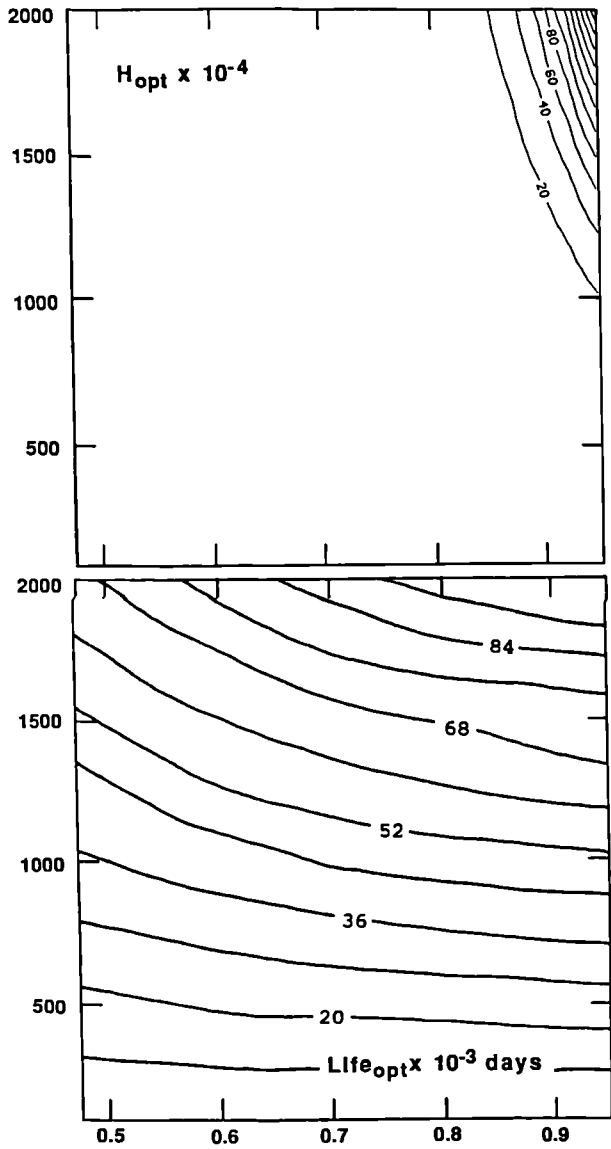


Fig. 5.12. Variation in *Cancer pagurus* optimal tactics with moult survival ω (abscissae) and intermoult survival v (ordinates). $K_r = 3$. The statistics, as described in the text, were calculated as described in Fig. 5.5.

pagurus, n_{opt} increases steadily as intermoult survival is increased, never actually reaching the maximum value of 50. The value of p_{opt} increases with increasing survival and is more strongly affected by moult survival than by intermoult survival. These patterns in p_{opt} and n_{opt} give a pattern of the lateness of reproduction which is quite different to that of *Carcinus maenas*. In that species, precocity (low values of $p_{opt}/(n_{opt}+1)$) occurred at high intermoult survival levels. In *Cancer pagurus* precocity occurs at low moult survival levels. The latter prediction is insensitive to the number of batches laid per instar.

5.3.3. *Hyas coarctatus*.

5.3.3.1 Fixed survival parameters.

The variation of H with p is shown for two survival regimes in Fig. 5.13. A new optimal statistic, b_{opt} , appears in this figure, which is the number of batches of eggs laid before survival reaches its pre-determined low level. With moderate rates of survival (those shown, regimes a and b) feasible values are obtained for H_{opt} (1980 and 342 respectively), but both p_{opt} and b_{opt} are rather large. With lower survival ($\omega < 0.75$, $v < 400$, not actually shown on the graph) the predicted p_{opt} and b_{opt} are lower and within the range observed or estimated in the field (Chapter three and Hartnoll 1963). At these lower survival rates, however, H_{opt} is of the order of tens rather than hundreds, which is unfeasibly low.

5.3.3.2. Variable survival parameters.

Contour plots of H_{opt} , p_{opt} , b_{opt} , lifetime and juvenile lifetime of the optimal tactic are given in Fig. 5.14. It is important to note that p_{opt} reaches its limit (16) at moderate survival levels. Consequently, the top right quarter of each contour plot represents an artificial result. At these higher survival rates, the model is predicting a tactic in which maturity is delayed beyond that observed in the field and laboratory (Chapters two and three). The terminal instar sizes

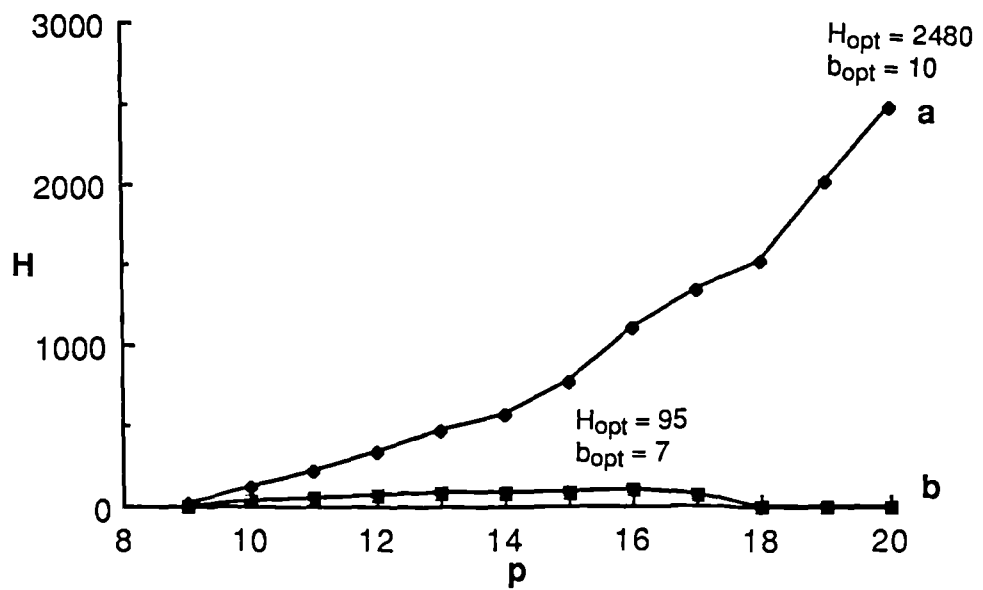
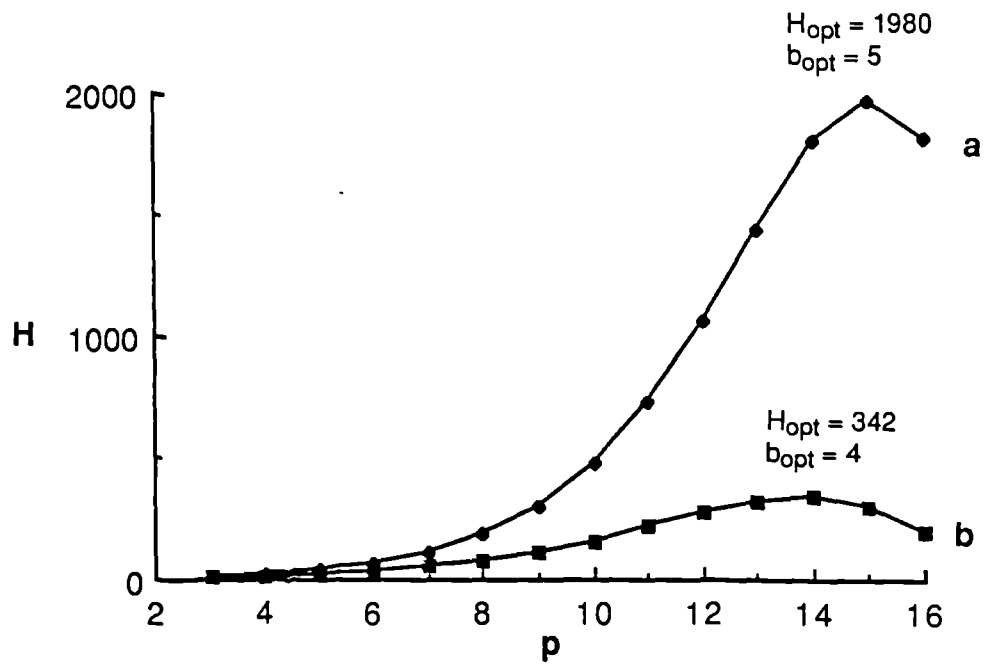


Fig. 5.13 (upper, *Hyas coarctatus*) and Fig. 5.15 (lower, *Inachus dorsettensis*). Lifetime egg production H versus p , for two survival regimes a and b. Regime a: $\omega = 0.8$, $v = 500$; regime b: $\omega = 0.75$, $v = 400$. Optimal lifetime egg production (H_{opt}) and the number of batches (b_{opt}) are indicated for each regime.

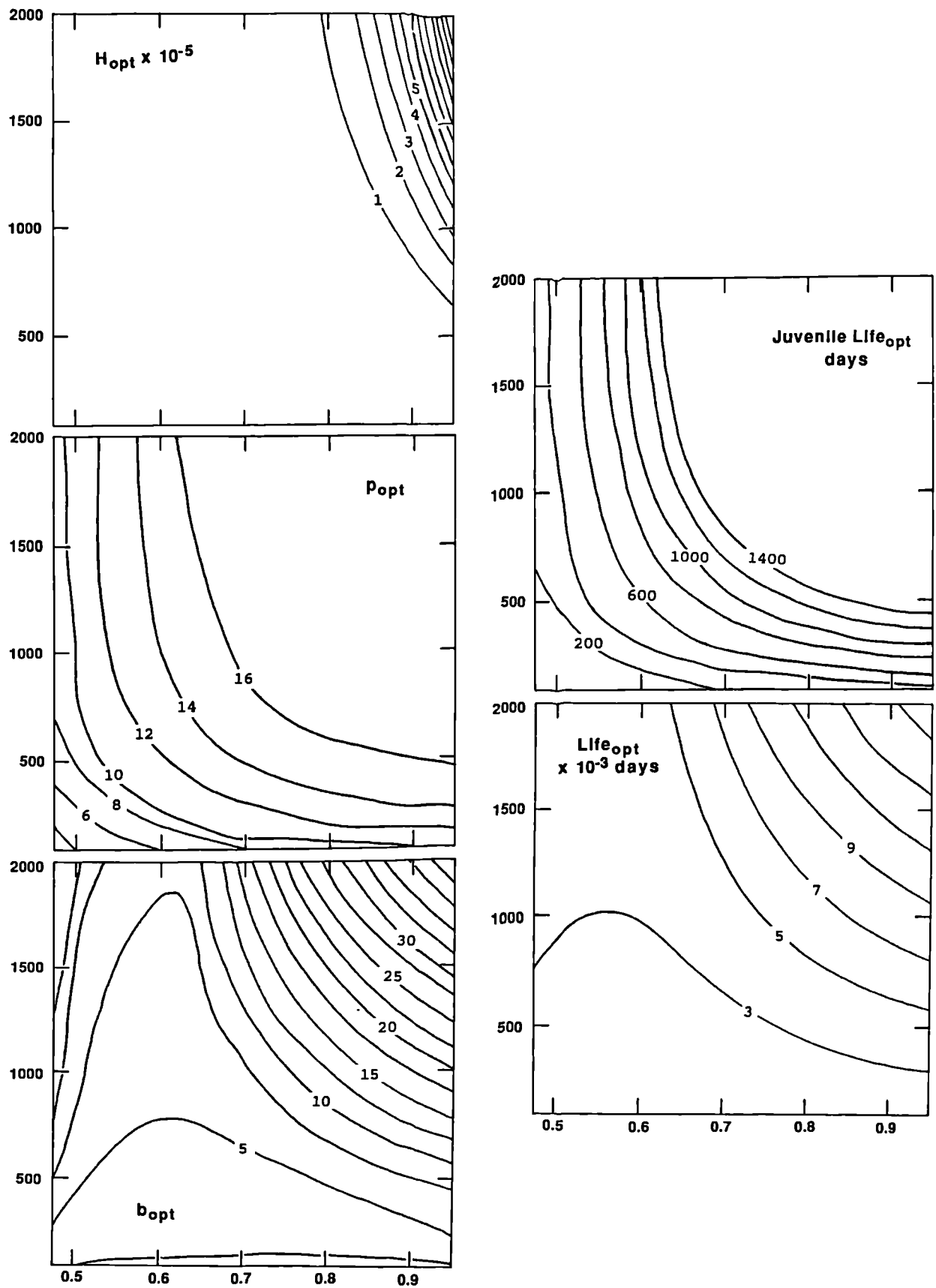


Fig. 5.14. Variation in *Hyas coarctatus* optimal tactics with moult survival ω (abscissae) and intermoult survival v (ordinates). The statistics, as described in the text, were calculated as described in Fig. 5.5.

associated with these tactics ($L_{p=16} = 185\text{mm}$ and greater) are considerably greater than those observed in British *Hyas coarctatus* (Chapter three and Hartnoll 1963).

At lower survival levels, p_{opt} , lifetime and juvenile lifetime increase with both moult and intermoult survival. The number of batches of eggs laid increases also, to a maximum of approximately 8. H_{opt} increases steadily, although this can not be seen from the contour plot; as H_{opt} increases greatly at the higher survival levels, this linear plot cannot represent the steady change at the lower levels. Values of H_{opt} in the 100s are obtained at certain survival combinations within this region, with b_{opt} not exceeding 5. The associated values of p_{opt} tend to be rather higher than those which are likely in the field however.

5.3.4. *Inachus dorsettensis*.

All of the figures for *Inachus dorsettensis* refer to a life history where instar 1 starts on Julian day 1. The model was run using other starting days (92, 183 and 274) and the results were found to be very similar to those shown. The predictions are, therefore, not sensitive to variation in recruitment time.

5.3.4.1. Fixed survival parameters.

Variation of H with p under the same two survival regimes as used for *Hyas coarctatus* is shown in Fig. 5.15. As with that species, H_{opt} is unfeasibly low at low survival rates ($\omega < 0.75$, $v < 400$, not shown on the graph) although the value of p_{opt} is close to that estimated in Chapter three. At slightly higher survival ($\omega = 0.75$, $v = 400$, regime b), p_{opt} is such that predicted size considerably exceeds that observed yet H_{opt} is still low (95). At the higher survival plotted (regime a), H_{opt} is obtained at the arbitrary maximum of $p = 20$, so the true H_{opt} and p_{opt} may be greater than that shown. Although the calculated lifetime egg production for $p = 20$ is feasible (2480), the corresponding size is far greater than that observed in Chapters two and three.

5.3.4.2. Variable survival parameters.

Contour plots equivalent to those for *Hyas coarctatus* are given in Fig. 5.16. As was the case for that species, p_{opt} reaches its limit (20) at the higher survival levels, that is, in the top right quarter of the plots. The interpretation will be restricted again, therefore, to the lower survival levels, those which do not cause p_{opt} to reach unfeasible values.

The plot of H_{opt} indicates a sharp rise only at the higher survival levels, those at which p_{opt} has reached its arbitrary maximum. The changes in H_{opt} at the more interesting lower survival levels cannot be seen in this plot. H_{opt} is clearly very low in this region however. Surprisingly, with H_{opt} being as low as it is, the number of batches predicted is very high: the model is predicting numbers of batches which are greater than those estimated in the field (Hartnoll 1963), which represent unfeasibly low lifetime egg productions.

The juvenile lifetimes predicted are in the observed range, although they are rather lower than is estimated in Chapter three. The overall lifetimes are very high, due to the above-mentioned prediction of numerous egg batches laid in the terminal instar.

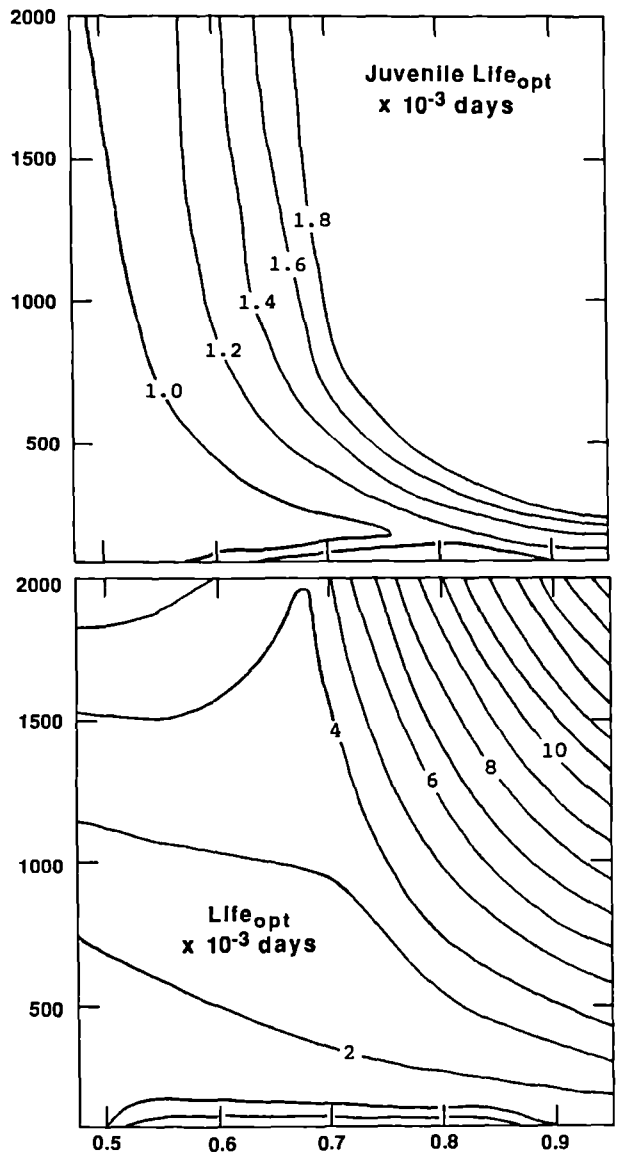
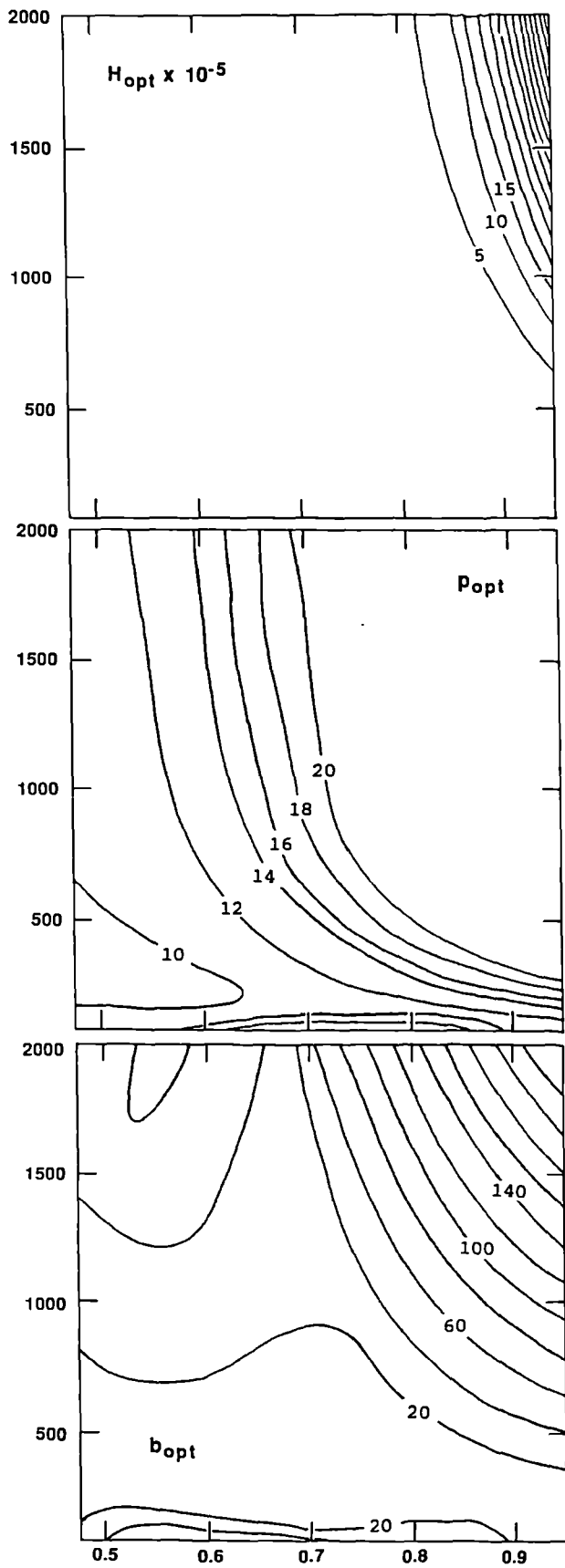


Fig. 5.16. Variation in *Inachus dorsettensis* optimal tactics with moult survival ω (abscissae) and intermoult survival v (ordinates). The statistics, as described in the text, were calculated as described in Fig. 5.5.

5.4. Discussion.

The *Carcinus maenas* and *Cancer pagurus* results will be discussed together, before separate discussion of the spider crab results. There are valuable comparisons to be made within these two groups, as the species within them have similar life histories. There are problems also which are peculiar to a particular group, especially the spider crabs, which merit separate discussion. At the end of this section the discussion will broaden to include all species, general comparisons will be made and general conclusions will be drawn.

As noted by Hartnoll and Gould (1988) there is considerable agreement between the fixed survival model results for *Carcinus maenas* and the observed life history. The predicted instar number at which maturity is attained is very similar to that found by Mohamedeen (1984) and the predicted total number of instars is slightly higher than has been estimated. The sizes of the model animals in their predicted instars are rather larger, however, than has been observed. Klein Breteler (1975a), working in the Wadden Sea, recorded the largest specimens as being approximately 50mm CW. Crothers (1967) estimated that females attained sexual maturity at 15-31mm CW depending upon season and that around 18 moults preceded terminal anecdyosis. At the northern end of the species' range in the Gulf of Maine Berrill (1982) found an absolute maximum female size of 70mm CW, with few individuals exceeding 50mm. There have been no observations of *Carcinus maenas* females as large as 248mm CW (predicted for the 25th instar) or even 199mm (20th instar).

This result may be due to overestimation of moult increment in the model. The equation, given here and in Hartnoll and Gould (1988), is based upon the laboratory data of Klein Breteler (1975b) and Mohamedeen and Hartnoll (1989). The moult increments of captive specimens tend to be smaller than those in the field (Hartnoll 1982) however, so one would expect under- rather than over-estimation.

In contrast, the sizes predicted for *Cancer pagurus* given the same survival assumptions, approximate closely to those observed in the field. The size at

maturity (19th instar) is very similar to that estimated by, for example, Bennett (1974) and Edwards (1979). The size during the penultimate instar (number 36) of the optimal tactic is far greater than the largest observed specimen of *C. pagurus*. However, the penultimate instar size of the near-optimal tactic ($L_{24}=233\text{mm}$) is close to that which has been observed by these authors.

One prediction which is common to both these species, assuming a fixed survival rate, is that a near-optimal lifetime egg production may result from a life schedule considerably shorter than that of the optimal tactic. In *C. pagurus* there is little increase in H when n exceeds 24, although H_{opt} occurs at $n=36$. *Carcinus maenas* has a similarly flat peak in H with respect to n . Thus, similar lifetime egg productions result from life schedules with n varying throughout these ranges. The fact that the actual values of n fall at the lower end of the predicted ranges, or below that range, suggests that there is a constraint upon final size or number of moults which may be undertaken by these species.

If such a constraint exists then it has special relevance to *Carcinus maenas*. In that species, unrealistically high values of n_{opt} are predicted when the number of batches per instar is increased. If, however, n is constrained then the optimal tactic for a female may be to produce only one batch of eggs per instar. Certainly, this is the tactic which gives the most realistic values of p_{opt} and n_{opt} , under both fixed and variable survival. In *Cancer pagurus* females, by contrast, no such selection for just a single batch of eggs per instar would be expected, as the number of batches has very little effect upon p_{opt} and n_{opt} .

There are similarities and differences in the effect of varying survival upon *Carcinus maenas* and *Cancer pagurus* life schedules. In general, increasing survival causes the prediction of a longer life schedule (higher n_{opt}) and later maturity (higher p_{opt}). This is to be expected given the constant, non age-specific, survival assumption and the size-related fecundity: if survival is increased then lifetime egg production will be increased by living through a greater number of instars (attaining a larger size) before maturity and before the terminal moult.

The differences between these two species relate to the differential effects of moult and intermoult survival variation. In the *Carcinus maenas* model p_{opt} increases only with moult survival whereas n_{opt} increases with both survival parameters. The overall effect is that precocity changes little with moult survival, as both p_{opt} and n_{opt} are increasing. With increased intermoult survival the predicted life history becomes more precocious, from reproducing about half way through the life history at low survival to reproducing about a quarter of the way through (in terms of the number of instars) at high survival. This gives us the counter-intuitive result of precocity being associated with high (intermoult) survival. In *Cancer pagurus* p_{opt} increases with both parameters but n_{opt} is affected most strongly by intermoult survival, leading to precocity at low moult survival levels. The biological significance of these moult and intermoult survival differences between species is unclear.

Interpretation of the spider crab results is rather problematic. The lower fecundity and low lifetime egg production of this group (Chapter four and Hartnoll 1963, Hines 1982) is evident. For *Hyas coarctatus* there are certain survival combinations which give a lifetime egg production in the hundreds, with predictions of terminal size and number of batches which are similar to those in the field. At most survival levels tested, a value is found for p_{opt} which is smaller than the computationally-imposed upper limit.

This is not the case for *Inachus dorsettensis*, however, in which p_{opt} often reaches the computational limit. The optimal tactic predicted for this species is, under almost all survival regimes, physiologically impossible or unfeasible. At high survival, an unrealistically large mature female laying many batches is predicted. As p_{opt} reaches the limit for p relatively early, it is likely that an unreasonably large p_{opt} would have been predicted at high survival levels had this been calculable. At the lower survival levels p_{opt} and b_{opt} are similar to those which have been estimated (Chapter three and Hartnoll 1963) but lifetime egg productions are extremely low.

There are several possible explanations for this *Inachus dorsettensis* result. One explanation is that this species may be adopting a suboptimal life history

tactic. Fig. 5.15 shows that a lifetime egg production of several hundred may be attained (at $\omega=0.8$, $v=500$) at a value of p which is within the range which is likely in the field. This value does not approach p_{opt} ; indeed, a true value for p_{opt} cannot be calculated under this survival regime as it exceeds the computational limit. A lower than optimal value for p could result from mechanical constraints precluding further moulting to the hypothetical larger sizes: the animal may function most effectively at a particular size and be ineffective beyond that size.

A second possible explanation is that this species' life history may be inappropriately represented by the model. The growth parameters, which were derived in Chapter four from laboratory experiments may be causing the simulated growth to differ considerably from that in the field. The size-specific fecundity parameters are more reliable as these are derived from field samples (Chapter four). The assumption of constant, non size-specific survival is another factor which has a marked effect upon the result. Additional runs of the model were performed with terminal instar mortality set at twice that of the juvenile instars, thus simulating a life history with extra risk associated with egg bearing. This had the effect of reducing the number of batches laid and reducing lifetime egg production still further, but had little effect upon p_{opt} .

It is likely that reduced survival during the terminal instar would bring the predictions for *Hyas coarctatus* closer to the observed pattern, even though this was not the case for *Inachus dorsettensis*. For *H. coarctatus* the predictions are generally more accurate apart from the number of batches which is rather high. Reduced terminal instar survival would reduce this number and would also reduce lifetime egg production. For both species it is likely that terminal instar survival differs from that of earlier instars. As speculated earlier, some extra risk may be associated with the carrying of eggs. Additionally, ageing of the animal's shell and the accumulation of epifauna (Hartnoll 1963) are likely to affect survival probability with longer instar durations.

One overall outcome of this work is the suggestion of postlarval survival rates which are likely in these species. In particular, lower postlarval survival is suggested for the spider crabs than for *Carcinus maenas* and *Cancer pagurus*. The very low fecundity of the spider crabs (Chapter four) implies, in addition, that larval survival is higher than in the more fecund species. If this is the case then the spider crabs have a ratio of early survival to postlarval survival which is considerably greater than that of the other two species.

The balance between early and late survivorship has been considered in some detail in the theoretical literature, in the context of the evolution of semelparity and iteroparity. Cole (1954) first considered the semelparity/iteroparity question and predicted that there was very little to be gained, in population growth terms, from breeding repeatedly. He suggested that the same intrinsic population growth rate was attained by producing n offspring repeatedly as by producing $n+1$ offspring then dying. Cole's result, as it became known, was controversial (Murdoch 1966, Gadgil and Bossert 1970, E. Bryant 1971) and was modified considerably when age-specific survival was taken into account (Charnov and Schaffer 1973). The analysis of the latter authors showed that the perennial reproductive habit with fecundity n was the equivalent of an annual with fecundity $n + P/C$ (where P = adult survivorship, C = juvenile survivorship). Thus if adult survivorship is very much greater than juvenile survivorship then a semelparous species would have to have a very high fecundity to be the equivalent of the iteroparous species. Iteroparity is likely to be selected for in these circumstances therefore. If adult survivorship is less than or equal to juvenile survivorship then it would be advantageous to breed only once.

The predominance of iteroparity amongst benthic marine invertebrates (Barnes and Hughes 1988) may be explained by Charnov and Schaffer's analysis. Survival is very low during the larval phase of crabs and other benthic invertebrates, so the value of P/C will be high. Iteroparity may be expected, then, under these circumstances. The spider crab females, as they breed only in the terminal instar, reproduce less repeatedly than the species which continue moulting after puberty. The results of this chapter suggest that P/C is lower in spider crabs than in the two other species studied. It is

tempting therefore to suggest a causative link between P/C and the less iteroparous habit of the spider crabs. Age-specific survival may control to some extent the level of iteroparity in the terminal instar, and may have influenced the evolution of the spider crab life history.

Another overall outcome of this work is the possible effect of moult, as distinct from intermoult, survival upon life history. These two survival parameters may have different effects upon life history tactic, as discussed earlier for *Carcinus maenas* and *Cancer pagurus*. The differential effect of the two parameters was found to be inconsistent between these two species. The spider crab model predicted, for both species, that the number of instars preceding maturity increased with both moult and intermoult survival; the two parameters had the same qualitative effect upon life history tactic.

The assumption of constant postlarval survival simply partitioned into two sources, moult and intermoult, probably represents a considerable simplification. Due to the experimental difficulty of ageing non-sessile crustaceans, there is a lack of data on the age-specificity of survival (Hartnoll 1985). It is commonly assumed in fish for example that predation pressure decreases, and thus survival probability increases, with age (Pitcher and Hart 1982). In crabs, however, individuals of all sizes are extraordinarily vulnerable when recently moulted. It may be that the animal which is best able to seek refuge from predation is the one which maximises survival through the moult. Body size, and the nature of the refuges available, will be highly significant in the ability to seek refuge. Thus, there is little reason to expect the common pattern of increasing survivorship with age in this group of animals. The age-specificity of survival depends very much upon the nature of the habitat and upon predation pressure.

Variation in survival between juvenile and adult, and with postlarval age generally, will be small relative to the difference between larval and postlarval survival. In varying survival in the model one is in effect varying the balance between larval and postlarval survival. If there is valid criticism to be made of the treatment of survival in the model, I believe that it relates to the lack of explicit representation of larval survival. This is a more significant omission than the lack of variation of postlarval survival with

age. Had this been included, however, it would have been one more parameter for which there is no supporting hard data.

Another shortcoming of the model relates to its use of lifetime egg production as its measure of fitness. This has the advantage of measurability but it ignores the possibility of variation in survival of the offspring. An ideal measure of fitness would be the number of offspring which survive to reproductive age themselves (Begon *et al.* 1990). Due to the difficulty in estimating this, it has been used in only a limited number of studies (eg. Sibly and Monk 1987). It is conceivable that fewer, larger eggs would have greater individual survival probabilities than more numerous, smaller eggs. Hines (1982), in his study of twenty species of brachyurans, demonstrated a clear interspecific trade-off between egg size and number of eggs per brood. If such a balance between number and size exists within a species, between individuals, then the consideration of egg number alone may be quite misleading. Reassuringly perhaps, no such intraspecific trade-off was found in *Hyas coarctatus* and *Inachus dorsettensis* in Chapter four.

There is another finding of Hines' (1982) study which is relevant to this life history model. He observed allometric constraints in brachyuran output, principally the strong relationship between female body size and several variables of reproductive effort. Such constraints challenge the assumption of theoretical studies that life history traits are free to evolve under demographic forces (eg. this study, Stearns 1976, 1980).

Despite the shortcomings of the model, some of which are inherent in the whole optimality modelling approach (Stearns 1980), some interesting possibilities have been raised. Survival differences are strongly suggested between the four species investigated. It is suggested that moult and intermoult survival variation can have different and unexpected effects depending upon species. Finally, in the spirit of Hartnoll and Gould (1988), the general effect of survival upon brachyuran life history evolution has been investigated, thus furthering the attempt to understand the different strategies and tactics observed in nature.

Chapter 6.

General Discussion.

Life history patterns have been studied in numerous crustaceans (Hartnoll 1985, Hines 1989) and various brachyurans (eg. Hartnoll and Gould 1988, Hines 1982, 1989) in an attempt to relate pattern to habitat and taxonomic rank. Two important component variables of these patterns are size and age at the puberty moult, the onset of maturity. Female body size is the most important factor affecting fecundity and reproductive output in the Brachyura (eg. Hines 1982, this study). The latter two variables are critically important in determining population growth rate and have thus featured prominently in the development of life history theory (Stearns 1976, 1989).

In studying female spider crab life histories, Hines (1981) envisaged the size at maturity to be critically balanced against the number of juvenile moults. Increasing the number of moults preceding maturity was considered to be a cost (in terms of survival probability) but the resultant increased size at maturity, and consequent fecundity, to be a benefit. That is essentially the philosophy underlying the present study. Size at puberty may be expected to be especially critical in spider crabs as the puberty moult is terminal, so the size at puberty represents the size throughout maturity (Hartnoll 1985, Hines 1989). Those brachyurans which continue moulting as adults may increase their body size considerably beyond pubertal size and, depending upon adult survival, have high reproductive output later in life. The particular moult number and size at puberty may, therefore, be less critical in those species.

Geographic variation in pubertal size has been noted in various brachyurans, mostly as information which was incidental to the main purpose of study (Hines 1989). Somerton (1981) found such variation in *Chionoecetes bairdi* and *C. opilio* in the eastern Bering Sea, which was of considerable consequence for fisheries management. The same study showed a significant increase in female size at maturity with temperature. Jones and Simons (1983) noted latitudinal variation of life history variables in the intertidal grapsid *Helice crassa* around New Zealand. Maximum size, pubertal size of females and brood size were found to increase with latitude, supporting similar earlier observations for marine animals generally. Hines (1989) studied size at puberty in particular, in three grapsid, one xanthid and one majid species on the east and west coasts of North America. The majid, *Scyra acutifrons*, is the only species

of these five in which females have a single ovigerous (terminal) instar. Geographic variation in either pubertal size or the size-frequency of mature females was found in the grapsids *Hemigrapsus nudis* and *Pachygrapsus crassipes* and the xanthid *Panopeus herbstii*. Variation occurred on a more local scale, among neighbouring populations, in *S. acutifrons* and the grapsid *Hemigrapsus oregonensis*. Disparate size structures were found for *S. acutifrons* populations, and this difference was accounted for by a difference in the number of juvenile moults (as many as seven) rather than by a difference in growth rate. The interpretation of the local variation result was that small scale factors, such as food availability, population density or substrate type, were more important than latitudinal factors in affecting pubertal size in those species. Differential predation pressure between the neighbouring populations may also have caused the observed size frequency differences in *S. acutifrons*, although it would appear that this factor was not considered.

The size structure differences in *Scyra acutifrons* (Hines 1989) were between populations with only fine differences in habitat. In another majid, *Libinia emarginata*, Aldrich (1974) found extreme size variation of mature animals between a rocky habitat population and a mud flat population. In the former habitat, adults were small and appeared to live for several years, on the basis of their epifaunal barnacles. On the mud flats, adults were large and carried few, small barnacles, indicating a short adult lifespan. It was suggested that the two different sizes represented evolved strategies (tactics) due to differential predation between habitats. The small adult females were capable of laying several small egg batches, whereas the large females could lay very few, large egg batches.

The modal size differences of mature animals found between sites in the present study were significant but small compared to, for example, differences between Hines' (1989) *S. acutifrons* populations. The entire observed mature size range could be accounted for by a difference in number of juvenile moults of four in *Hyas coarctatus* and three in *Inachus dorsettensis* (Chapter three). The results of Chapters two and three suggest that both species may undergo one extra juvenile moult on average at the Laxey site relative to the Bradda site. Small differences in growth rate may also have contributed to this variation; no size-related

difference in moult increment or intermoult period was detected in preliminary analysis of the laboratory growth experiment, but field conditions at those sites may have affected growth. Equally, differential predation between sites may have affected the size frequency distributions.

In addition to size differences in these species considerable variation in abundance was noted, between sites and between this study and the one conducted thirty years ago (Hartnoll 1961, 1963). The possibility of changes in abundance being due to disturbance (commercial scallop dredging) was discussed earlier (section 2.4). This well-documented source of disturbance may have affected not only abundance, but size frequency also. *Hyas coarctatus* at the site to the south west of the island had a smaller maximum size, in females especially, than was found in the earlier study. The likely effect of dredging, although unconfirmed in these particular species, is to increase postlarval mortality rates. The potential consequence for abundance is obvious. A possible consequence for the size at which an individual undergoes the maturity moult is suggested by the model of Chapter five. The model predicts that increased postlarval mortality leads to a decreased instar number (and size) at maturity in females of both spider crab species. The results for *H. coarctatus* support this prediction, therefore, but those for *Inachus dorsettensis* do not.

The possibility of genetic differentiation between the two spider crab populations was discussed earlier in the context of causation of the size structure differences (section 2.4). The larvae of *Hyas coarctatus* were estimated to spend over two months in the plankton and the larvae of *Inachus dorsettensis* about one month. Both estimates were based upon laboratory rearing results and considerable error may have been incurred in extrapolating to field conditions. Even if the estimation of larval duration is accurate, it is not safe to assume that larval dispersal results in genetic homogeneity between populations. Relatively little is known of the realised dispersal of marine animals, and there are conflicting examples in the literature. At one extreme, Scheltema (1971a,b) observed larvae of continental shelf species along the entire length of ocean currents in the Atlantic, and inferred that genetic exchange was occurring between widely separated populations. Other studies have shown, however, that larval dispersal may not always be far-reaching (Johanneson

1988) and that the potential duration may not always be realised (Todd *et al.* 1988).

The genetic homogeneity of populations has a bearing also on whether one might expect local adaptation to habitat conditions. Underwood and Fairweather (1989) considered local adaptation to be unlikely when dispersal results in few offspring returning to the parental population. Under these non-self-recruiting conditions, offspring are likely to be subject to different selective pressures to the parents. Traits which confer a selective advantage in the parent population may not necessarily confer the same advantage to the offspring. In such an absence of consistent selective pressure, specific adaptation to local conditions is unlikely.

Not surprisingly, data which quantify these ideas are scarce. It is difficult to say how different habitat conditions must be and how limited the return of larvae to the parent population must be, in order to preclude local adaptation. In the studies cited earlier (Aldrich 1974, Hines 1989) local adaptation of life history tactics was strongly suggested. In both those studies and the present study there is little information on larval dispersal patterns and none on genetic differentiation. In *Chionoecetes opilio*, genetic homogeneity has been observed in geographically separate and morphologically different populations (Davidson *et al.* 1985). Those authors concluded that there was an exchange of pelagic larvae, on the basis of estimated larval duration and typical summer water circulation. The morphological differences were thought to be due to differences between habitats in conditions for juvenile growth. Precise patterns of larval dispersal are not easily studied in benthic marine invertebrates. The study of genetic differentiation between populations is relatively straightforward, however, and offers considerable insight into these problems.

The predominance of larval development amongst marine invertebrates has inspired much work on possible reasons for the evolution of that mode of development. These studies were considered earlier (sections 1 and 5.1) and will not be discussed further here; the present results relate to different aspects of marine invertebrate reproductive patterns and offer no new insights into the evolution of development mode. Aside from questions of why larval development exists, the consequences have long

been recognised as being important. These include the population genetic consequences, as discussed above, and also the consequences for the dynamics of recruitment (eg. Roughgarden *et al.* 1988, Underwood and Fairweather 1989). A larval phase, in which the many numerous offspring are subject to massive mortality, leads to recruitment which is very variable in time and space. It is likely therefore that populations of (benthic) postlarvae will fluctuate through time, for reasons which are only indirectly linked to reproductive output of the parent population. It is likely also that there will be gaps in these species' distributions, due to failure of larvae to arrive at particular sites. Hypotheses and models of marine population dynamics must take account of this variability in recruitment (Underwood and Fairweather 1989).

Population densities of *Hyas coarctatus* and *Inachus dorsettensis* will be affected by variability in recruitment: they may be expected to fluctuate over time. The abundance changes between the earlier study (Hartnoll 1963) and this one should therefore be interpreted rather cautiously. Abundance may have varied with time irrespective of the disturbance caused by scallop dredging. No data are available on temporal variation at either site, although a comparison may soon be possible with data which are currently being collected (D.R. Jones pers. comm.). Such a comparison would be relatively inexact, being based upon catch-per-unit-effort rather than absolute density. As described earlier (section 2.4) there are difficulties in obtaining quantitative abundance estimates in these mobile, subtidal species.

As larval survival is of such consequence in demographic terms, there has been considerable interest in the variability and causes of that survival (eg. Lasker and Sherman 1981). Larval survival was not considered explicitly in the model of Chapter five, although it is likely that it would have had considerable effect. The balance between larval and postlarval survival, in particular, may be important (section 5.4). The model has, so far, considered moult and intermoult survival in only the postlarval animals (Chapter five, Hartnoll and Gould 1988). Survival variation of larvae may also be an important determinant of reproductive tactic, as this is the stage at which most mortality occurs. A future application of the model may be to vary both larval and postlarval survival. For the latter, moult and intermoult survival could be varied in parallel to give, in effect, a single

postlarval survival parameter. The predicted optimal tactics would represent possible responses to the balance between survival in the two phases of life. Such results would be complementary to those already obtained, and would add weight to the speculation (section 5.4) on early and late survival in spider crabs.

The model of Chapter five predicted optimal precocity and longevity in response to the postlarval survival rates. Moults and intermoult survival were incorporated separately, as they are likely to differ considerably from each other (Hartnoll 1985, Hartnoll and Gould 1988): during the moult and immediate postmoult a crab is extraordinarily vulnerable to predators. Egg size was assumed to be constant within a species, and this was shown to be true in *Hyas coarctatus* and *Inachus dorsettensis* (Chapter four). Lifetime egg production was used as the measure of a female's reproductive success. Ideally, one should consider the number of offspring surviving to maturity rather than lifetime egg production. The former is potentially a more meaningful measure of an individual's fitness but our approach was, by necessity, limited to the simpler alternative. The many unknowns of larval survival and dispersal, as discussed earlier, preclude the incorporation of this potentially more powerful measure of fitness.

Life history patterns may be modelled more easily, and with greater confidence, in many terrestrial systems. An example from the literature serves to illustrate the differences in life history modelling between terrestrial insects and benthic Crustacea. Sibly and Monk (1987) considered grasshopper life cycles which are seasonal with non-overlapping generations. Eggs are laid during the summer, which lay dormant over the winter, then hatch to develop into reproductive adults in the following summer. Egg size was considered to be traded-off against juvenile development time: a balance was suggested, between producing few large hatchlings which would be able to breed early in the following summer, or more numerous, smaller hatchlings which would breed relatively later. Their model predicted the number of offspring surviving to reproduce in the summer following egg laying. Thus, an optimal egg size was predicted. Comparison with field data revealed that one species

adopted the predicted optimal egg size at all of three sites, but another species laid consistently larger eggs than was predicted.

This approach was made possible by the existence of field data on egg, juvenile and adult survival rates (Monk 1985). The trade-off between egg size and development period was supported by laboratory results. Juvenile development period was expected to be critical to a female's reproductive success, as there was a limited, well-characterised period during the summer in which offspring could grow and reproduce. The shortest development period was therefore most likely to result in successful reproduction. A similar trade-off between egg size and development period, given a fixed allocation of resources to reproduction, has been assumed in many models (cited in Sibly and Monk 1987), including those of development mode in benthic invertebrates (following on from Vance 1973a,b). It is more difficult to demonstrate this trade-off in marine aquatic species which have planktonic larvae, compared to terrestrial species; laboratory experiments may show development time of larvae from different sized eggs, but only under conditions which are very different to those in the field. Survival rates, all-important in Sibly and Monk's model, are also more difficult, or impossible, to determine for many marine aquatic species.

There are more general difficulties in adopting an optimality-based, adaptationist approach, which applies to work on organisms in all habitats. These relate not to, for example, the ease with which parameters may be estimated, but to the applicability of the adaptationist approach itself. This approach, when applied to life history patterns, assumes that the life history has been moulded, by natural selection, to give optimal solutions to the problems posed by particular habitats. The approach, the adaptationist programme, has been criticised by Gould and Lewontin (1979). Their main argument is that the organism should be considered as a whole, that is, considered at the level at which selection acts, rather than as a collection of unitary traits. In considering the organism as a whole, the emphasis is placed upon the integration of traits within the individual, and the constraints of phylogeny and ontogeny. Gould and Lewontin (1979) criticised also the acceptance of adaptationist explanations

of evolved patterns on the grounds of plausibility alone. These criticisms have been countered (Mayr 1983) with the argument that extreme reductionism is the pitfall, rather than adaptationism itself. That author advocates a middle course between the holistic approach, which explains very little if taken to extremes, and the reductionist approach. The holistic approach is useful if appropriate questions are asked about integrated components of the system. Similarly, the adaptationist approach is useful if one has a realistic conception of natural selection and of the whole organism.

Life history studies, as pursued here, focus on whole organisms. The emphasis is upon the individual, and upon the balance between life history variables. In modelling life history patterns, some of the problems which are outlined above are avoided. Rather than simply constructing possible explanations for life history phenomena, a mathematical model predicts optimal solutions. The optimal solutions are then compared with observed phenomena. Thus, one begins to assess, rather than assume, the adaptive significance of life history patterns.

Summary.

1. The size structure of two populations was studied for the spider crabs *Hyas coarctatus* and *Inachus dorsettensis*, and was related to the results of a laboratory growth experiment. Size structures of mature animals were of especial interest as these species have only a single mature instar and the size of that instar is a critical determinant of brood size. Consistent small differences in modal size at maturity were found in both sexes of both species between the populations. The differences may have been caused by either or both of habitat-related factors or genetic differences between populations.
2. Size frequency data for juveniles were rather sparse, revealing few instar modes, and could not be used to determine growth rates in the natural habitat.
3. Lower abundances were found for both species around the south west of the Isle of Man than were found in a study conducted thirty years earlier (Hartnoll 1961, 1963). A lower maximum size was found in *Hyas coarctatus*, especially in the females, relative to the earlier study. It is suggested that these differences are related to disturbance by scallop dredging in the area. No time-lapse comparison is available for an undredged area to the east of the island, the second study site, but *Inachus dorsettensis* was far more abundant there than around the south west.
4. Sex ratios were found to be biased in favour of males in the juveniles, especially so for *Inachus dorsettensis*, and in favour of females in the adults (except for *Hyas coarctatus* at one of the sites). It is not known which of the possible factors was responsible for this observed switch.
5. Laboratory relative growth analysis indicated a moult of pre-puberty in males of both spider crab species, and a clear morphometric difference between juveniles and adults. The latter result was used to differentiate between the two groups for the purposes of comparing maturity moult increments with juvenile increments in male *Hyas coarctatus*.
6. In the laboratory growth experiment, percentage moult increment decreased slightly with temperature in *Hyas coarctatus*, but not in *Inachus dorsettensis*. Only in juvenile male *I. dorsettensis* did percentage increment decrease significantly with premoult size. The general lack of

relationship with premoult size is consistent with results for other determinate crustacean species.

7. Percentage increment was smaller at maturity than at the juvenile moults in both sexes of *Hyas coarctatus*. In the females this was thought to be due to pre-puberty allocation of resources to ovarian development. An opposite result was found in female *Inachus dorsettensis*, which develops its ovaries only after the terminal moult.

8. Intermoult period increased with body size in *Hyas coarctatus* and, in the females, decreased with temperature. A decrease with temperature was shown in female *Inachus dorsettensis*, but no relationship with body size was found.

9. Synthesis of the laboratory growth data suggests that *Hyas coarctatus* spends only one year as a juvenile (5-10 instars), and that *Inachus dorsettensis* females spend two to three years (8-11 juvenile instars).

10. Brood size was strongly related to body size in both *Hyas coarctatus* and *Inachus dorsettensis*. The first-laid batch of eggs was smaller than those laid subsequently in *I. dorsettensis*. There was no intraspecific trade-off between egg size and number per batch, and no variation of egg size with body size.

11. Reproductive allocation by weight was similar for both species and similar to that reported for other brachyurans (brood mass \approx 10% of body mass). Energetic allocation was three to four times higher than allocation by weight. Reproductive effort was greater in *Inachus dorsettensis* than *Hyas coarctatus*.

12. A simulation model was developed to predict optimal precocity and longevity, in response to postlarval moult and intermoult survival, for various brachyuran species. Pubertal and terminal moulting were predicted to be delayed in response to increasing postlarval survival.

13. For *Carcinus maenas* and *Cancer pagurus* the model predicted a flat peak in lifetime egg production with respect to terminal instar number. Thus, a near-optimal lifetime egg production could be attained by early

terminal moulting. For *C. pagurus*, the near-optimal tactic corresponded to that observed in the field. For *C. maenas*, the predicted terminal sizes were larger than those observed.

14. Low lifetime egg production was predicted by the model for *Hyas coarctatus* and *Inachus dorsettensis*. There was considerable agreement between predicted optimal tactics and those observed for the former species, but not for the latter.

15. Lower postlarval survival rates are suggested by the model for the spider crab species than for *Carcinus maenas* and *Cancer pagurus*. This may have implications for the evolution of the life history patterns in the spider crabs relative to other brachyurans.

References.

- Adelung, D. (1971) Studies on the moulting physiology of decapod crustaceans as exemplified by the shore crab *Carcinus maenas*. *Helg. wiss. Meeres*. **22**: 66-119.
- Adiyodi, R.G. and Subramoniam, T. (1983) Arthropoda - Crustacea. Ch. 18, in: Oogenesis, oviposition and oosorption, Eds. Adiyodi, K.G. and Adiyodi, R.G. Vol. I, Reproductive biology of invertebrates. Wiley Interscience, Chichester.
- Aldrich, J.C. (1974) Allometric constraints on energy relationships in the spider crab *Libinia emarginata* (Leach). *Biol. Bull. mar. biol. Lab., Woods Hole* **147**: 257-73.
- Aldrich, J.C. (1975) Individual variability in oxygen consumption rates of fed and starved *Cancer pagurus* and *Maia squinado*. *Comp. Biochem. Physiol.* **51A**: 175-83.
- Allan, J.D. (1976) Life history patterns in zooplankton. *Am. Nat.* **110**: 165-80.
- Alvey, N., Galwey, N. and Lane, P. (1982) An introduction to Genstat. Academic Press, London.
- Alvey, N.G. et al. (1983) GENSTAT. A general statistical program. Parts I and II. Lawes Agricultural Trust, Rothamsted.
- Amsler, M.O. and George, R.Y. (1984) Seasonal variation in the biochemical composition of the embryos of *Callinectes sapidus* Rathbun. *J. Crust. Biol.* **4**: 546-53.
- Anger, K. (1984) Development and growth in larval and juvenile *Hyas coarctatus* (Decapoda, Majidae) reared in the laboratory. *Mar. Ecol. Prog. Ser.* **19**: 115-23.
- Backhaus, J.O. (1985) A three-dimensional model for the simulation of shelf sea dynamics. *Dt. hydrogr. Z.* **38**: 165-87.
- Backhaus, J.O. and Hainbucher, D. (1987) A finite difference general circulation model for shelf seas and its application to low frequency variability on the north European shelf. pp. 221-44, in: Three-dimensional models of marine and estuarine dynamics, Eds. Nihoul, J.C.J. and Jamart, B.M. Elsevier, Amsterdam.
- Bagenal, T.B. (1966) The ecological and geographical aspects of the fecundity of the plaice. *J. mar. biol. Ass. U.K.* **46**: 161-86.

Barnes, H. and Barnes, M. (1968) Egg numbers, metabolic efficiency of egg production and fecundity; local and regional variations in a number of common cirripedes. *J. Exp. Mar. Biol. Ecol.* 2: 135-53.

Barnes, R.D. (1987) *Invertebrate zoology*. Saunders, Philadelphia.

Barnes, R.S.K. and Hughes, R.N. (1988) *An introduction to marine ecology*. Blackwell Scientific, Oxford.

Begon, M., Harper, J.L. and Townsend, C.R. (1990) *Ecology: individuals, populations and communities*. 2nd. Ed., Blackwell Scientific, Oxford.

Bennett, D.B. (1974a) Growth of the edible crab (*Cancer pagurus* L.) off south-west England. *J. mar. biol. Ass. U.K.* 54: 803-23.

Bennett, D.B. (1974b) The effects of pot immersion time on catches of crabs *Cancer pagurus* L. and lobsters *Homarus gammarus* (L.). *J. Cons. Int. Explor. Mer* 35: 332-6.

Bennett, D.B. and Brown, C.G. (1983) Crab (*Cancer pagurus*) migrations in the English channel. *J. mar. biol. Ass. U.K.* 63: 371-98.

Berrill, M. (1982) The life cycle of the green crab *Carcinus maenas* at the northern end of its range. *J. Crust. Biol.* 2: 31-9.

Bhattacharya, C.G. (1967) A simple method of resolution of a distribution into Gaussian components. *Biometrics* 23: 115-35.

Botsford, L.W. (1985) Models of growth. pp. 171-88, in: *Factors in adult growth*, Ed. Wenner, A.M. Vol. 3, *Crustacean Issues*, Ed. Schram, F.R. A.A. Balkema, Rotterdam.

Brafield, A.E. and Llewellyn, M.J. (1982) *Animal energetics*. Blackie, Glasgow.

Brand, A.R., Allison, E.H. and Murphy, E.J. (in press) North Irish Sea scallop fisheries: a review of changes. in: *An international compendium of scallop biology and culture*, Ed. Shumway, S.E. World Aquac. Soc. and Nat. Shellfish Assoc.

Brand, A.R., Wilson, U.A.W., Hawkins, S.J., Allison, E.H. and Duggan, N.A. (1991) Pectinid fisheries, spat collection, and the potential for stock enhancement in the Isle of Man. *ICES Mar. Sci. Symp.* 192: 79-86.

Bruce, J.R., Colman, J.S. and Jones, N.S. (1963) *Marine fauna of the Isle of Man and its surrounding seas*. Liverpool University Press, Liverpool.

Bryant, E. (1971) Life-history consequences of natural selection: Cole's result. *Am. Nat.* 105: 75-6.

Bückmann, D. and Adelung, D. (1964) The effect of environmental factors on growth and moulting rhythm in the shore crab, *Carcinus maenas*. *Helg. wiss. Meeres.* 10: 91-103.

Burrows, M.T. (1988) The comparative biology of *Chthalamus stellatus* (Poli) and *Chthalamus montagui* Southwood. Unpubl. Ph.D. thesis, University of Manchester.

Butler, T.H. (1960) Maturity and breeding of the Pacific edible crab, *Cancer magister* Dana. *J. Fish. Res. Bd. Canada* 17: 641-6.

Caddy, J.F. (1973) Underwater observations on tracks of dredges and trawls and some effects of dredging on a scallop ground. *J. Fish. Res. Bd. Canada* 30: 173-80.

Calow, P. (1978) Life cycles - An evolutionary approach to the physiology of reproduction, development and ageing. Chapman and Hall, London.

Calow, P. (1979) The cost of reproduction - A physiological approach. *Biol. Rev.* 54: 23-40.

Calow, P. (1981) Resource utilization and reproduction. Ch. 10, pp. 245-70, in: *Physiological ecology: An evolutionary approach to resource use*, Eds. Townsend, C.R. and Calow, P. Blackwell, Oxford.

Carlisle, D.B. (1957) On the hormonal inhibition of moulting in decapod Crustacea. II. The terminal anecdyesis in crabs. *J. mar. biol. Ass. U.K.* 36: 291-307.

Cassie, R.M. (1954) Some uses of probability paper in the analysis of size frequency distributions. *Aust. J. Mar. Freshw. Res.* 5: 513-22.

Chapman, C.J., Mason, J. and Kinnear, J.A.M. (1977) Diving observations on the efficiency of dredges used in the Scottish fishery for the scallop, *Pecten maximus* (L.). *Scot. Fish. Res. Rep.* 10: 1-16.

Charnov, E.L. and Schaffer, W.M. (1973) Life history consequences of natural selection: Cole's result revisited. *Am. Nat.* 107: 791-3.

Cheung, T.S. (1966) The development of egg-membranes and egg attachment in the shore crab, *Carcinus maenas*, and some related decapods. *J. mar. biol. Ass. U.K.* 46: 373-400.

Christiansen, F.B. and Fenchel, T.M. (1979) Evolution of marine invertebrate reproductive patterns. *Theor. Pop. Biol.* 16: 267-82.

Christiansen, M.E. (1969) Crustacea Decapoda Brachyura. Vol. 2, Marine invertebrates of Scandinavia. Universitetsforlaget, Oslo.

Christiansen, M.E. (1973) The complete larval development of *Hyas araneus* (Linneus) and *Hyas coarctatus* Leach (Decapoda, Brachyura, Majidae) reared in the laboratory. *Norw. J. Zool.* 21: 63-89.

Clarke, A. (1987) Temperature, latitude and reproductive effort. *Mar. Ecol. Prog. Ser.* 38: 89-99.

Clarke, M.R.B. (1980) The reduced major axis of a bivariate sample. *Biometrika* 67: 441-6.

Cock, A.G. (1966) Genetical aspects of metrical growth and form in animals. *Quart. Rev. Biol.* 41: 131-90.

Cole, L.C. (1954) The population consequences of life history phenomena. *Quart. Rev. Biol.* 29: 103-37.

Conan, G.Y. and Comeau, M. (1986) Functional maturity and terminal molt of male snow crab, *Chionoecetes opilio*. *Can. J. Fish. Aquat. Sci.* 43: 1710-9.

Conan, G.Y., Elner, R.W. and Moriyasu, M. (1990) Review of literature on life histories in the genus *Chionoecetes* in the light of the recent findings on growth and maturity of *C. opilio* in eastern Canada. *Proc. Int. Symp. King & Tanner Crabs* 163-79.

Conan, G.Y. and Gunderson, K.R. (1979) Growth curve of tagged lobsters (*Homarus gammarus*) in Norwegian waters as inferred from the relative increase in size at moulting and frequency of moult. *Rapp. P.-v. Reun. Cons. Int. Explor. Mer* 175: 155-66.

Conan, G.Y., Moriyasu, M., Comeau, M., Mallet, P., Cormier, R., Chiasson, Y. and Chiasson, H. (1988) Growth and maturation of snow crab (*Chionoecetes opilio*). *Proceedings of the International Workshop on Snow Crab Biology, December 8-10, 1987, Montreal, Quebec.* Eds. Jamieson G.S. and McKone W.D. *Can. Manus. Rep. Fish. Aquat. Sci.* 2005: 45-66.

Connell, J.B. (1970) a predator-prey system in the marine intertidal region. I. *Balanus glandula* and several predatory species of *Thais*. *Ecol. Monogr.* 40: 49-78.

- Coull, B.C. and Bell, S.S. (1983) Biotic assemblages: populations and communities. pp. 283-319, in: Behavior and ecology, Eds. Vernberg, F.J. and Vernberg, W.B. Vol. 7, The biology of Crustacea, Eds. Bliss, D.E., Vernberg, F.J. and Vernberg, W.B. Academic Press, New York.
- Crisp, D.J. (1984) Energy flow measurements. Ch. 9, pp. 284-372, in: Methods for the study of marine benthos, Eds. Holme, N.A. and McIntyre, A.D., 2nd. Ed., Blackwell, Oxford.
- Crothers, J.H. (1967) The biology of the shore crab *Carcinus maenas* (L.). 1. The background - anatomy, growth and life history. *Field Studies* 2: 407-34.
- Dalla Via, J. (1985) Oxygen consumption and temperature change in the shrimp *Palaemon elegans*. *Mar. Ecol. Prog. Ser.* 26: 199-206.
- Davidson, K., Roff, J.C. and Elner, R.W. (1985) Morphological, electrophoretic and fecundity characteristics of Atlantic snow crab *Chionoecetes opilio*, and implications for fisheries management. *Can. J. Fish. Aquat. Sci.* 42: 474-82.
- Day, R. and McEdward, L. (1984) Aspects of the physiology and ecology of pelagic larvae of marine benthic invertebrates. pp. 93-120, in: Marine plankton life cycle strategies, Eds. Steidinger, K.A. and Walker, L.M. CRC Press, Florida.
- Demeusy, N. (1957) Respiratory metabolism of the fiddler crab *Uca pugilator* from two different latitudinal populations. *Biol. Bull. mar. biol. Lab., Woods Hole* 113: 245-53.
- Dennell, R. (1960) Integument and exoskeleton. pp. 449-72, in: The physiology of Crustacea, Ed. Waterman, T.H. Academic Press, New York.
- Diaz, H., Conde, J.E. and Bevilacqua, M. (1983) A volumetric method for estimating fecundity in Decapoda. *Mar. Ecol. Prog. Ser.* 10: 203-6.
- Diesel, R. (1986) Optimal mate searching strategy in the symbiotic spider crab *Inachus phalangium* (Decapoda). *Ethology* 72: 311-28.
- Diesel, R. (1988) Male-female association in the spider crab *Inachus phalangium*: the influence of female reproductive stage and size. *J. Crust. Biol.* 8: 63-9.
- Donaldson, W.E. (1988) Growth of males after reaching sexual maturity in the genus *Chionoecetes*. Proceedings of the International Workshop on Snow Crab Biology, December 8-10, 1987, Montreal, Quebec. Eds. Jamieson G.S. and McKone W.D. *Can. Manus. Rep. Fish. Aquat. Sci.* 2005: 100-20.

- Donaldson, W.E. and Adams, A.E. (1989) Ethogram of behavior with emphasis on mating for the tanner crab *Chionoecetes bairdi* Rathbun. *J. Crust. Biol.* 9: 37-53.
- Donaldson, W.E., Cooney, R.T. and Hilsinger, J.R. (1981) Growth, age and size at maturity of tanner crab, *Chionoecetes bairdi* M.J.Rathbun, in the northern Gulf of Alaska (Decapoda, Brachyura). *Crustaceana* 40: 286-302.
- Edwards, E. (1965) Observations on the growth of the edible crab (*Cancer pagurus*). *Rapp. P.-v. Reun. Cons. Int. Explor. Mer* 156: 62-70.
- Edwards, E. (1967) The Yorkshire crab stocks. M.A.F.F. Fisheries Laboratory, Burnham-on-Crouch.
- Edwards, E. (1979) The edible crab and its fishery in British waters. Fishing News Books, Farnham (UK).
- Farmer, A.S. (1973) Age and growth in *Nephrops norvegicus* (Decapoda: Nephropidae). *Mar. Biol.* 23: 315-25.
- de Figueiredo, M.J. and Thomas, H.J. (1967) On the biology of the Norway lobster, *Nephrops norvegicus* (L.). *J. Cons. Int. Explor. Mer* 31: 89-101.
- Fingerman, M. (1987) *The endocrine mechanisms of crustaceans.* *J. Crust. Biol.* 7: 1-24.
- Foyle, T.P., O'Dor, R.K. and Elner, R.W. (1989) Energetically defining the thermal limits of the snow crab. *J. Exp. Biol.* 145: 371-93.
- Gadgil, M. and Bossert, W.H. (1970) Life historical consequences of natural selection. *Am. Nat.* 104: 1-24.
- Gadgil, M. and Solbrig, O.T. (1972) The concept of r- and K-selection: evidence from wild flowers and some theoretical considerations. *Am. Nat.* 106: 14-31.
- Gould, S.J. and Lewontin, R.C. (1979) The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proc. R. Soc. Lond.* B205: 581-98.
- Grahame, J. and Branch, G.M. (1985) Reproductive patterns of marine invertebrates. *Oceanogr. Mar. Biol. Ann. Rev.* 23: 373-98.
- Grant, A. (1990) Mode of development and reproductive effort in marine invertebrates: should there be any relationship? *Funct. Ecol.* 4: 128-30.

- Griffiths, D. (1977) Caloric variation in Crustacea and other animals. *J. Anim. Ecol.* **46**: 593-605.
- Halberg, F., Shankaraiah, K., Giese, A.C. and Halberg, F. (1987) The chronology of marine invertebrates: methods of analysis. pp. 331-84, in: *General aspects: seeking unity in diversity*, Eds. Giese, A.C., Pearse, J.S. and Pearse, V.B. Vol. IX, *Reproduction of Marine Invertebrates*, Ed. Giese, A.C. The Boxwood Press, Pacific Grove, CA.
- Harding, J.P. (1949) The use of probability paper for the graphical analysis of polymodal frequency distributions. *J. mar. biol. Ass. U.K.* **28**: 141-53.
- Hart, A. and Begon, M. (1982) The status of general reproductive-strategy theories, illustrated in winkles. *Oecologia* **52**: 37-42.
- Hartnoll, R.G. (1961) Studies on the biology of Manx spider crabs. Unpubl. Ph.D. thesis, University of Liverpool.
- Hartnoll, R.G. (1963) The biology of Manx spider crabs. *Proc. Zool. Soc. Lond.* **141**: 423-96.
- Hartnoll, R.G. (1969) Mating in the Brachyura. *Crustaceana* **16**: 161-81.
- Hartnoll, R.G. (1972) The biology of the burrowing crab, *Corystes cassivelaunus*. *Bijdr. Dierk.* **42**: 139-55.
- Hartnoll, R.G. (1978) The effect of salinity and temperature in the post-larval growth of the crab *Rhithropanopeus harrisii*. pp. 349-58, in: *Physiology and behaviour of marine organisms*, Eds. McLusky, D.S. and Berry, A.J. Vol. 12, *European symposia on Marine Biology*. Pergamon Press, Oxford.
- Hartnoll, R.G. (1982) Growth. Ch. 3, pp. 111-96, in: *Embryology, morphology and genetics*, Ed. Abele, L.G. Vol. 2, *The biology of Crustacea*, Eds. Bliss, D.E. and Abele, L.G. Academic Press, New York.
- Hartnoll, R.G. (1985) Growth, sexual maturity and reproductive output. pp. 101-28, in: *Factors in adult growth*, Ed. Wenner, A.M. Vol. 3, *Crustacean Issues*, Ed. Schram, F.R. A.A. Balkema, Rotterdam.
- Hartnoll, R.G. (in press) Brachyura. Ch. 17, in: *Reproduction of marine invertebrates*, Eds. Clarke, W. and Hand, C. The Boxwood Press, Pacific Grove, CA.
- Hartnoll, R.G. and Gould, P. (1988) Brachyuran life history strategies and the optimisation of egg production. *Symp. Zool. Soc. Lond.* **59**: 1-9.

- Havenhand, J.N. and Todd, C.D. (1989) Reproductive effort of the nudibranch molluscs *Adalaria proxima* (Alder and Hancock) and *Onchidoris muricata* (Mueller): An evaluation of techniques. *Funct. Ecol.* 3: 153-63.
- Haynes, E., Karinen, J.F., Watson, J. and Hopson, D.J. (1976) Relation of number of eggs and egg length to carapace width in the brachyuran crabs *Chionoecetes bairdi* and *C. opilio* from the Gulf of St. Lawrence. *J. Fish. Res. Bd. Canada* 33: 2592-5.
- Hebert, P.D.N. (1978) The population biology of *Daphnia* (Crustacea, Daphnidae). *Biol. Rev.* 53: 387-426.
- Hiatt, R.W. (1948) The biology of the lined shore crab *Pachygrapsus crassipes* Randall. *Pacif. Sci.* 2: 135-213.
- Hilsinger, J.R. (1976) Aspects of the reproductive biology of female snow crabs, *Chionoecetes bairdi*, from Prince William Sound and the adjacent Gulf of Alaska. *Mar. Sci. Comm.* 2: 201-35.
- Hines, A.H. (1978) Reproduction in three species of intertidal barnacles from central California. *Biol. Bull. mar. biol. Lab., Woods Hole* 154: 262-81.
- Hines, A.H. (1979) The comparative reproductive ecology of three species of intertidal barnacles. pp. 213-34, in: *Reproductive ecology of marine invertebrates*, Ed. Stancyk, S.E. University of South Carolina Press, Columbia.
- Hines, A.H. (1981) Life history strategies of spider crabs. *Am. Zool.* 21: 990.
- Hines, A.H. (1982) Allometric constraints and variables of reproductive effort in brachyuran crabs. *Mar. Biol.* 69: 309-20.
- Hines, A.H. (1986) Larval problems and perspectives in life histories of marine invertebrates. *Bull. Mar. Sci.* 39: 506-25.
- Hines, A.H. (1989) Geographic variation in size at maturity in Brachyuran crabs. *Bull. Mar. Sci.* 45: 356-68.
- Hirshfield, M.F. and Tinkle, D.W. (1975) Natural selection and the evolution of reproductive effort. *Proc. Nat. Acad. Sci. USA* 72: 2227-31.
- Holland, D.L. (1978) Lipid reserves and energy metabolism in the larvae of benthic marine invertebrates. pp. 85-123, in: *Biochemical and biophysical perspectives in marine biology*, Eds. Malins, D.C. and Sargent, J.R. Academic Press, London.

- Huber, M.E. (1985) Non-random mating with respect to mate size in the crab *Trapezia* (Brachyura, Xanthidae). *Mar. Behav. Physiol.* **12**: 19-32.
- Hughes, R.N. and Roberts, D.J. (1980) Reproductive effort of winkles (*Littorina* spp.) with contrasted methods of reproduction. *Oecologia* **47**: 130-6.
- Huxley, J.S. (1924) The variation in the width of the abdomen in immature fiddler-crabs considered in relation to its relative growth rate. *Am. Nat.* **58**: 468-75.
- Huxley, J.S. (1932) Problems of relative growth. Methuen, London.
- Ingle, R.W. (1980) British crabs. Oxford University Press, Oxford.
- Jamieson, G.S., Bailey, R., Conan, G.Y., Elner, R.W., McKone, W.D. and Taylor, D.M. (1988) Workshop Report. Proceedings of the International Workshop on Snow Crab Biology, December 8-10, 1987, Montreal, Quebec. Eds. Jamieson G.S. and McKone W.D. *Can. Manus. Rep. Fish. Aquat. Sci.* **2005**: 1-15.
- Johannesson, K. (1988) The paradox of Rockall: why is a brooding gastropod (*Littorina saxatilis*) more widespread than one having a planktonic larval dispersal stage (*L. littorea*). *Mar. Biol.* **99**: 507-13.
- Jones, M.B. and Simons, M.J. (1983) Latitudinal variation in reproductive characteristics of a mud crab, *Helice crassa* (Grapsidae). *Bull. Mar. Sci.* **33**: 656-70.
- Khan, M.A. and Williamson, D.I. (1970) Seasonal changes in the distribution of Chaetognatha and other plankton in the eastern Irish Sea. *J. Exp. Mar. Biol. Ecol.* **5**: 285-303.
- Klein Breteler, W.C.M. (1975a) Growth and molting of juvenile shore crabs, *Carcinus maenas*, in a natural population. *Neth. J. Sea Res.* **9**: 86-99.
- Klein Breteler, W.C.M. (1975b) Laboratory experiments on the influence of environmental factors on the frequency of molting and the increase in size at molting of juvenile shore crabs, *Carcinus maenas*. *Neth. J. Sea Res.* **9**: 100-20.
- Klein Breteler, W.C.M. (1975c) Oxygen consumption and respiratory levels of juvenile shore crabs *Carcinus maenas*, in relation to weight and temperature. *Neth. J. Sea Res.* **9**: 243-54.
- Klein Breteler, W.C.M. (1975d) Food consumption, growth and energy metabolism of juvenile shore crabs, *Carcinus maenas*. *Neth. J. Sea Res.* **9**: 255-72.

Kurata, H. (1962) Studies on the age and growth of Crustacea. Bull. Hokkaido reg. Fish. Res. Lab. 24: 1-115.

Lasker, R. and Sherman, K. (1981) The early life history of fish: recent studies. Rapp. P.-v. Reun. Cons. Int. Explor. Mer 178: 1-607.

Laws, E.A. and Archie, J.W. (1981) Appropriate use of regression analysis in marine biology. Mar. Biol. 65: 13-6.

Leffler, C.W. (1972) Some effects of temperature on the growth and metabolic rate of juvenile blue crabs, *Callinectes sapidus*, in the laboratory. Mar. Biol. 14: 104-10.

Lovett, D.L. and Felder, D.L. (1989) Application of regression techniques to studies of relative growth in crustaceans. J. Crust. Biol. 9: 529-39.

MacArthur, R.H. and Wilson, E.O. (1967) The theory of island biogeography. Princeton University Press, Princeton, N.J.

Macdonald, P.D.M. and Pitcher, T.J. (1979) Age-groups from size-frequency data: a versatile and efficient method of analysing distribution mixtures. J. Fish. Res. Bd. Canada 36: 987-1001.

Macleod, J.A.A., Thorpe, J.P. and Duggan, N.A. (1985) A biochemical genetic study of population structure in queen scallop (*Chlamys opercularis*) stocks in the northern Irish Sea. Mar. Biol. 87: 77-82.

Mason, J., Chapman, C.J. and Kinnear, J.A.M. (1979) Population abundance and dredge efficiency studies on the scallop, *Pecten maximus* (L.). Rapp. P.-v. Reun. Cons. Int. Explor. Mer 175: 91-6.

Mauchline, J. (1977) Growth of shrimps, crabs and lobsters - an assessment. J. Cons. Int. Explor. Mer 37: 162-9.

Mayr, E. (1983) How to carry out the adaptationist program? Am. Nat. 121: 324-34.

McLeese, D. and Watson, J. (1968) Oxygen consumption of the spider crab (*Chionoecetes opilio*) and the American lobster (*Homarus americanus*) at a low temperature. J. Fish. Res. Bd. Canada 25: 1729-32.

Mileikovsky, S.A. (1971) Types of larval development in marine bottom invertebrates, their distribution and ecological significance: a re-evaluation. Mar. Biol. 10: 193-213.

- Miller, R.J. and Watson, J. (1976) Growth per molt and limb regeneration in the spider crab *Chionoecetes opilio*. J. Fish. Res. Bd. Canada 33: 1644-9.
- Mohamedeen, H. (1984) Studies on laboratory growth of decapod crustaceans. Unpubl. Ph.D. thesis, University of Liverpool.
- Mohamedeen, H. and Hartnoll, R.G. (1989) Larval and postlarval growth of individually reared specimens of the common shore crab *Carcinus maenas* (L.). J. Exp. Mar. Biol. Ecol. 134: 1-24.
- Monk, K.A. (1985) Effect of habitat on the life history strategies of some British grasshoppers. J. Anim. Ecol. 54: 163-77.
- Moriyasu, M., Conan, G.Y., Mallet, P., Chiasson, Y. and Lacroix, H. (1987) Growth at moult, moulting season and mating of snow crab (*Chionoecetes opilio*) in relation to functional and morphometric maturity. ICES Shellfish Committee CM K:21: 1-14.
- Mort, M.A. (1991) Bridging the gap between ecology and genetics: the case of freshwater zooplankton. Trends Ecol. Evol. 6: 41-5.
- Murdoch, W.W. (1966) Population stability and life history phenomena. Am. Nat. 100: 45-51.
- Paine, R.T. (1966) Endothermy in bomb calorimetry. Limn. & Oceanogr. 11: 126-9.
- Palmer, A.R. and Strathmann, R.R. (1981) Scale of dispersal in varying environments and its implication for life histories of marine invertebrates. Oecologia 48: 308-18.
- Parry, G.D. (1981) The meanings of r- and K-selection. Oecologia 48: 260-4.
- Parsons, T.R., Maita, Y. and Lalli, C.M. (1984) A manual of chemical and biological methods for seawater analysis. Pergamon Press, Oxford.
- Paul, A.J. and Fuji, A. (1989) Bioenergetics of the Alaskan crab *Chionoecetes bairdi* (Decapoda: Majidae). J. Crust. Biol. 9: 25-36.
- Phillipson, J. (1964) A miniature bomb calorimeter for small biological samples. Oikos 15: 130-9.
- Pianka, E.R. (1970) On r- and K-selection. Am. Nat. 104: 592-7.
- Pianka, E.R. (1972) r and K selection or b and d selection? Am. Nat. 106: 581-8.

- Pianka, E.R. (1976) Natural selection of optimal reproductive tactics. *Am. Zool.* 16: 775-84.
- Pitcher, T.J. and Hart, P.J.B. (1982) *Fisheries ecology*. Croom Helm, London.
- Raffaelli, D.G. and Hughes, R.N. (1978) The effects of crevice size and availability on populations of *Littorina rudis* and *Littorina neritoides*. *J. Anim. Ecol.* 47: 71-83.
- Ramster, J.W. and Hill, H.W. (1969) Current systems in the N. Irish Sea. *Nature* 224: 59-61.
- Ricker, W.E. (1973) Linear regressions in fishery research. *J. Fish. Res. Bd. Canada* 30: 409-34.
- Roughgarden, J. (1989) The evolution of marine life cycles. Ch. 12, pp. 270-300, in: *Mathematical evolutionary theory*, Ed. Feldman, M.W. Princeton University Press, Princeton, N.J.
- Roughgarden, J., Gaines, S. and Possingham, H. (1988) Recruitment dynamics in complex life cycles. *Science* 241: 1460-6.
- Schaffer, W.M. (1979) The theory of life-history evolution and its application to Atlantic salmon. *Symp. Zool. Soc. Lond.* 44: 307-26.
- Scheirer, C.J., Ray, W.S. and Hare, N. (1976) The analysis of ranked data derived from completely randomised factorial designs. *Biometrics* 32: 429-34.
- Scheltema, R.S. (1971a) Larval dispersal as a means of genetic exchange between geographically separated populations of shallow-water benthic marine gastropods. *Biol. Bull. mar. biol. Lab., Woods Hole* 140: 284-322.
- Scheltema, R. (1971b) The dispersal of the larvae of shoal-water benthic invertebrate species over long distances by ocean currents. pp. 7-28, in: *European Marine Biology Symposium*, Ed. Crisp, D.J. Cambridge University Press, New York.
- Shen, C.J. (1935) An investigation of the post-larval development of the shore crab *Carcinus maenas*, with special reference to the external secondary sexual characters. *Proc. Zool. Soc. Lond.* 1935: 1-33.
- Sibly, R. and Calow, P. (1983) An integrated approach to life-cycle evolution using selective landscapes. *J. Theor. Biol.* 102: 527-47.
- Sibly, R.M. and Calow, P. (1986) *Physiological ecology of animals: an evolutionary approach*. Blackwell Scientific, Oxford.

- Sibly, R. and Monk, K. (1987) A theory of grasshopper life cycles. *Oikos* 48: 186-94.
- Simpson, J.H. (1971) Density stratification and microstructure in the western Irish Sea. *Deep Sea Res.* 18: 309-19.
- Simpson, J.H. (1981) The shelf-sea fronts: implications of their existence and behaviour. *Phil. Trans. R. Soc. Lond. A* 302: 531-46.
- Simpson, J.H. and Bowers, D. (1979) Shelf sea fronts adjustments revealed by satellite IR imagery. *Nature* 280: 648-51.
- Skinner, D.M. (1985) Molting and regeneration. pp. 43-146, in: *Integuments, Pigments and Hormonal Processes*, Eds. Bliss, D.E. and Mantel, L.H. Vol. 9, *The Biology of Crustacea*, Academic Press, Orlando.
- Skinner, D.M., Graham, D.E., Holland, C.A., Mykles, D.L., Soumoff, C. and Yamaoka, L.H. (1985) Control of molting in Crustacea. pp. 3-14, in: *Crustacean growth: factors in adult growth*, Ed. Wenner, A.M. A. A. Balkema, Rotterdam.
- Slinn, D.J. and Eastham, J.F. (1984) Routine hydrographic observations in the Irish Sea off Port Erin, Isle of Man, during 1972-1981 inclusive. *Annales Biologiques CIEM* 38: 42-3.
- Slobodkin, L.B. (1954) Population dynamics in *Daphnia obtusata* Kurz. *Ecol. Monogr.* 24: 69-88.
- Slobodkin, L.B. and Richman, S. (1961) Calories/gm in species of animals. *Nature* 191: 299.
- Smith, R.J. (1980) Rethinking allometry. *J. Theor. Biol.* 87: 97-111.
- Sokal, R.R. and Rohlf, F.J. (1981) *Biometry. The principles and practice of statistics in biological research.* 2nd. Ed., W.H. Freeman & Co., San Francisco.
- Somerton, D.A. (1981) Regional variation in the size of maturity of two species of tanner crab (*Chionoecetes bairdi* and *C. opilio*) in the eastern Bering Sea, and its use in defining management subareas. *Can. J. Fish. Aquat. Sci.* 38: 163-74.
- Somerton, D.A. and Meyers, W.S. (1983) Fecundity differences between primiparous and multiparous female Alaskan tanner crab (*Chionoecetes bairdi*). *J. Crust. Biol.* 3: 183-6.

- Southwood, T.R.E. (1977) Habitat, the templet for ecological strategies? *J. Anim. Ecol.* **46**: 337-65.
- Southwood, T.R.E. (1988) Tactics, strategies and templets. *Oikos* **52**: 3-18.
- Stearns, S.C. (1976) Life history tactics: a review of the ideas. *Quart. Rev. Biol.* **51**: 3-47.
- Stearns, S.C. (1977) The evolution of life history traits: a critique of the theory and a review of the data. *Ann. Rev. Ecol. Syst.* **8**: 145-71.
- Stearns, S.C. (1980) A new view of life-history evolution. *Oikos* **35**: 266-81.
- Stearns, S.C. (1983) A natural experiment in life-history evolution: field data on the introduction of mosquitofish (*Gambusia affinis*) to Hawaii. *Evolution* **37**: 601-17.
- Stearns, S.C. (1989) Trade-offs in life-history evolution. *Funct. Ecol.* **3**: 259-68.
- Strathmann, R.R. (1978) The evolution and loss of feeding larval stages of marine invertebrates. *Evolution* **32**: 894-906.
- Strathmann, R.R. (1985) Feeding and non-feeding larval development and life-history evolution in marine invertebrates. *Ann. Rev. Ecol. Syst.* **16**: 339-61.
- Thompson, R.J. and Hawryluk, M. (1990) Physiological energetics of the snow crab, *Chionoecetes opilio*. *Proc. Int. Symp. King & Tanner Crabs* 283-91.
- Thorson, G. (1946) Reproduction and larval development of Danish marine bottom invertebrates. With special reference to the planktonic larvae in the Sound (Oresund). *Meddelelser fra Kommissionen for Danmarks Fiskeri- og Havundersogelser, Serie: Plankton* **4**: 1-523.
- Thorson, G. (1950) Reproductive and larval ecology of marine bottom organisms. *Biol. Rev.* **25**: 1-45.
- Todd, C.D. and Doyle, R.W. (1981) Reproductive strategies of marine benthic invertebrates: a settlement-timing hypothesis. *Mar. Ecol. Prog. Ser.* **4**: 75-83.
- Todd, C.D. and Havenhand, J.N. (1990) Mode of development and reproductive effort in marine invertebrates: is there any relationship? *Funct. Ecol.* **4**: 132-3.
- Todd, C.D., Havenhand, J.N. and Thorpe, J.P. (1988) Genetic differentiation, pelagic larval transport and gene flow between local populations of the

intertidal marine mollusc *Adalaria proxima* (Alder and Hancock). *Funct. Ecol.* 2: 441-5.

Underwood, A.J. (1974) On models for reproductive strategies in marine benthic invertebrates. *Am. Nat.* 108: 874-8.

Underwood, A.J. and Fairweather, P.G. (1989) Supply-side ecology and benthic marine assemblages. *Trends Ecol. Evol.* 4: 16-20.

Vance, R.R. (1973a) On reproductive strategies in marine benthic invertebrates. *Am. Nat.* 107: 339-52.

Vance, R.R. (1973b) More on reproductive strategies in marine benthic invertebrates. *Am. Nat.* 107: 353-61.

Vance, R.R. (1974) Reply to Underwood. *Am. Nat.* 108: 879-80.

Vernberg, F.J. (1959) Studies on the physiological variation between tropical and temperate zone fiddler crabs of the genus *Uca*. III. The influence of temperature acclimation on oxygen consumption of whole organisms. *Biol. Bull. mar. biol. Lab., Woods Hole* 117: 582-93.

Vernet-Cornubert, G. (1958) Biologie generale de *Pisa tetraodon*. *Bull. Inst. Oceanogr. Monaco* 1113: 1-52.

Vernet-Cornubert, G. (1960) Influence de l'ablation des pedoncules oculaires sur la mue, la ponte et les caracteres sexuels externes de *Pisa tetraodon* Pennant. *Bull. Inst. Oceanogr. Monaco* 1186: 1-24.

Warner, G.F. (1977) The biology of crabs. Elek Science, London.

Watson, J. (1970) Maturity, mating and egg laying in the spider crab *Chionoecetes opilio*. *J. Fish. Res. Bd. Canada* 27: 1607-16.

Wear, R.G. (1974) Incubation in British decapod Crustacea, and the effects of temperature on the rate and success of embryonic development. *J. mar. biol. Ass. U.K.* 54: 745-62.

Weekes, A.J. (1986) A GENSTAT primer. Edward Arnold, London.

Wenner, A.M. (1972) Sex ratio as a function of size in marine Crustacea. *Am. Nat.* 106: 321-50.

Wenner, A.M., Fusaro, C. and Oaten, A. (1974) Size at onset of sexual maturity and growth rate in crustacean populations. *Can. J. Zool.* 52: 1095-106.

White, R.G., Hill, A.E. and Jones, D.A. (1988) Distribution of *Nephrops norvegicus* (L.) larvae in the western Irish Sea: an example of advective control on recruitment. J. Plankton Res. 10: 735-47.

Willows, R.I. (1990) Mode of development and reproductive effort in marine invertebrates: no relationship predicted by life-history theory? Funct. Ecol. 4: 130-2.

Zar, J.H. (1984) Biostatistical analysis. 2nd. Ed., Prentice-Hall International Inc., Englewood Cliffs, N.J.

Appendices.

Appendix 1. A FORTRAN 77 program (IBM VFORTRAN) for the calculation of simple growth statistics from raw data. See section 3.2 for further description.

```

PROGRAM GROWTH1

C Program for preliminary analysis of growth experiment data.
C Version 1, to analyse female results.
C Andy Bryant, 23xi89. Modified, for actual use, 3iv90, 25v90.
C Datafile of temperatures (GroTemp DATA) is read in on channel 1,
C (2 x 500 data) and stored in Temp(1...500) and TempPE(1...500).
C Datafile of CL's and dates is read in on channel 2.
C Results are written to channel 3.
C
C Subroutine PLOT added to plot temperatures using GINO, 25v90.
C
C In datafile, the 2nd CL and 2nd date may be missing (denoted in the
C file as 0.0 or 0 as appropriate). If this is found to be the case,
C the program writes missing values to the output file as asterisks.
C
C All variables are declared and F77 type-name rules ignored.
C
C DayM1, DayM2 - experimental day of moults 1 and 2.
C D1, M1, Y1, D2, M2, Y2 - day, month and year of moults 1 and 2.
C IntP - calculated intermoult period.
C N - number of observations in datafile.
C CL1, CL2, CL3 - 1st, 2nd & 3rd carapace lengths (read in from file).
C IntT - mean temperature calculated for the intermoult period.
C TempM1, TempM2 - mean temp. for moults 1 & 2 (n=6, see notes).
C Temp - array of temperatures read in (one for each day of expt.).
C TempPE - same as Temp but the temperatures of Port Erin bay.
C M - information about moulting to maturity, for each animal.

      INTEGER DayM1, DayM2, D1, M1, Y1, D2, M2, Y2, IntP, N, M
      REAL CL1, CL2, CL3, IntT, TempM1, TempM2, Temp(500), TempPE(500)

      DO 10 I = 1, 500
        READ(1,*) Temp(I), TempPE(I)
10     CONTINUE

C     CALL PLOT(TempPE)

      READ(2,*) N
      DO 100 I = 1, N

        READ(2,20) CL1, CL2, CL3, D1, M1, Y1, D2, M2, Y2, M
20     FORMAT(3(F5.2,1X), 7I3)

        DayM1 = IDAY(D1,M1,Y1)
        X = 0.0
        DO 25 J = DayM1 - 3, DayM1 + 2
          X = X + Temp(J)
25     CONTINUE
        TempM1 = X / 6.0

```

```

        IF (CL3 .GT. 0.0) THEN
            DayM2 = IDAY(D2,M2,Y2)
            IntP = DayM2 - DayM1

            X = 0.0
            DO 30 J = DayM1, DayM2 - 1
                X = X + Temp(J)
30          CONTINUE
            IntT = X / IntP

            X = 0.0
            DO 40 J = DayM2 - 3, DayM2 + 2
                X = X + Temp(J)
40          CONTINUE
            TempM2 = X / 6.0

            WRITE(3,60) CL1, CL2, CL3, TempM1, TempM2, IntT, IntP, M
        ELSE
            WRITE(3,70) CL1, CL2, TempM1, M
        END IF
60      FORMAT(1X, 3F6.2, 3F5.1, I4, I3)
70      FORMAT(1X, 2F6.2, 3X, '* ', F5.1, 3(3X, '* '), I2)

100     CONTINUE
        END

```

C Find (integer) expt. day from an actual date, month and year.

```

        INTEGER D, M, Y, Acc(16)
        DATA Acc/ 15, 46, 77, 105, 136, 166, 197, 227, 258,
&                289, 319, 350, 380, 411, 442, 470/

        IF (Y .EQ. 88) THEN
            IF (M .EQ. 11) IDAY = D - 15
            IF (M .EQ. 12) IDAY = Acc(1) + D
        END IF
        IF (Y .EQ. 89) IDAY = Acc(M+1) + D
        IF (Y .EQ. 90) IDAY = Acc(M+13) + D
        END

```

C Plots a graph of temperatures passed to parameter Y.

```

        REAL X(500), Y(500)

        DO 10 I = 1, 500
            X(I) = REAL(I)
10       CONTINUE
        CALL GINO
        CALL SAVDRA
        CALL DEVPAP(200.0, 200.0, 0)
        CALL WINDO2(0.0, 200.0, 0.0, 200.0)
        CALL AXISCA(1, 10, 0.0, 20.0, 2)
        CALL AXISCA(1, 10, 0.0, 500.0, 1)
        CALL GRID(-2, 1, 1)
        CALL GRAPOL(X, Y, 500)
        CALL DEVEND
        CALL GINEND
        END

```

Appendix 2. A Pascal program (Turbo Pascal, Borland International Inc.) for the segmented regression analysis of Lovett and Felder (1989). See section 3.2 for further description.

```

PROGRAM TwoLines (input, output, DataFile, RFile);

    {Program to find a point of inflexion in a positively
    correlated [y,x] relationship. The data are iteratively
    partitioned into 2 groups and a model II regression line
    is fitted to each group. By examining the fit of the
    lines one can determine the best breakpoint on the x axis.
    Andy Bryant, 20xi90. Method : Lovett & Felder 1989. See notes}

CONST  Max = 300;                                {max. number of data pairs}

TYPE   ArrayType = ARRAY[1..Max] OF real;

VAR
    n,                                           {amount of array which is used}
    i,                                           {general purpose loop identifier}
    Num : integer;                               {number of data pairs in a group}

    XCurr,                                       {current breakpoint on X axis}
    XInc,                                       {increment to next breakpoint}
    XMax,                                       {max. value found in array X}
    Alpha, Beta,                                {regression coefficients}
    Temp, Temp1, Temp2,                         {temporary real variables}
    SSR, RR, CombRR : real;                     {sum sq. residuals & rand. residuals}

    DataFile, RFile : text;                     {data and result files}

    FileName1, FileName2 : string[12];         {names of data and result files (DOS)}

    X,                                           {X axis variate}
    Y : ArrayType;                              {Y axis variate}

```



```
PROCEDURE ReadData; {Reads DataFile into arrays X and Y, and calculates
                    XMax. Prompts user and reads XCurr and XInc from
                    the default input.}
```

```
BEGIN {ReadData}
  n := 0;
  XMax := -99.0;
  writeln(output);
  write(output, 'Program TwoLines. Enter the name of your datafile : ');
  readln(input, FileName1);
  assign(DataFile, FileName1);
  reset(DataFile);
  WHILE NOT eof(DataFile) DO
    BEGIN
      n := n + 1;
      readln(DataFile, X[n], Y[n]);
      IF X[n] > XMax THEN XMax := X[n]
    END;
  close(DataFile);
  writeln(output);
  write(output, 'Enter the first breakpoint (X axis) : ');
  readln(input, XCurr);
  write(output, 'Enter the increment between successive breakpoints : ');
  readln(input, XInc);
  writeln(output)
END; {ReadData}
```

```
PROCEDURE Regress(Start, Finish : integer;
                  VAR Alpha, Beta, SSR, RR : real;
                  VAR Num : integer);

  {performs regression on the data in global arrays X and Y
   using elements Start to Finish. Calculates coefficients
   and the fit. See notes.}
```

```
CONST Small = 1.0E-6;
```

```
VAR
  i,                               {general purpose loop identifier}
  Lag,                              {difference between position in X and RunsX}
  R,                                {No. of runs of sign change}
  Coin : integer;                  {number of coinciding X values in runs test}
  m, n : longint;                 {No. of residuals >0.0 and <0.0 respectively}

  SumX, SumSqX, SumY, SumSqY,      {sums and sums of squares of X and Y}
  Diff,                            {Difference between X[i] and X[i+1]}
  ER, VR,                          {expected no. of runs and its variance}
  Temp, Temp1 : real;              {temporary variables}

  RunsX, RunsY : ArrayType;       {X and Y arrays set up for runs test}
```

```

BEGIN {Regress}

SumX := 0.0; SumSqX := 0.0;
SumY := 0.0; SumSqY := 0.0;
SSR := 0.0;
Num := Finish - Start + 1;

{perform reduced major axis regression}
FOR i := Start TO Finish DO
  BEGIN
    SumX := SumX + X[i]; SumSqX := SumSqX + sqr(X[i]);
    SumY := SumY + Y[i]; SumSqY := SumSqY + sqr(Y[i])
  END;
Temp := SumSqY - sqr(SumY)/Num;
Temp1 := SumSqX - sqr(SumX)/Num;
Beta := sqrt(Temp / Temp1);
Alpha := SumY/Num - Beta*SumX/Num;

{calculate SSR}
FOR i := Start TO Finish DO
  SSR := SSR + sqr(Y[i] - Alpha - Beta*X[i]);

{deal with any equal values within X[Start...Finish]}
Lag := 0; i := Start - 1;
WHILE i < Finish DO
  BEGIN {while}
    i := i + 1;
    RunsX[i-Lag] := X[i];
    Diff := abs( X[i+1] - X[i] );
    IF (Diff > Small) OR (i = Finish) THEN RunsY[i-Lag] := Y[i]
    ELSE
      BEGIN {else}
        Temp := Y[i]; Coin := 1;
        REPEAT
          i := i + 1; Coin := Coin + 1;
          Temp := Temp + Y[i];
          Diff := abs( X[i+1] - X[i] )
        UNTIL (Diff > Small) OR (i = Finish);
        Lag := Lag + Coin - 1;
        RunsY[i-Lag] := Temp / Coin
      END {else}
    END; {while}

{omit median value of RunsX if number of obs. is odd}
IF odd(Num - Lag) THEN
  BEGIN {if}
    FOR i := (Finish-Lag) DIV 2 + 1 TO Finish-Lag-1 DO
      BEGIN {for}
        RunsX[i] := RunsX[i+1]; RunsY[i] := RunsY[i+1]
      END; {for}
    Lag := Lag + 1
  END; {if}

```

```

{runs test proper}
  m := 0; n := 0; R := 1;
  Temp := RunsY[Start] - (Alpha + Beta*RunsX[Start]);
  IF Temp > 0.0 THEN m := m + 1 ELSE IF Temp < 0.0 THEN n := n + 1;
  FOR i := Start+1 TO Finish-Lag DO
    BEGIN {for}
      Temp1 := RunsY[i] - (Alpha + Beta*RunsX[i]);
      IF Temp1 > 0.0 THEN m := m + 1 ELSE IF Temp1 < 0.0 THEN n := n + 1;
      IF ((Temp1 > 0.0) AND (Temp < 0.0)) OR ((Temp1 < 0.0) AND (Temp > 0.0))
      THEN R := R + 1;
      Temp := Temp1
    END; {for}
  Temp := 2.0 * m * n;
  ER := 1.0 + Temp/(m+n);
  VR := Temp * (Temp-m-n) / (sqr(m+n) * (m+n-1.0));
  RR := (R + 0.5 - ER) / sqrt(VR);

  {* FOR i := Start TO Finish DO
    writeln(i:5, ' X,Y',X[i]:8:4,Y[i]:8:4, ' RunsX,Y',RunsX[i]:8:4,RunsY[i]:
    writeln;
    writeln('Alpha', Alpha:8:4, ' Beta', Beta:8:4);
    writeln('SSR', SSR:8:4);
    writeln('Num', Num:4, ' Lag', Lag:4);
    writeln('m', m:4, ' n', n:4, ' R', R:4);
    writeln('ER', ER:8:4, ' VR', VR:8:4, ' RR', RR:8:4);
    writeln *}

END; {procedure Regress}

FUNCTION Runs( Alpha1, Beta1, Alpha2, Beta2 : real;
              Break, Finish : integer) : real;

  {The randomness of residuals is returned by this function,
  calculated from the whole data set which has been regressed in
  two groups : regression coefficients Alpha1 and Beta1 refer
  to elements 1 to Break-1, Alpha2 and Beta2 refer to elements
  Break to Finish. The median observation is not omitted.}

CONST Small = 1.0E-6;

VAR
  i,                               {general purpose loop identifier}
  Lag,                              {difference between position in X and RunsX}
  R,                                {No. of runs of sign change}
  Coin                               {number of coinciding X values in runs test}
  m, n                             : longint; {No. of residuals >0.0 and <0.0 respectively}

  Diff,                             {absolute difference between X[i] and X[i+1]}
  ER, VR,                           {expected no. of runs and its variance}
  Temp, Temp1                       : real;   {temporary variables}

  RunsX, RunsY                     : ArrayType; {X and Y arrays set up for runs test}

```

```

BEGIN {Runs}

{deal with any equal values within X[1...Finish]}
Lag := 0; i := 0;
WHILE i < Finish DO
  BEGIN {while}
    i := i + 1;
    RunsX[i-Lag] := X[i];
    Diff := abs( X[i+1] - X[i] );
    IF (Diff > Small) OR (i = Finish) THEN RunsY[i-Lag] := Y[i]
    ELSE
      BEGIN {else}
        Temp := Y[i]; Coin := 1;
        REPEAT
          i := i + 1; Coin := Coin + 1;
          Temp := Temp + Y[i];
          Diff := abs( X[i+1] - X[i] );
          IF i < Break THEN Break := Break - 1
          UNTIL (Diff > Small) OR (i = Finish);
          Lag := Lag + Coin - 1;
          RunsY[i-Lag] := Temp / Coin
        END {else}
      END; {while}

{runs test proper}
m := 0; n := 0; R := 1;
Temp := RunsY[1] - (Alpha1 + Beta1*RunsX[1]);
IF Temp > 0.0 THEN m := m + 1 ELSE IF Temp < 0.0 THEN n := n + 1;
FOR i := 2 TO Finish-Lag DO
  BEGIN {for}
    IF i < Break THEN Temp1 := RunsY[i] - (Alpha1 + Beta1*RunsX[i])
    ELSE Temp1 := RunsY[i] - (Alpha2 + Beta2*RunsX[i]);
    IF Temp1 > 0.0 THEN m := m + 1 ELSE IF Temp1 < 0.0 THEN n := n + 1;
    IF ((Temp1 > 0.0) AND (Temp < 0.0)) OR ((Temp1 < 0.0) AND (Temp > 0.0))
    THEN R := R + 1;
  (*   writeln('i=',i:2,RunsY[i]:8:1,(RunsY[i]-Temp1):8:2,' m=',m:2,' n=',n:2,
    Temp := Temp1
  END; {for}
  Temp := 2.0 * m * n;
  ER := 1.0 + Temp/(m+n);
  VR := Temp * (Temp-m-n) / (sqr(m+n) * (m+n-1.0));

  Temp := (R + 0.5 - ER) / sqrt(VR);
  Runs := (R + 0.5 - ER) / sqrt(VR);

  (* FOR i := 1 TO Finish DO
    writeln(i:5,' X,Y',X[i]:8:4,Y[i]:8:4,' RunsX,Y',RunsX[i]:8:4,RunsY[i]:8
    writeln;
    writeln('Break', Break:4, ' Finish', Finish:4, ' Lag', Lag:4);
    writeln('m', m:4, ' n', n:4, ' R', R:4);
    writeln('ER', ER:8:4, ' VR', VR:8:4, ' Runs', Temp:8:4);
    writeln *)
END; {function Runs}

```

```

BEGIN {main program}

  ReadData;
  write(output, 'Enter a name for the results file : ');
  readln(input, FileName2);
  writeln(output);
  write(output, 'Calculation in progress...');
  assign(RFile, FileName2);
  rewrite(RFile);
  writeln(output);  writeln(output);
  writeln(RFile, 'Data from file : ', FileName1);
  writeln(RFile);
  writeln(RFile, 'Breakpoint Group n      Alpha      Beta          SSR
                  '      CombSSR CombRR');

  i := 1;
  REPEAT
    WHILE (X[i] < XCurr) AND (i < n-5) DO i := i + 1;
    IF i < n-5 THEN
      BEGIN
        Regress(1, i-1, Alpha, Beta, SSR, RR, Num);
        writeln(RFile, XCurr:8:3, '      1', Num:6, Alpha:10:3, Beta:9:3,
                  SSR:13:2, RR:9:2);
        Temp := SSR;  Temp1 := Alpha;  Temp2 := Beta;
        Regress(i, n, Alpha, Beta, SSR, RR, Num);
        Temp := Temp + SSR;
        CombRR := Runs(Temp1, Temp2, Alpha, Beta, i, n);
        writeln(RFile, '      2', Num:6, Alpha:10:3, Beta:9:3,
                  SSR:13:2, RR:9:2, Temp:12:2, CombRR:8:2);
        writeln(RFile)
      END;
      XCurr := XCurr + XInc;
    UNTIL (XCurr > X[n]) OR (i >= n-5);

  (* Temp := Runs( 0.56 , 0.4366, 0.56 , 0.4366, 4, n); *)

  Regress(1, n, Alpha, Beta, SSR, RR, Num);
  writeln(RFile, 'Whole data set', Num:5, Alpha:10:3, Beta:9:3,
            SSR:13:2, RR:9:2);

  writeln(output, 'Calculation complete. Results are in file ', FileName2);
  writeln(output, 'End of program. ');
  writeln(output);
  close(RFile)

END. {main program}

```

Appendix 3. FORTRAN 77 programs (IBM VFORTRAN) for implementation of the *Carcinus maenas* model and visualisation of its results. See section 5.2.1 and Fig. 5.2.

```
PROGRAM CARCINUS

C   Carcinus reproductive strategies simulation program.
C   Version 1.7 Andy Bryant 9v90 (started 22/11/88).
C   Same as version 1.5 except subroutine SOURCESM added (and calls
C   to that subroutine) and PLOT1 and PLOT2 removed.
C
C   Subroutine MAINCALC corrected (re. K > 1), 25/6/89.
C
C   Protected the survival calculation against underflow, 14xi89.
C
C   Implicit FORTRAN typing rules ignored (nomenclature used is
C   mainly that of the original model, Dr.P.Gould 5/8/86).
C   All variables are declared except loop identifiers, I, J and M,
C   and also temporary real variables, TEMP, TEMP1, TEMP2 etc.
C
C   Variables / Constants :
C
C   NMAX - maximum number of instars allowed. NMAXA = NMAX + 1.
C   A, B, C, MU, OMEGA, NU, K, KA, L - usage as in original model.
C   TAU0(I) - duration of instar I assuming no egg production.
C   X0(I) - survival to instar I assuming no egg production.
C   H(P,N) - total hatched egg production for a given [P,N] schedule.
C           This is real rather than integer for the purposes of
C           plotting using GINO. Strictly, it should be an integer.
C   LIFE(P,N) - lifetime in days for a given [P,N] life schedule.
C   HOPT, POPT, NOPT, LIFEOPT - optimal values of H, P, N and LIFE
C           respectively.
C   OAS - size of the arrays of optima. The size (both dimensions) of
C           the arrays PA, NA, HA and LIFEA (see below).
C   PA, NA, HA, LIFEA and MMORT - two-dimensional arrays of values of
C           POPT, NOPT, HOPT, LIFEOPT AND MOULTM respectively. Their
C           elements represent ranges of the two lifetime survival
C           parameters, OMEGA and NU. OMEGA is the first dimension;
C           NU is the second dimension. Array MMORT is moult mortality
C           as a % of total lifetime mortality as calculated by subroutine
C           SOURCESM. See subroutine VS.
C   ANEC - anecysis constant A(C/NU) as described by Dr.P.Gould 25/7/88.
C   MINANEC, MAXANEC - minimum and maximum values which ANEC takes
C           (calculated by MAINCALC from KA, NU(N+1) and C).
C
C   CHECK - error checking status of the program.
C           CHECK = 0, no error checking information is output.
C           CHECK = 1, some error checking information is output.
C
C
C   COMMON block IDATA is used to group input data. COMMON blocks
C   O1DATA and O2DATA are used to contain logically discrete groups
C   of output data. O1DATA contains the initially produced output;
C   see subroutines INITCALC and MAINCALC. O2DATA contains the two-
C   dimensional arrays of optima calculated by subroutine VS.
C   Subroutines needing any of these may declare the
C   variables then access the appropriate block.
C
C
```

```

INTEGER K, KA, NU, NMAX, NMAXA, CHECK, OAS, POPT, PA, NOPT, NA
PARAMETER (NMAX = 50, NMAXA = NMAX + 1, OAS = 20, CHECK = 0)
REAL LAMBDA, A, B, C, L, MU, OMEGA, TAU0, X0, LIFE, LIFEOPT,
& LIFEA, H, HOPT, HA, ANEC, MINANEC, MAXANEC, MMORT
DIMENSION L(NMAXA), MU(NMAXA), K(NMAXA), OMEGA(NMAXA), NU(NMAXA),
& TAU0(NMAXA), X0(NMAXA), H(2:NMAXA,NMAX), LIFE(2:NMAXA,NMAX),
& PA(OAS,OAS), NA(OAS,OAS), HA(OAS,OAS), LIFEA(OAS,OAS),
& MMORT(OAS,OAS)
COMMON /IDATA/ LAMBDA, A, B, C, MU, OMEGA, K, KA, NU
COMMON /O1DATA/ L, TAU0, X0, H, LIFE, HOPT, POPT, NOPT, LIFEOPT,
& ANEC, MINANEC, MAXANEC
COMMON /O2DATA/ PA, NA, HA, LIFEA, MMORT

CALL READIN
CALL INITCALC
CALL MAINCALC
C CALL SOURCESM(TEMP)
CALL TABH
CALL PLOTH(0)
C CALL VS(100, 2000, 100, 0.475, 0.950, 0.025)
END

SUBROUTINE READIN

C Reads the data file into the variables in common block IDATA.
C Subroutine PRINTOUT called if CHECK = 1.
C Precondition : data file must be connected to channel 1 and
C of the format shown in lines 10 and 30.

INTEGER K, KA, NU, NMAX, NMAXA, CHECK, POPT, NOPT
PARAMETER (NMAX = 50, NMAXA = NMAX + 1, CHECK = 0)
REAL LAMBDA, A, B, C, L, MU, OMEGA, TAU0, X0, LIFE, H, HOPT,
& LIFEOPT, ANEC, MINANEC, MAXANEC
DIMENSION L(NMAXA), MU(NMAXA), K(NMAXA), OMEGA(NMAXA), NU(NMAXA),
& TAU0(NMAXA), X0(NMAXA), H(2:NMAXA,NMAX), LIFE(2:NMAXA,NMAX)
COMMON /IDATA/ LAMBDA, A, B, C, MU, OMEGA, K, KA, NU
COMMON /O1DATA/ L, TAU0, X0, H, LIFE, HOPT, POPT, NOPT, LIFEOPT,
& ANEC, MINANEC, MAXANEC

10 READ(1,10) L(1), LAMBDA, A, B, C, KA
   FORMAT(F4.2, /, F5.1, /, F5.3, /, F6.3, /, F4.1, /, I1)
   DO 20 I = 1, NMAXA
     READ(1,30) J, MU(I), K(I), OMEGA(I), NU(I)
20 CONTINUE
30 FORMAT(I2, F5.2, I2, F5.2, I5)
   IF (CHECK .EQ. 1) CALL PRINTOUT
END

```

SUBROUTINE PRINTOUT

C Input parameters of model written to screen.
 C Called from subroutine READIN if CHECK = 1.

```

INTEGER K, KA, NU, NMAX, NMAXA, CHECK, POPT, NOPT
PARAMETER (NMAX = 50, NMAXA = NMAX + 1, CHECK = 0)
REAL LAMBDA, A, B, C, L, MU, OMEGA, TAU0, X0, LIFE, H, HOPT,
& LIFEOPT, ANEC, MINANEC, MAXANEC
DIMENSION L(NMAXA), MU(NMAXA), K(NMAXA), OMEGA(NMAXA), NU(NMAXA),
& TAU0(NMAXA), X0(NMAXA), H(2:NMAXA,NMAX), LIFE(2:NMAXA,NMAX)
COMMON /IDATA/ LAMBDA, A, B, C, MU, OMEGA, K, KA, NU
COMMON /OLDATA/ L, TAU0, X0, H, LIFE, HOPT, POPT, NOPT, LIFEOPT,
& ANEC, MINANEC, MAXANEC
  
```

```

PRINT*, 'NMAXA  L(1)  LAMBDA  A      B      C      KA'
WRITE(*,10) NMAXA, L(1), LAMBDA, A, B, C, KA
10  FORMAT(1X, I5, F7.2, F8.1, 3F7.3, I3, /)
PRINT*, ' I  MU(I)   K(I) OMEGA(I) NU(I)'
DO 20 I = 1, NMAXA
  WRITE(*,30) I, MU(I), K(I), OMEGA(I), NU(I)
20  CONTINUE
30  FORMAT(1X, I2, F7.2, I6, F9.2, I6)
PRINT*
END
  
```

SUBROUTINE INITCALC

C Performs initial calculations of L, TAU0 and X0 (assuming no
 C egg production). The appropriate elements of H and LIFE (ie.
 C those which will not be set by subroutine MAINCALC) are
 C initialised to zero.
 C Precondition : IDATA have been read in (by subroutine READIN).

```

INTEGER K, KA, NU, NMAX, NMAXA, CHECK, POPT, NOPT
PARAMETER (NMAX = 50, NMAXA = NMAX + 1, CHECK = 0)
REAL LAMBDA, A, B, C, L, MU, OMEGA, TAU0, X0, LIFE, H, HOPT,
& LIFEOPT, ANEC, MINANEC, MAXANEC
DIMENSION L(NMAXA), MU(NMAXA), K(NMAXA), OMEGA(NMAXA), NU(NMAXA),
& TAU0(NMAXA), X0(NMAXA), H(2:NMAXA,NMAX), LIFE(2:NMAXA,NMAX)
COMMON /IDATA/ LAMBDA, A, B, C, MU, OMEGA, K, KA, NU
COMMON /OLDATA/ L, TAU0, X0, H, LIFE, HOPT, POPT, NOPT, LIFEOPT,
& ANEC, MINANEC, MAXANEC
  
```



```

    TAU0(1) = A * L(1) + B
    X0(1) = 1.0
    IF (CHECK .EQ. 1) WRITE(*,5)
5   FORMAT(2X, 'I', 11X, 'L(I)', 20X, 'TAU0(I)', 15X, 'X0(I)')
    DO 10 I = 2, NMAXA
        L(I) = L(I-1) * (1.0 + MU(I-1) * EXP(-L(I-1) / LAMBDA) )
        TAU0(I) = A * L(I) + B
        TEMP = -TAU0(I-1)/NU(I-1)
        IF (TEMP .GT. -170.0) THEN
            X0(I) = X0(I-1) * OMEGA(I-1) * EXP(TEMP)
        ELSE
            X0(I) = 0.0
        END IF
        IF (CHECK .EQ. 1) WRITE(*,20) I, L(I), TAU0(I), X0(I)
10  CONTINUE
20  FORMAT(1X, I2, 2F24.17, F24.20)
    IF (CHECK .EQ. 1) PRINT*

    DO 50 I = 3, NMAXA
        DO 50 J = 1, I-2
            H(I,J) = 0.0
            LIFE(I,J) = 0.0
50  CONTINUE
    END

```

SUBROUTINE MAINCALC

```

C   Performs the main body of calculations of the model,
C   ie. calculating the elements of LIFE and H, and the optima HOPT,
C   POPT, NOPT and LIFEOPT.
C   Precondition : subroutine INITCALC has been called.
C
C   'Local' variables ie. other than those in the COMMON blocks:
C
C   AH - accumulated egg production (incremented for each mature instar).
C       Real, not integer, for the same reasons that H is real (see
C       description of variables at start of main program body).
C   E - egg production during any given mature instar, I (P <= I < N+1).
C       Real again, not integer.
C   P - first instar in which eggs are laid (first mature instar).
C   N - instar immediately preceding terminal anecdysis.
C   TAUCURR - duration of the current instar, I (P <= I <= N), in days.
C   TAUPREV - duration of the previous instar, I-1 (assigned the value
C             of TAUCURR at the end of the DO 30 loop).
C   TAUA - duration of terminal anecdysis, in days.
C   ALIFE - accumulated lifetime (incremented for each instar).
C   XCURR - current value of survival (survival to any mature instar I).
C   XPREV - previous value of survival (from which XCURR is calculated),
C           assigned the value of XCURR at the end of the DO 30 loop.

```

```

    INTEGER K, KA, NU, NMAX, NMAXA, CHECK, POPT, NOPT,
&         N, P
    PARAMETER (NMAX = 50, NMAXA = NMAX + 1, CHECK = 0)
    REAL LAMBDA, A, B, C, L, MU, OMEGA, TAU0, X0, LIFE, H, LIFEOPT,
&       AH, E, HOPT, TAUCURR, TAUPREV, TAUA, ALIFE, ANEC,
&       XCURR, XPREV, MINANEC, MAXANEC
    DIMENSION L(NMAXA), MU(NMAXA), K(NMAXA), OMEGA(NMAXA), NU(NMAXA),
&           TAU0(NMAXA), X0(NMAXA), H(2:NMAXA,NMAX), LIFE(2:NMAXA,NMAX)
    COMMON /IDATA/ LAMBDA, A, B, C, MU, OMEGA, K, KA, NU
    COMMON /O1DATA/ L, TAU0, X0, H, LIFE, HOPT, POPT, NOPT, LIFEOPT,
&           ANEC, MINANEC, MAXANEC

```

```

TAUA = (KA + 0.5) * C
HOPT = 0.0

DO 50 N = 1, NMAX

TEMP = 1.0 + (KA-3.0) * (4.0*KA-11.0) / (3.0 * (2.0*KA-5.0))
TEMP1 = TEMP - ( (KA-3.0) * (KA-2.0) / 6.0 * (C/NU(N+1)) )
TEMP2 = EXP(-3.0*C/NU(N+1)) * TEMP1
ANEC = EXP(-C/NU(N+1)) + EXP(-2.0*C/NU(N+1)) + TEMP2

DO 50 P = 2, N+1

ALIFE = 0.0
AH = 0.0

DO 10 I = 1, P-1
ALIFE = ALIFE + TAU0(I)
CONTINUE

IF (P .LE. N) THEN
DO 30 I = P, N
TAUCURR = A*L(I) + B + C*K(I)
ALIFE = ALIFE + TAUCURR
IF (I .EQ. P) THEN
XPREV = X0(I-1)
TAUPREV = TAU0(I-1)
END IF
TEMP = -TAUPREV/NU(I-1)
IF (TEMP .GT. -170.0) THEN
XCURR = XPREV * OMEGA(I-1) * EXP(TEMP)
ELSE
XCURR = 0.0
END IF
TEMP1 = 0.0
DO 20 J = 1, K(I)
TEMP1 = TEMP1 + EXP(-J*C/NU(I))
CONTINUE
E = L(I)**3 * XCURR * TEMP1
AH = AH + E
XPREV = XCURR
TAUPREV = TAUCURR
CONTINUE
ELSE
XPREV = X0(N)
TAUPREV = TAU0(N)
END IF

TEMP = -TAUPREV/NU(N)
IF (TEMP .GT. -170.0) THEN
XCURR = XPREV * OMEGA(N) * EXP(TEMP)
ELSE
XCURR = 0.0
END IF
ALIFE = ALIFE + TAUA
E = L(N+1)**3 * XCURR * ANEC
AH = AH + E

```

```

        LIFE(P,N) = ALIFE
        H(P,N) = AH
        IF (AH .GT. HOPT) THEN
            HOPT = AH
            LIFEOPT = ALIFE
            POPT = P
            NOPT = N
        END IF
50    CONTINUE
    END

```

SUBROUTINE SOURCESM(MOULTM)

```

C    Calculates the sources of mortality, from the moult (MOULTM) and
C    from the intermoult (INTM), which together make up total lifetime
C    mortality. This is done for the optimal strategy only.
C    See 'Sources of mortality, ADB l11190'.
C    Precondition : subroutines INITCALC and MAINCALC have been called.
C
C    'Local' variables ie. other than those in the COMMON blocks:
C
C    TAUCURR - duration of the current instar, I, in days.
C    TAUPREV - duration of the previous instar, I-1.
C    XCURR - current value of survival (survival to any mature instar I).
C    XPREV - previous value of survival (from which XCURR is calculated).
C    TEMPCURR - current value of temporary variable, the quantity that
C               is checked for range before exponentiation.
C    TEMPPREV - previous value of temporary variable.

```

```

        INTEGER K, KA, NU, NMAX, NMAXA, CHECK, POPT, NOPT
        PARAMETER (NMAX = 50, NMAXA = NMAX + 1, CHECK = 0)
        REAL LAMBDA, A, B, C, L, MU, OMEGA, TAU0, X0, LIFE, H, LIFEOPT,
&          HOPT, TAUCURR, TAUPREV, ANEC, MOULTM, INTM,
&          XCURR, XPREV, MINANEC, MAXANEC, TEMPCURR, TEMPPREV
        DIMENSION L(NMAXA), MU(NMAXA), K(NMAXA), OMEGA(NMAXA), NU(NMAXA),
&          TAU0(NMAXA), X0(NMAXA), H(2:NMAXA,NMAX), LIFE(2:NMAXA,NMAX)
        COMMON /IDATA/ LAMBDA, A, B, C, MU, OMEGA, K, KA, NU
        COMMON /OLDATA/ L, TAU0, X0, H, LIFE, HOPT, POPT, NOPT, LIFEOPT,
&          ANEC, MINANEC, MAXANEC

```

```

MOULTM = 0.0
INTM = 0.0

DO 10 I = 1, POPT-1
  TEMP = -TAU0(I) / NU(I)
  IF (TEMP .GT. -170.0) THEN
    INTM = INTM + (1.0 - EXP(TEMP)) * X0(I)
    MOULTM = MOULTM + (1.0 - OMEGA(I)) * X0(I) * EXP(TEMP)
  ELSE
    INTM = INTM + X0(I)
  END IF
10 CONTINUE

IF (POPT .LE. NOPT) THEN
  DO 20 I = POPT, NOPT
    TAUCURR = A*L(I) + B + C*K(I)
    IF (I .EQ. POPT) THEN
      XPREV = X0(I-1)
      TAUPREV = TAU0(I-1)
      TEMPPREV = TEMP
    END IF
    IF (TEMPPREV .GT. -170.0) THEN
      XCURR = XPREV * OMEGA(I-1) * EXP(TEMPPREV)
    ELSE
      XCURR = 0.0
    END IF

    TEMPCURR = -TAUCURR / NU(I)
    IF (TEMPCURR .GT. -170.0) THEN
      INTM = INTM + (1.0 - EXP(TEMPCURR)) * XCURR
      MOULTM = MOULTM + (1.0 - OMEGA(I)) * XCURR * EXP(TEMPCURR)
    ELSE
      INTM = INTM + XCURR
    END IF

    TEMPPREV = TEMPCURR
    XPREV = XCURR
    TAUPREV = TAUCURR
20 CONTINUE
  ELSE
    XPREV = X0(NOPT)
    TAUPREV = TAU0(NOPT)
    TEMPPREV = TEMP
  END IF

  IF (TEMPPREV .GT. -170.0) THEN
    XCURR = XPREV * OMEGA(NOPT) * EXP(TEMPPREV)
    INTM = INTM + XCURR * ANEC
  END IF

  MOULTM = MOULTM / (MOULTM + INTM)
END

```

SUBROUTINE TABH

C Tabulates H for the full range of values of P and N. The table
 C is printed with P as columns and N as rows (the reverse of the
 C conventional representation of [P,N] matrices) to allow easy
 C comparison of results with those of P.Gould's program.
 C Subroutines PARAM and CONV are called.
 C Preconditions : subroutine MAINCALC has been called
 C and NMAX = 20, 30, 40 or 50.
 C 'Local' array variable : PVALUE(1:10) which holds 10 values of P
 C (for column headings) for the table currently being written.

```

  INTEGER K, KA, NU, NMAX, NMAXA, CHECK, POPT, NOPT,
&      N, P, PVALUE(10), IY, IM, ID
  PARAMETER (NMAX = 50, NMAXA = NMAX + 1, CHECK = 0)
  REAL LAMBDA, A, B, C, L, MU, OMEGA, TAU0, X0, LIFE, H, HOPT,
&      LIFEOPT, ANEC, MINANEC, MAXANEC
  DIMENSION L(NMAXA), MU(NMAXA), K(NMAXA), OMEGA(NMAXA), NU(NMAXA),
&      TAU0(NMAXA), X0(NMAXA), H(2:NMAXA,NMAX), LIFE(2:NMAXA,NMAX)
  COMMON /IDATA/ LAMBDA, A, B, C, MU, OMEGA, K, KA, NU
  COMMON /O1DATA/ L, TAU0, X0, H, LIFE, HOPT, POPT, NOPT, LIFEOPT,
&      ANEC, MINANEC, MAXANEC
  
```

```

  CALL PARAM(1, 1.0, 1.0, 1, 1)
  
```

```

  WRITE(*,15)
15  FORMAT(//, 10X, 'Optimal strategy for these parameters :', //)
  WRITE(*,20) NINT(HOPT)
20  FORMAT(10X, 'H      = ', I8, '/', 11X, 'opt', /)
  WRITE(*,25) POPT
25  FORMAT(10X, 'p      = ', I2, '/', 11X, 'opt', /)
  WRITE(*,30) NOPT
30  FORMAT(10X, 'n      = ', I2, '/', 11X, 'opt', /)
  CALL CONV(LIFEOPT, IY, IM, ID)
  WRITE(*,35) NINT(LIFEOPT), IY, IM, ID
35  FORMAT(10X, 'Life    = ', I5, ' days', /, 14X, 'opt', /,
&      19X, '= ', I2, ' years, ', I2, ' months, ', I2, ' days.')
```

```

  DO 80 I = 2, NMAX-8, 10
    DO 40 J = 1, 10
      PVALUE(J) = I + J - 1
40    CONTINUE
      WRITE(*,50) 1
50    FORMAT(/, I1, /)
      WRITE(*,60) ( PVALUE(J), J = 1, 10 )
60    FORMAT(1X, ' N', 10(6X, 'P=', I2), 4X, 'N')
      DO 80 N = 1, NMAX
        WRITE(*,70) N, ( NINT( H(P,N) ), P=I, I+9 ), N
70      FORMAT(1X, I2, 10I10, I5)
80    CONTINUE
  END
  
```

```

  SUBROUTINE PARAM(I, MINOMEGA, MAXOMEGA, NUMIN, NUMAX)
  
```

C Writes the input parameters of the model to the default output.
 C Version 2 (2/3/89), with just the first element of arrays MU, K,
 C OMEGA and NU displayed (assuming therefore that all elements are
 C the same as the first). GLIB subroutines are used.
 C If I=1 then the call has come from TABH - print the appropriate
 C title and do not use the other 4 arguments.
 C If I=2 then the call has come from PRVS - print the appropriate
 C title and print out the other 4 arguments.

```

INTEGER K, KA, NU, NMAX, POPT, NOPT, NUMIN, NUMAX
PARAMETER (NMAX = 50, NMAXA = NMAX + 1)
REAL LAMBDA, A, B, C, L, MU, OMEGA, TAU0, X0, LIFE, LIFEOPT,
& H, HOPT, MINOMEGA, MAXOMEGA, ANEC, MINANEC, MAXANEC
CHARACTER*8 TODAY, CURRTIME
DIMENSION L(NMAXA), MU(NMAXA), K(NMAXA), OMEGA(NMAXA), NU(NMAXA),
& TAU0(NMAXA), X0(NMAXA), H(2:NMAXA,NMAX), LIFE(2:NMAXA,NMAX)
COMMON /IDATA/ LAMBDA, A, B, C, MU, OMEGA, K, KA, NU
COMMON /OLDATA/ L, TAU0, X0, H, LIFE, HOPT, POPT, NOPT, LIFEOPT,
& ANEC, MINANEC, MAXANEC

CALL DATE(TODAY)
CALL TIME(CURRTIME)
WRITE(*,10) TODAY, CURRTIME
10 FORMAT(10(/), 10X, 'Crab Reproductive Strategies (program 1).', //,
& 10X, 'Date : ', A8, 5X, 'Time : ', A8, '.', //)
IF (I .EQ. 1) THEN
  WRITE(*,20) NMAX
ELSE
  WRITE(*,30)
END IF
20 FORMAT(10X, 'Tabulation of H (lifetime hatched egg production)', //,
& 10X, 'for all possible values of p and n (n <= ', I2, ').', ///)
30 FORMAT(10X, 'Tabulation of the optima for a range of values', //,
& 10X, 'of the survival parameters, Omega and Nu.', ///)

WRITE(*,40) L(1)
40 FORMAT(1X, 'Parameters of the model :', //, 1X, 'Initial size = ',
& F4.1, 'mm')
WRITE(*,50) LAMBDA, MU(1)
50 FORMAT(1X, 'Moult increment parameters : Lambda = ', F4.1,
& ' Mu = ', F4.2)
WRITE(*,60) A, B, C
60 FORMAT(1X, 'Instar duration parameters : A = ', F4.2,
& ' B = ', F4.1, ' C = ', F4.1, /)
WRITE(*,70) K(1), KA
70 FORMAT(1X, 'Egg batches per instar : Before anecdysis = ',
& I1, ' After anecdysis = ', I1, /)
WRITE(*,80) X0(1)
80 FORMAT(1X, 'Initial population density = ', F3.1)
IF (I .EQ. 1) THEN
  WRITE(*,90) OMEGA(1), NU(1)
ELSE
  WRITE(*,100) MINOMEGA, MAXOMEGA, NUMIN, NUMAX
END IF
90 FORMAT(1X, 'Survival probability parameters : Omega = ', F5.3,
& ' Nu = ', I4)
100 FORMAT(1X, 'Survival probability parameters : Omega = ', F5.3,
& ' - ', F5.3, /, 36X, 'Nu = ', I4, ' - ', I4)
IF (I .EQ. 1) THEN
  WRITE(*,110) ANEC
ELSE
  WRITE(*,120) MINANEC, MAXANEC
END IF
WRITE(*,130)
110 FORMAT(1X, 'Anecdysis constant = ', F4.2)
120 FORMAT(1X, 'Anecdysis constant : Min. = ', F4.2, ' Max. = ', F4.2)
130 FORMAT(1X, '(calculated from KA, Nu during anecdysis and C)')
END

```

SUBROUTINE PLOTH(I)

C Plots H as the dependant variable against 2 predictor variables,
C P (2,3,...,NMAXA) and N (1,2,...,NMAX). If I=1 then a contour
C plot is produced. If I<>1 then an isometric projection surface
C plot is produced. GINO routines are used to generate SAVDRA code.

```
INTEGER K, KA, NU, NMAX, NMAXA, CHECK, POPT, NOPT
PARAMETER (NMAX = 50, NMAXA = NMAX + 1, CHECK = 0)
REAL LAMBDA, A, B, C, L, MU, OMEGA, TAU0, X0, LIFE, H, HOPT,
& ANEC, MINANEC, MAXANEC, LIFEOPT, W(6000)
DIMENSION L(NMAXA), MU(NMAXA), K(NMAXA), OMEGA(NMAXA), NU(NMAXA),
& TAU0(NMAXA), X0(NMAXA), H(2:NMAXA,NMAX), LIFE(2:NMAXA,NMAX)
COMMON /IDATA/ LAMBDA, A, B, C, MU, OMEGA, K, KA, NU
COMMON /O1DATA/ L, TAU0, X0, H, LIFE, HOPT, POPT, NOPT, LIFEOPT,
& ANEC, MINANEC, MAXANEC
```

```
CALL GINO
CALL SAVDRA
CALL DEVPAP(200.0, 200.0, 0)
CALL WINDO2(0.0, 200.0, 0.0, 200.0)
IF (I .EQ. 1) THEN
  CALL SETFRA(0)
  CALL DRACON(NMAX, 2.0, REAL(NMAXA), NMAX, 1.0, REAL(NMAX),
& H, 10, 1, 6000, W)
ELSE
  CALL ISOPRJ(NMAX, 2.0, REAL(NMAXA), NMAX, 1.0, REAL(NMAX),
& H, 1, 6000, W)
END IF
CALL DEVEND
CALL GINEND
END
```

SUBROUTINE VS(NUMIN, NUMAX, NUINC, MINOMEGA, MAXOMEGA, INCOMEGA)

C Varies the survival parameters NU and OMEGA (all elements) in the
C ranges NUMIN : NUMAX and MINOMEGA : MAXOMEGA respectively, with
C increments NUINC and INCOMEGA respectively. For each [NU,OMEGA]
C combination, subroutines INITCALC and MAINCALC are called to
C perform lifetime calculations. The arrays PA, NA, HA, LIFEA and
C MMORT are used to hold the parameters of the optimal strategies
C calculated for the range of values of NU and OMEGA.
C 'Local' variables : IMAX and JMAX, the maximum value that the loop
C identifiers I and J respectively will reach. These
C two are calculated at the start of this subroutine
C from the arguments of the subroutine. I is used to
C vary OMEGA. J is used to vary NU.
C Preconditions : subroutine READIN must have been called and, to
C prevent the upper bound of the arrays being
C exceeded, IMAX <= OAS and JMAX <= OAS.

```

INTEGER K, KA, NU, NMAX, NMAXA, CHECK, OAS, POPT, PA, NOPT, NA,
&     NUMIN, NUMAX, NUINC, IMAX, JMAX
PARAMETER (NMAX = 50, NMAXA = NMAX + 1, OAS = 20, CHECK = 0)
REAL LAMBDA, A, B, C, L, MU, OMEGA, TAU0, X0, LIFE, LIFEOPT,
&     LIFEA, H, HOPT, HA, MINOMEGA, MAXOMEGA, INCOMEGA,
&     ANEC, MINANEC, MAXANEC, MMORT
DIMENSION L(NMAXA), MU(NMAXA), K(NMAXA), OMEGA(NMAXA), NU(NMAXA),
&     TAU0(NMAXA), X0(NMAXA), H(2:NMAXA,NMAX), LIFE(2:NMAXA,NMAX),
&     PA(OAS,OAS), NA(OAS,OAS), HA(OAS,OAS), LIFEA(OAS,OAS),
&     MMORT(OAS,OAS)
COMMON /IDATA/ LAMBDA, A, B, C, MU, OMEGA, K, KA, NU
COMMON /O1DATA/ L, TAU0, X0, H, LIFE, HOPT, POPT, NOPT, LIFEOPT,
&     ANEC, MINANEC, MAXANEC
COMMON /O2DATA/ PA, NA, HA, LIFEA, MMORT

IMAX = NINT( (MAXOMEGA - MINOMEGA + INCOMEGA) / INCOMEGA )
JMAX = (NUMAX - NUMIN + NUINC) / NUINC
IF (CHECK .EQ. 1) PRINT*, 'IMAX=', IMAX, 'JMAX=', JMAX

MINANEC = 99.9
MAXANEC = 0.0

DO 50 I = 1, IMAX
  DO 50 J = 1, JMAX
    DO 10 M = 1, NMAXA
      OMEGA(M) = MINOMEGA + (I-1)*INCOMEGA
      NU(M) = NUMIN + (J-1)*NUINC
10    CONTINUE

    IF (CHECK .EQ. 1) PRINT*, 'I=', I, 'J=', J
    IF (CHECK .EQ. 1) PRINT*, 'OMEGA=', OMEGA(1), 'NU=', NU(1)

    CALL INITCALC
    CALL MAINCALC
    CALL SOURCESM(TEMP)

    PA(I,J) = POPT
    NA(I,J) = NOPT
    HA(I,J) = HOPT
    LIFEA(I,J) = LIFEOPT
    MMORT(I,J) = TEMP
    IF (ANEC .LE. MINANEC) MINANEC = ANEC
    IF (ANEC .GE. MAXANEC) MAXANEC = ANEC
50  CONTINUE
C  CALL PRVS(MINOMEGA, INCOMEGA, IMAX, NUMIN, NUINC, JMAX)
C  CALL TABMMORT(MMORT,MINOMEGA, INCOMEGA, NUMIN, NUINC, OAS)
CALL SAVEVS(MINOMEGA, INCOMEGA, IMAX, NUMIN, NUINC, JMAX)
END

```



```

SUBROUTINE PRVS(MINOMEGA, INCOMECA, IMAX, NUMIN, NUINC, JMAX)

C      Prints out the results of subroutine VS in a format similar to
C      that of P.Gould's program. The arrays PA, NA, HA and LIFEA are
C      tabulated, along with the appropriate values of OMEGA and NU.
C      The values of OMEGA and NU are calculated (TEMP1/TEMP2 and M
C      respectively) in the same way as done in subroutine VS.
C      Subroutine CONV is called to convert lifetimes to yrs, mos & days.
C      Subroutine PARAM is called to display the input parameters etc.
C      Preconditions : none other than those required by subroutine VS.
C      'Local' variables : HI - half of IMAX. If IMAX is odd then HI is
C                          rounded up rather than truncated.
C                          M, TEMP1, TEMP2 - see above comment.
C                          IY, IY1, IM, IM1, ID, ID1 - integers representing
C                          years, months and days (see subroutine CONV).

      INTEGER OAS, PA, NA, NUMIN, NUMAX, NUINC, IMAX, JMAX, HI, M,
&          IY, IY1, IM, IM1, ID, ID1
      PARAMETER (OAS = 20)
      REAL LIFEA, HA, MINOMEGA, MAXOMEGA, INCOMECA, MMORT
      DIMENSION PA(OAS,OAS), NA(OAS,OAS), HA(OAS,OAS), LIFEA(OAS,OAS),
&          MMORT(OAS,OAS)
      COMMON /O2DATA/ PA, NA, HA, LIFEA, MMORT

      MAXOMEGA = MINOMEGA + (IMAX - 1)*INCOMECA
      NUMAX = NUMIN + (JMAX - 1)*NUINC
      CALL PARAM(2, MINOMEGA, MAXOMEGA, NUMIN, NUMAX)

      HI = IMAX / 2
      IF (IMAX - HI*2 .EQ. 1) HI = HI + 1

      WRITE(*,5)
5      FORMAT(7(/))
      WRITE(*,10)
10     FORMAT(2(2X,'Omega',4X,'Nu',2X,'p',5X,'n',9X,'H',5X,'Lifetime',8X)
&          / 2(16X,'opt',3X,'opt',7X,'opt',3X,'(y:m:d)',8X) )

      DO 50 I = 1, HI

          PRINT*
          TEMP1 = MINOMEGA + (I-1)*INCOMECA
          TEMP2 = TEMP1 + HI*INCOMECA

          DO 50 J = 1, JMAX

              M = NUMIN + (J-1)*NUINC
              CALL CONV( LIFEA(I,J), IY, IM, ID)
              IF (I .EQ. HI .AND. IMAX-HI*2 .NE. 0) THEN
                  WRITE(*,20) TEMP1,M,PA(I,J),NA(I,J),NINT(HA(I,J)),IY,IM,ID
              ELSE
                  CALL CONV( LIFEA(I+HI,J), IY1, IM1, ID1)
                  WRITE(*,30) TEMP1,M,PA(I,J),NA(I,J),NINT(HA(I,J)),IY,IM,ID,
&          TEMP2,M,PA(I+HI,J),NA(I+HI,J),NINT(HA(I+HI,J)),IY1,IM1,ID1
              END IF
20          FORMAT(2X,F5.3,2X,I4,2(4X,I2),2X,I8,2X,2(I2,':'),I2)
30          FORMAT( 2(2X,F5.3,2X,I4,2(4X,I2),2X,I8,2X,2(I2,':'),I2,8X) )
50     CONTINUE
      END

```

```

SUBROUTINE TABMMORT(MMORT,MINOMEGA,INCOMEGA,NUMIN,NUINC,OAS)

C   Tabulates MMORT, a real array, for the range of values of Nu
C   and Omega as determined by their minima and increments.
C   All 20*20 elements of MMORT are tabulated. The rows and columns
C   of MMORT are reversed relative to the storage of this array.
C   GLIB routines are called. OAS is assumed to be 20.

      INTEGER NUMIN, NUINC, OAS
      REAL MINOMEGA, INCOMEGA, MMORT(OAS,OAS)
      CHARACTER*8 TODAY, CURRTIME

      CALL DATE(TODAY)
      CALL TIME(CURRTIME)
      WRITE(*,10) TODAY, CURRTIME
10   FORMAT(10X, 'Crab Reproductive Strategies (program 1).',//,
&         10X, 'Date : ', A8, 5X, 'Time : ', A8, '.',///,
&         10X, 'Moult mortality as % of total lifetime mortality'///)
      WRITE(*,20)
20   FORMAT(10X, 'Omega (moult survival)')
      WRITE(*,30) (MINOMEGA + 2.0*INCOMEGA*I, I = 0, 9)
30   FORMAT(8X, 10(F5.3, 5X) )
      WRITE(*,40)
40   FORMAT(3X, 'Nu')
      DO 50 I = 1, OAS
          ITEMP = NUMIN + (I-1)*NUINC
          WRITE(*,60) ITEMP, ( MMORT(J,I), J = 1, 20 )
50   CONTINUE
60   FORMAT(1X, I4, 3X, 20(1X, F4.3) )
      WRITE(*,'(//)')
      END

SUBROUTINE CONV(X, IY, IM, ID)

C   Converts a real number X (a number of days) into its component
C   integer parts of years (IY), months (IM) and days (ID). X itself
C   is unchanged. One month is taken as 30 days. One year is taken
C   as 360 days (so that 12 30-day months equal 1 360-day year).

      IY = INT( X/360.0 )
      IREM = INT( X - IY*360.0 )
      IM = IREM / 30
      ID = IREM - IM*30
      END

SUBROUTINE SAVEVS(MINOMEGA, INCOMEGA, IMAX, NUMIN, NUINC, JMAX)

C   Saves the results of subroutine VS to a formatted file.
C   Precondition : channel 3 is connected to a disk file of
C   the appropriate characteristics.

```

```

INTEGER K, KA, NU, NMAX, NMAXA, CHECK, OAS, POPT, PA, NOPT, NA
PARAMETER (NMAX = 50, NMAXA = NMAX + 1, OAS = 20, CHECK = 0)
REAL LAMBDA, A, B, C, L, MU, OMEGA, TAU0, X0, LIFE, LIFEOPT,
& LIFEA, H, HOPT, HA, ANEC, MINANEC, MAXANEC, MMORT
DIMENSION L(NMAXA), MU(NMAXA), K(NMAXA), OMEGA(NMAXA), NU(NMAXA),
& TAU0(NMAXA), X0(NMAXA), H(2:NMAXA,NMAX), LIFE(2:NMAXA,NMAX),
& PA(OAS,OAS), NA(OAS,OAS), HA(OAS,OAS), LIFEA(OAS,OAS),
& MMORT(OAS,OAS)
COMMON /IDATA/ LAMBDA, A, B, C, MU, OMEGA, K, KA, NU
COMMON /O1DATA/ L, TAU0, X0, H, LIFE, HOPT, POPT, NOPT, LIFEOPT,
& ANEC, MINANEC, MAXANEC
COMMON /O2DATA/ PA, NA, HA, LIFEA, MMORT

M = 1
WRITE(3,10) M,L(1),LAMBDA,MU(1),A,B,C,K(1),KA,MINANEC,MAXANEC
10  FORMAT(I1 / F4.2, F6.1, F6.2, F6.3, F7.3, F5.1, 2I2, 2F5.2)
WRITE(3,20) MINOMEGA, INCOMEGA, IMAX, NUMIN, NUINC, JMAX
20  FORMAT(1X, 2F6.3, I4, 2I6, I4)
DO 50 I = 1, IMAX
    DO 50 J = 1, JMAX
        WRITE(3,60) PA(I,J), NA(I,J), HA(I,J), LIFEA(I,J), MMORT(I,J)
50  CONTINUE
60  FORMAT(1X, 2I3, F12.1, F10.2, F24.18)
END

```

PROGRAM CRAB2

```

C   Program to read back a file of results produced by CARCINUS
C   VFORTTRAN or CANCER VFORTTRAN, to tabulate and plot those results.
C   Version 1.5 Andy Bryant 9ii91 (started 31/1/89).
C
C   This version also accepts results from INAC VFORTTRAN for plotting
C   (but not for tabulation). If data are from INAC ie. M=3 in
C   INDATA, then PRVS, PARAM, CALCPN and TABMMORT should not be
C   called.
C
C   Data structures and usage as described earlier, except common
C   block INDATA which contains miscellaneous variables read in at
C   the start of the input file. Also, array PN which is the lateness
C   of reproduction of the optimum strategy (= PA / (NA+1) ).

```

```

INTEGER PA,BA,NA, OAS, NUMIN, NUINC, IMAX, JMAX, K1, KA, M
PARAMETER (OAS = 20, CHECK = 0)
REAL A, B, C, MU1, L1, BETA0, BETA1, MINANEC, MAXANEC,
& LIFEA, HA, MINOMEGA, INCOMEGA, Y, MMORT, JLIFEA, PN
DIMENSION PA(OAS,OAS), NA(OAS,OAS), HA(OAS,OAS), LIFEA(OAS,OAS),
& Y(OAS,OAS), MMORT(OAS,OAS), PN(OAS,OAS), BA(OAS,OAS), JLIFEA(OAS,OAS)
COMMON /O2DATA/ PA, NA, HA, LIFEA, MMORT, BA, JLIFEA
COMMON /INDATA/ M, LAMBDA, A, B, C, MU1, L1, K1, KA,
& BETA0, BETA1, MINANEC, MAXANEC

```

```

CALL READVS(MINOMEGA, INCOMEGA, IMAX, NUMIN, NUINC, JMAX)
C CALL PRVS(MINOMEGA, INCOMEGA, IMAX, NUMIN, NUINC, JMAX)
C CALL CALCPN(PA, NA, PN, OAS)
C CALL CONVX(BA, Y, OAS)
C CALL TABPANA(PA, MINOMEGA, INCOMEGA, NUMIN, NUINC, OAS)
C CALL TABMMORT(PN, MINOMEGA, INCOMEGA, NUMIN, NUINC, OAS)
CALL PLVS(LIFEA, OAS, 4)
END

SUBROUTINE READVS(MINOMEGA, INCOMEGA, IMAX, NUMIN, NUINC, JMAX)

C Reads the results contained in a formatted file, which is
C connected to channel 3. The data are presumed to have been
C calculated and written by subroutines VS and SAVEVS respectively
C of program CRAB1 VFORTRAN.
C Precondition : channel 3 is connected to a disk file of
C the appropriate characteristics, with the correct structure.

INTEGER PA,BA,NA, OAS, NUMIN, NUINC, IMAX, JMAX, K1, KA, M
PARAMETER (OAS = 20, CHECK = 0)
REAL A, B, C, MU1, L1, BETA0, BETA1, MINANEC, MAXANEC,
& LIFEA, HA, MINOMEGA, INCOMEGA, X, MMORT, JLIFEA
DIMENSION PA(OAS,OAS), NA(OAS,OAS), HA(OAS,OAS), LIFEA(OAS,OAS),
& MMORT(OAS,OAS), BA(OAS,OAS), JLIFEA(OAS,OAS)
COMMON /O2DATA/ PA, NA, HA, LIFEA, MMORT, BA, JLIFEA
COMMON /INDATA/ M, LAMBDA, A, B, C, MU1, L1, K1, KA,
& BETA0, BETA1, MINANEC, MAXANEC

READ(3,10) M
10 FORMAT(I1)
IF (M .EQ. 1) THEN
  READ(3,20) L1, LAMBDA, MU1, A, B, C, K1, KA, MINANEC, MAXANEC
ELSE IF (M .EQ. 2) THEN
  READ(3,30) L1, BETA0, BETA1, A, C, K1
END IF
20 FORMAT(F4.2, F6.1, F6.2, F6.3, F7.3, F5.1, 2I2, 2F5.2)
30 FORMAT(F4.2, 3F6.3, F6.1, I2)
READ(3,40) MINOMEGA, INCOMEGA, IMAX, NUMIN, NUINC, JMAX
40 FORMAT(1X, 2F6.3, I4, 2I6, I4)
IF (CHECK .EQ. 1) PRINT*, MINOMEGA, IMAX, NUMIN, JMAX
DO 50 I = 1, IMAX
  DO 50 J = 1, JMAX
    IF (M .EQ. 1 .OR. M .EQ. 2) THEN
      READ(3,60) PA(I,J), NA(I,J), HA(I,J), LIFEA(I,J), MMORT(I,J)
      PRINT*, PA(I,J), NA(I,J), HA(I,J), LIFEA(I,J)
    ELSE IF (M .EQ. 3) THEN
      READ(3,70) PA(I,J), BA(I,J), HA(I,J), LIFEA(I,J), JLIFEA(I,J)
    END IF
50 CONTINUE
60 FORMAT(1X, 2I3, F12.1, F10.2, F24.18)
70 FORMAT(1X, I3, I4, F12.1, 2F10.2)
END

```

```

SUBROUTINE PRVS(MINOMEGA, INCOMEGA, IMAX, NUMIN, NUINC, JMAX)

C Prints out the results of subroutine VS in a format similar to
C that of P.Gould's program. The arrays PA, NA, HA and LIFEA are
C tabulated, along with the appropriate values of OMEGA and NU.
C The values of OMEGA and NU are calculated (TEMP1/TEMP2 and M
C respectively) in the same way as done in subroutine VS.
C Subroutine CONV is called to convert lifetimes to yrs, mos & days.
C Preconditions : in COMMON INDATA, M=1 OR M=2.
C 'Local' variables : HI - half of IMAX. If IMAX is odd then HI is
C rounded up rather than truncated.
C M, TEMP1, TEMP2 - see above comment.
C IY, IY1, IM, IM1, ID, ID1 - integers representing
C years, months and days (see subroutine CONV).
C This subroutine is the same as that of the same name in
C program CRAB1 VFORTRAN.

INTEGER OAS, PA, NA, NUMIN, NUINC, NUMAX, IMAX, JMAX, HI, M,
& IY, IY1, IM, IM1, ID, ID1, BA
PARAMETER (OAS = 20)
REAL LIFEA, HA, MINOMEGA, INCOMEGA, MAXOMEGA, MMORT, JLIFEA
DIMENSION PA(OAS,OAS), NA(OAS,OAS), HA(OAS,OAS), LIFEA(OAS,OAS),
& MMORT(OAS,OAS), BA(OAS,OAS), JLIFEA(OAS,OAS)
COMMON /O2DATA/ PA, NA, HA, LIFEA, MMORT, BA, JLIFEA

MAXOMEGA = MINOMEGA + (IMAX - 1)*INCOMEGA
NUMAX = NUMIN + (JMAX - 1)*NUINC
CALL PARAM(MINOMEGA, MAXOMEGA, NUMIN, NUMAX)

HI = IMAX / 2
IF (IMAX - HI*2 .EQ. 1) HI = HI + 1

WRITE(*,5)
5 FORMAT(7(/))
WRITE(*,10)
10 FORMAT(2(2X,'Omega',4X,'Nu',2X,'p',5X,'n',9X,'H',7X,'Lifetime',8X)
& / 2(16X,'opt',3X,'opt',7X,'opt',5X,'(y:m:d)',8X) )

DO 50 I = 1, HI

PRINT*
TEMP1 = MINOMEGA + (I-1)*INCOMEGA
TEMP2 = TEMP1 + HI*INCOMEGA

DO 50 J = 1, JMAX

M = NUMIN + (J-1)*NUINC
CALL CONV( LIFEA(I,J), IY, IM, ID)
IF (I .EQ. HI .AND. IMAX-HI*2 .NE. 0) THEN
WRITE(*,20) TEMP1,M,PA(I,J),NA(I,J),NINT(HA(I,J)),IY,IM,ID
ELSE
CALL CONV( LIFEA(I+HI,J), IY1, IM1, ID1)
WRITE(*,30) TEMP1,M,PA(I,J),NA(I,J),NINT(HA(I,J)),IY,IM,ID,
& TEMP2,M,PA(I+HI,J),NA(I+HI,J),NINT(HA(I+HI,J)),IY1,IM1,ID1
END IF
20 FORMAT(2X,F5.3,2X,I4,2(4X,I2),2X,I8,3X,I3,':',I2,':',I2)
30 FORMAT(2(2X,F5.3,2X,I4,2(4X,I2),2X,I8,3X,I3,':',I2,':',I2,8X) )
50 CONTINUE
PRINT*
END

```

```

SUBROUTINE PARAM(MINOMEGA, MAXOMEGA, NUMIN, NUMAX)

C   Writes the input parameters of the model to the default output.
C   Copied over from CARCINUS VFORTRAN. GLIB subroutines are used.
C   Precondition: in INDATA, M=1 or M=2.

INTEGER PA,BA,NA, OAS, NUMIN, NUINC, NUMAX, IMAX, JMAX, K1, KA, M
PARAMETER (OAS = 20, CHECK = 0)
REAL A, B, C, MU1, L1, BETA0, BETA1, MINANEC, MAXANEC,
& LIFEA, HA, MINOMEGA, INCOMEGA, MAXOMEGA, X, MMORT, JLIFEA
CHARACTER*8 TODAY, CURRTIME
DIMENSION PA(OAS,OAS), NA(OAS,OAS), HA(OAS,OAS), LIFEA(OAS,OAS),
& MMORT(OAS,OAS), BA(OAS,OAS), JLIFEA(OAS,OAS)
COMMON /O2DATA/ PA, NA, HA, LIFEA, MMORT, BA, JLIFEA
COMMON /INDATA/ M, LAMBDA, A, B, C, MU1, L1, K1, KA,
& BETA0, BETA1, MINANEC, MAXANEC

CALL DATE(TODAY)
CALL TIME(CURRTIME)
IF (M .EQ. 1) THEN
  WRITE(*,10) TODAY, CURRTIME
ELSE IF (M .EQ. 2) THEN
  WRITE(*,20) TODAY, CURRTIME
END IF
10  FORMAT(10(/),10X,'Carcinus Reproductive Strategies (program 2).',//
& 10X, 'Date : ', A8, 5X, 'Time : ', A8, '.', //)
20  FORMAT(10(/),10X,'Cancer Reproductive Strategies (program 2).',//
& 10X, 'Date : ', A8, 5X, 'Time : ', A8, '.', //)
WRITE(*,30)
30  FORMAT(10X, 'Tabulation of the optima for a range of values',/,
& 10X, 'of the survival parameters, Omega and Nu.', ///)

WRITE(*,40) L1
40  FORMAT(1X, 'Parameters of the model :', //, 1X, 'Initial size =',
& F4.1, 'mm')
IF (M .EQ. 1) THEN
  WRITE(*,50) LAMBDA, MU1
  WRITE(*,60) A, B, C
  WRITE(*,70) K1, KA
ELSE IF (M .EQ. 2) THEN
  WRITE(*,55) BETA0, BETA1
  WRITE(*,65) A, C
  WRITE(*,75) K1
END IF
50  FORMAT(1X, 'Moult increment parameters : Lambda = ', F4.1,
& ' Mu = ', F4.2)
55  FORMAT(1X, 'Moult increment parameters : Beta0 = ', F5.3,
& ' Beta1 = ', F5.3)
60  FORMAT(1X, 'Instar duration parameters : A = ', F4.2,
& ' B = ', F4.1, ' C = ', F4.1, /)
65  FORMAT(1X, 'Instar duration parameters : A = ', F5.3,
& ' C = ', F5.1, /)
70  FORMAT(1X, 'Egg batches per instar : Before anecdysis = ',
& I1, ' After anecdysis = ', I1, /)
75  FORMAT(1X, 'Egg batches per instar (all instars) = ', I1, /)
WRITE(*,100) MINOMEGA, MAXOMEGA, NUMIN, NUMAX
100 FORMAT(1X, 'Survival probability parameters : Omega = ', F5.3,
& ' - ', F5.3, /, 36X, 'Nu = ', I4, ' - ', I4)
IF (M .EQ. 1) THEN
  WRITE(*,110) MINANEC, MAXANEC
END IF
110 FORMAT(1X, 'Anecdysis constant : Min. = ', F4.2, ' Max. = ', F4.2/
& 1X, '(calculated from KA, Nu during anecdysis and C)')
END

```

```

SUBROUTINE TABPANA(PANA, MINOMEGA, INCOMEGA, NUMIN, NUINC, OAS)

C   Tabulates PANA, an integer array, for the range of values of Nu
C   and Omega as determined by their minima and increments.
C   All 20*20 elements of PANA are tabulated. The rows and columns
C   are reversed relative to the storage of this array.
C   GLIB routines are called. OAS is assumed to be 20.
C   PANA is either array PA or array NA.

INTEGER PANA, NUMIN, NUINC, OAS
DIMENSION PANA(OAS,OAS)
REAL MINOMEGA, INCOMEGA
CHARACTER*8 TODAY, CURRTIME

CALL DATE(TODAY)
CALL TIME(CURRTIME)
WRITE(*,10) TODAY, CURRTIME
10  FORMAT(10X, 'Crab Reproductive Strategies (program 2).',//,
&      10X, 'Date : ', A8, 5X, 'Time : ', A8, '.',//)

WRITE(*,20)
20  FORMAT(10X, 'Omega (moult survival)')
WRITE(*,30) (MINOMEGA + 2.0*INCOMEGA*I, I = 0, 9)
30  FORMAT(8X, 10(F5.3, 5X) )
WRITE(*,40)
40  FORMAT(3X, 'Nu')
DO 50 I = 1, OAS
    ITEMP = NUMIN + (I-1)*NUINC
    WRITE(*,60) ITEMP, ( PANA(J,I), J = 1, 20 )
50  CONTINUE
60  FORMAT(1X, I4, 2X, 20(3X, I2) )
WRITE(*,'(//)')
END

SUBROUTINE TABMMORT(MMORT,MINOMEGA,INCOMEGA,NUMIN,NUINC,OAS)

C   Tabulates MMORT, a real array, for the range of values of Nu
C   and Omega as determined by their minima and increments.
C   All 20*20 elements of MMORT are tabulated. The rows and columns
C   of MMORT are reversed relative to the storage of this array.
C   GLIB routines are called. OAS is assumed to be 20.

INTEGER NUMIN, NUINC, OAS
REAL MINOMEGA, INCOMEGA, MMORT(OAS,OAS)
CHARACTER*8 TODAY, CURRTIME

```

```

CALL DATE(TODAY)
CALL TIME(CURRTIME)
WRITE(*,10) TODAY, CURRTIME
10  FORMAT(10X, 'Crab Reproductive Strategies (program 2).',//,
&      10X, 'Date : ', A8, 5X, 'Time : ', A8, '.', ' ',//,
&      10X, 'Moult mortality as % of total lifetime mortality'//)
WRITE(*,20)
20  FORMAT(10X, 'Omega (moult survival)')
WRITE(*,30) (MINOMEGA + 2.0*INCOMEGA*I, I = 0, 9)
30  FORMAT(8X, 10(F5.3, 5X) )
WRITE(*,40)
40  FORMAT(3X, 'Nu')
DO 50 I = 1, OAS
    ITEMP = NUMIN + (I-1)*NUINC
    WRITE(*,60) ITEMP, ( MMORT(J,I), J = 1, 20 )
50  CONTINUE
60  FORMAT(1X, I4, 3X, 20(1X, F4.2) )
WRITE(*, '(//)')
END

```

SUBROUTINE CONV(X, IY, IM, ID)

C Converts a real number X (a number of days) into its component
C integer parts of years (IY), months (IM) and days (ID). X itself
C is unchanged. One month is taken to be 30.4375 days. One year
C is taken to be 365.25 days

```

IY = INT( X/365.25 )
REM = MOD( X,365.25 )
IM = INT( REM/30.4375 )
ID = NINT( REM - IM*30.4375 )
END

```

SUBROUTINE CALCPN(PA, NA, PN, OAS)

C Calculates a square two-dimensional array, PN, from square two-
C dimensional arrays PA and NA (all of dimensions OAS).

```

INTEGER PA, NA, OAS
REAL PN
DIMENSION PA(OAS,OAS), NA(OAS,OAS), PN(OAS,OAS)

DO 50 I = 1, OAS
    DO 50 J = 1, OAS
        PN(I,J) = REAL( PA(I,J) ) / REAL( NA(I,J)+1 )
50  CONTINUE
END

```



```

SUBROUTINE CONVX(X, Y, OAS)

C   Converts a square two-dimensional integer array (ie. PA or NA
C   in COMMON block O2DATA), X, of dimensions OAS, into
C   a real array Y. X itself is unchanged.

INTEGER X, OAS
REAL Y
DIMENSION X(OAS,OAS), Y(OAS,OAS)

DO 50 I = 1, OAS
  DO 50 J = 1, OAS
    Y(I,J) = REAL( X(I,J) )
50 CONTINUE
END

SUBROUTINE PLVS(X, OAS, M)

C   Plots the results read in by READVS, which were in turn produced
C   by subroutine VS of program CRAB1. A square two-dimensional
C   array X and its dimensions OAS are passed as arguments.
C   Precondition : OAS <= 20 and subroutine READVS has been called.
C   If M=1 then the array being passed (to X) is Y (real version of
C   array PA, converted by subroutine CONVX).
C   If M=2 then the array being passed (to X) is Y (real version of
C   array NA, converted by subroutine CONVX).
C   If M=3 then the array being passed (to X) is HA.
C   If M=4 then the array being passed (to X) is LIFEA.
C   If M=5 then the array being passed (to X) is PN.
C   If M=6 then the array being passed (to X) is MMORT.
C   If M=7 then the array being passed (to X) is Y (real version of
C   array BA, converted by subroutine CONVX).
C   If M=8 then the array being passed (to X) is JLIFEA.

INTEGER OAS, ITITLE(20)
REAL X(OAS,OAS), W(1000)

```

```

CALL GINO
CALL SAVDRA
CALL DEVPA(200.0, 200.0, 0)
CALL WINDO2(0.0, 200.0, 0.0, 200.0)
C CALL ISOPRJ(OAS, 0.475, 0.950, OAS, 100.0, 2000.0, X, 0, 1000, W)
CALL SETSCA(0.05, 200.0, 1)
CALL SETFRA(0)
IF (M .EQ. 1) THEN
  CALL TITSTR('V*VALUES OF P OF THE OPTIMAL STRATEGY FOR A RANGE O
&F VALUES OF OMEGA AND NU.')
  CALL GRDCON(OAS,0.475,0.950,OAS,100.0,2000.0, X, 10, 0)
  ELSE IF (M .EQ. 2) THEN
    CALL TITSTR('V*VALUES OF N OF THE OPTIMAL STRATEGY FOR A RANGE
&OF VALUES OF OMEGA AND NU.')
    CALL LEVELS(10.0, 49.0)
    CALL LABCON(0, 1, 60.0, 0)
    CALL GRDCON(OAS,0.475,0.950,OAS,100.0,2000.0, X, 14, 0)
  ELSE IF (M .EQ. 3) THEN
    CALL TITSTR('O*LPTIMAL EGG PRODUCTION (H) FOR A RANGE OF VALUES
&OF OMEGA AND NU.')
    CALL GRDCON(OAS,0.475,0.950,OAS,100.0,2000.0, X, 10, 0)
  ELSE IF (M .EQ. 4) THEN
    CALL TITSTR('L*LIFETIME OF THE OPTIMAL STRATEGY FOR A RANGE OF
&VALUES OF OMEGA AND NU.')
    CALL LEVELS(4000.0, 100000.0)
    CALL LABCON(0, 1, 60.0, 0)
    CALL GRDCON(OAS,0.475,0.950,OAS,100.0,2000.0, X, 13, 0)
  ELSE IF (M .EQ. 5) THEN
    CALL TITSTR('V*VALUES OF P/(N+1) OF THE OPTIMAL STRATEGY FOR A
& RANGE OF VALUES OF OMEGA AND NU.')
    CALL GRDCON(OAS,0.475,0.950,OAS,100.0,2000.0, X, 10, 0)
  ELSE IF (M .EQ. 6) THEN
    CALL TITSTR('M*LOULT MORTALITY OF THE OPTIMAL STRATEGY FOR A RAN
&GE OF VALUES OF OMEGA AND NU.')
    CALL GRDCON(OAS,0.475,0.950,OAS,100.0,2000.0, X, 10, 0)
  ELSE IF (M .EQ. 7) THEN
    CALL TITSTR('N*LUMBER OF BATCHES OF THE OPTIMAL STRATEGY FOR A R
&ANGE OF VALUES OF OMEGA AND NU.')
    CALL GRDCON(OAS,0.475,0.950,OAS,100.0,2000.0, X, 10, 0)
  ELSE IF (M .EQ. 8) THEN
    CALL TITSTR('J*LUVENILE LIFETIME OF THE OPTIMAL STRATEGY FOR A R
&ANGE OF VALUES OF OMEGA AND NU.')
    CALL GRDCON(OAS,0.475,0.950,OAS,100.0,2000.0, X, 10, 0)
  END IF
CALL SOFCHA
CALL CONSPA(7.0, -15.0, 0.0, 0.0)
CALL MOVTO2(70.0, -2.0)
CALL CHASTR('O*LMEGA (MOULT SURVIVAL)')
CALL MOVTO2(-2.0, 70.0)
CALL CHASWI(1)
CALL CHAANG(90.0)
CALL CHASTR('N*LU (INTERMOULT SURVIVAL)')
CALL DEVEND
CALL GINEND
END

```

Appendix 4. Derivation of intermoult period relationship with body size (equation (15), Chapter 5) for *Cancer pagurus* females.

Data from Edwards (1965), animals maintained in laboratory tanks:

CW / mm	Intermoult period / days
22.0	21
27.6	71
34.5	90
42.8	130
41.5	130
45.3	121
45.1	169
67.9	199

Annual moult frequency (AMF) in the field, data from Bennett (1974):

CW / mm	% AMF	n	Intermoult period / days (est.) *
115	100	4	365
125	82	11	445
135	69	29	529

* period = $100/\%AMF * 365$ days

Bennett (1974) gives data for one smaller and several larger size classes, but the numbers which moulted are such that estimation of intermoult period would have involved great potential error. These data were therefore discarded.

A least squares regression through the origin, using the combined intermoult period data shown above, gave the following result:

Period = $3.434 * CW$ days

Several problems may be identified in this procedure:

1. The data are from two different studies employing different conditions (laboratory and field).
2. The estimation of intermoult period from annual moult frequency is imprecise, but represents the only information available on larger individuals of *Cancer pagurus*.
3. The regression analysis considers each data point to have equal weight. If it were possible to calculate weights for the data points then a weighted analysis would have been preferable.
4. The fitted line has been forced through the origin, to avoid the prediction of negative intermoult periods for the very small individuals.

Appendix 5. A FORTRAN 77 program (IBM VFORTRAN) for implementation of the *Hyas coarctatus* model. See section 5.2.3.

```
PROGRAM HYAS

C Hyas reproductive strategies simulation program.
C Version 1.1 Andy Bryant 13xi90 (started 11x90).
C
C Program is based loosely upon CARCINUS VFORTRAN.
C
C Implicit FORTRAN typing rules ignored (nomenclature used is
C mainly that of the original model, P.Gould 5/8/86, etc.).
C All variables are declared except loop identifiers, I, J and M,
C and also temporary real variables, TEMP, TEMP1, TEMP2 etc.
C
C Variables / Constants :
C
C NMAX - maximum number of instars allowed. NMAXA = NMAX + 1.
C A, B, C, OMEGA, NU, L - usage as in my formulation & orig. model.
C TAUJ(I) - duration of instar I.
C XJ(I) - survival to instar I.
C H(P) - total hatched egg production for a given [P] schedule.
C This is real rather than integer for the purposes of
C plotting using GINO. Strictly, it should be an integer.
C LIFE(P) - lifetime in days for a given [P] life schedule, measured
C to the point at which survival falls below the level
C ALLDEAD in subroutine SUBSCALC.
C BATCHES(P) - number of egg batches laid in the life schedule [P].
C E(P,J) - eggs produced in the j'th batch for life schedule [P].
C HOPT, POPT, BOPT, LIFEOPT, JLIFEOPT - values of H, P, BATCHES, LIFE
C juvenile lifespan respectively which correspond to optimal H.
C OAS - size of the arrays of optima. The size (both dimensions) of
C the arrays PA, HA, BA, JLIFEA and LIFEA (see below).
C PA, HA, BA, LIFEA and JLIFEA - two-dimensional arrays of values of
C POPT, HOPT, BOPT, LIFEOPT and JLIFEOPT respectively. Their
C elements represent ranges of the two lifetime survival
C parameters, OMEGA and NU. OMEGA is the first dimension;
C NU is the second dimension. See subroutine VS.
C
C
C
C COMMON block IDATA is used to group input data. COMMON blocks
C O1DATA and O2DATA are used to contain logically discrete groups
C of output data. O1DATA contains the initially produced output;
C see subroutines INITCALC and SUBSCALC. O2DATA contains the
C arrays of optima calculated by subroutine VS.
C Subroutines needing any of these may declare the
C variables then access the appropriate block.
C
C
```

```

INTEGER NMAX, NMAXA, NMIN, BATCHES, POPT, BOPT, OAS, PA, BA
PARAMETER (NMAX = 15, NMAXA = NMAX + 1, NMIN = 2, OAS = 20)
REAL ALPHA, BETA, ALPHAT, BETAT, A, B, C, L, TAUJ, XJ, H, E,
& OMEGA, NU, SDAY, EGGSA, EGGSB, INCUB, ALPHT, BETT, DELTA,
& LIFE, JLIFE, HOPT, LIFEOPT, JLIFEOPT, HA, LIFEA, JLIFEA
DIMENSION L(NMAX), TAUJ(NMAX), XJ(NMAX), H(NMAXA), E(NMAXA,5),
& LIFE(NMAXA), JLIFE(NMAXA), BATCHES(NMAXA), PA(OAS,OAS),
& HA(OAS,OAS), BA(OAS,OAS), LIFEA(OAS,OAS), JLIFEA(OAS,OAS),
& Y(OAS,OAS)
COMMON /IDATA/ ALPHA, BETA, ALPHAT, BETAT, A, B, C, OMEGA, NU,
& SDAY, EGGSA, EGGSB, INCUB, ALPHT, BETT, DELTA
COMMON /O1DATA/ L, TAUJ, XJ, H, E, LIFE, JLIFE, BATCHES,
& HOPT, POPT, BOPT, LIFEOPT, JLIFEOPT
COMMON /O2DATA/ PA, HA, BA, LIFEA, JLIFEA

```

```

CALL SETPARAM
C CALL INITCALC
C CALL SUBSCALC( NMIN )
C CALL TABH( NMIN )
CALL VS(100.0, 2000.0, 100.0, 0.475, 0.950, 0.025, NMIN)
C CALL TABPN(PA, 0.475, 0.950, 100.0, 2000.0, OAS)
C CALL CONVX(BA, Y, OAS)
CALL PLVS( LIFEA, OAS, 4, 0.475, 0.950, 100.0, 2000.0)
END

```

SUBROUTINE SETPARAM

C Sets the parameters in common block IDATA and L(1) in O1DATA.

```

INTEGER NMAX, NMAXA, BATCHES, POPT, BOPT
PARAMETER (NMAX = 15, NMAXA = NMAX + 1)
REAL ALPHA, BETA, ALPHAT, BETAT, A, B, C, L, TAUJ, XJ, H, E,
& OMEGA, NU, SDAY, EGGSA, EGGSB, INCUB, ALPHT, BETT, DELTA,
& LIFE, JLIFE, HOPT, LIFEOPT, JLIFEOPT
DIMENSION L(NMAX), TAUJ(NMAX), XJ(NMAX), H(NMAXA), E(NMAXA,5),
& LIFE(NMAXA), JLIFE(NMAXA), BATCHES(NMAXA)
COMMON /IDATA/ ALPHA, BETA, ALPHAT, BETAT, A, B, C, OMEGA, NU,
& SDAY, EGGSA, EGGSB, INCUB, ALPHT, BETT, DELTA
COMMON /O1DATA/ L, TAUJ, XJ, H, E, LIFE, JLIFE, BATCHES,
& HOPT, POPT, BOPT, LIFEOPT, JLIFEOPT

```

```

L(1) = 2.74
ALPHA = 0.007
BETA = 1.33
ALPHAT = 0.555
BETAT = 1.23
A = 57.1
B = 2.12
C = 3.34
SDAY = 165.0
EGGSA = 8.01
EGGSB = 0.217
INCUB = 365.25
ALPHT = 10.2
BETT = 3.2
DELTA = 78.0
OMEGA = 0.800
NU = 500.0
END

```

```

SUBROUTINE INITCALC

C   Performs initial calculations of L, TAUJ and XJ.
C   Function PERIOD is called to calculate TAUJ.
C
C   Precondition : subroutine SETPARAM has been called.
C
C   Variables :
C   I - the instar currently being considered.
C   TEMP - the value of L(1).
C   TEMP1 - start day of instar I.
C   TEMP2 - general use temporary variable.

INTEGER NMAX, NMAXA, BATCHES, POPT, BOPT
PARAMETER (NMAX = 15, NMAXA = NMAX + 1)
REAL ALPHA, BETA, ALPHAT, BETAT, A, B, C, L, TAUJ, XJ, H, E,
& OMEGA, NU, SDAY, EGGSA, EGGSB, INCUB, ALPHT, BETT, DELTA,
& LIFE, JLIFE, HOPT, LIFEOPT, JLIFEOPT
DIMENSION L(NMAX), TAUJ(NMAX), XJ(NMAX), H(NMAXA), E(NMAXA,5),
& LIFE(NMAXA), JLIFE(NMAXA), BATCHES(NMAXA)
COMMON /IDATA/ ALPHA, BETA, ALPHAT, BETAT, A, B, C, OMEGA, NU,
& SDAY, EGGSA, EGGSB, INCUB, ALPHT, BETT, DELTA
COMMON /OLDATA/ L, TAUJ, XJ, H, E, LIFE, JLIFE, BATCHES,
& HOPT, POPT, BOPT, LIFEOPT, JLIFEOPT

TEMP = L(1)
TAUJ(1) = PERIOD(SDAY, TEMP)
TEMP1 = SDAY + TAUJ(1)
IF (TEMP1 .GT. 365.25) TEMP1 = AMOD(TEMP1,365.25)
XJ(1) = 1.0
DO 10 I = 2, NMAX
  TEMP2 = BETA ** (I-1)
  L(I) = ALPHA * (TEMP2 - 1.0) / (BETA - 1.0) + TEMP2 * TEMP
  TAUJ(I) = PERIOD(TEMP1, L(I))
  TEMP1 = TEMP1 + TAUJ(I)
  IF (TEMP1 .GT. 365.25) TEMP1 = AMOD(TEMP1,365.25)
  TEMP2 = -TAUJ(I-1) / NU
  IF (TEMP2 .GT. -170.0) THEN
    XJ(I) = XJ(I-1) * OMEGA * EXP(TEMP2)
  ELSE
    XJ(I) = 0.0
  END IF
C   PRINT*, 'I, L, TAUJ & XJ'
C   WRITE(*,'(I3, 2F10.3, F10.5 /)') I, L(I), TAUJ(I), XJ(I)
10 CONTINUE
END

FUNCTION PERIOD(TR, L)

C   Solves the intermoult period equation by Newton-Raphson iteration
C   starting at day TR. Called by subroutine INITCALC.
C
C   TR - start day of intermoult period.
C   L - size of animal in the instar being investigated.
C   P, Q, R - see P.Gould's 20ix90 formulation on intermoult period.
C   PE1, PE2 - initial/improved period estimates (iteratively updated)
C   PI - 2 * Pi / 365.25

```

```

PARAMETER (SMALL = 0.01)
REAL ALPHA, BETA, ALPHAT, BETAT, A, B, C, OMEGA, NU, SDAY, EGGSA,
& EGGSB, INCUB, ALPHT, BETT, DELTA, TR, L, P, Q, R, PI, PE1, PE2
COMMON /IDATA/ ALPHA, BETA, ALPHAT, BETAT, A, B, C, OMEGA, NU,
& SDAY, EGGSA, EGGSB, INCUB, ALPHT, BETT, DELTA

PI = 0.0172
P = A + B*L - C*ALPHT
R = C * BETT / PI
Q = R * SIN( PI*(TR-DELTA) )

C PRINT*, 'Start day, L, then P, Q and R:'
C WRITE(*, '(F10.2, F10.3)') TR, L
C WRITE(*, '(F9.3, 2F10.3)') P, Q, R
PE1 = 350
I = 1
C PRINT*, 'I=', I, ' TAU=', PE1
10 PE2 = PE1 - ( PE1**2 - P*PE1 + Q - R*SIN( PI*(TR-DELTA+PE1) ) )
& / ( 2*PE1 - P - PI*R*COS( PI*(TR-DELTA+PE1) ) )
I = I + 1
C PRINT*, 'I=', I, ' TAU=', PE2
TEMP = ABS( PE2 - PE1 )
PE1 = PE2
IF (TEMP .GT. SMALL) GO TO 10

PERIOD = PE2
END

SUBROUTINE SUBSCALC( NMIN )

C Performs subsequent calculations relating to all the terminal
C anecdyces which are possible. Argument NMIN is the minimum value
C which n is allowed to take. Data in OLDATA are affected - the
C elements of the arrays H, LIFE and BATCHES in this common block
C which are affected are NMIN + 1 to NMAXA.
C
C Precondition : subroutine INITCALC has been called.
C
C Variables / constants :
C XCURR - current value of survival (start of instar, then at the
C end of incubation of 1st batch of eggs, then the 2nd etc).
C ALLDEAD - all are assumed to be dead when XCURR reaches this.
C LTERM - size of animal in terminal instar.
C EGGNO - egg number, as calculated from LTERM and data in IDATA.
C JLIFE - lifetime of animal in its juvenile instars.
C I - value of n currently being considered.
C J - the number of batches of eggs laid so far.
C TEMP - lifetime so far.
C TEMP1 - number of eggs laid so far.
C TEMP2 - used to protect exponentiations against underflow, and
C general very temporary use.

```



```

INTEGER NMAX, NMAXA, BATCHES, POPT, BOPT, NMIN
PARAMETER (NMAX = 15, NMAXA = NMAX + 1, ALLDEAD = 1.0E-4)
REAL ALPHA, BETA, ALPHAT, BETAT, A, B, C, L, TAUJ, XJ, H, E,
& OMEGA, NU, SDAY, EGGSA, EGGSB, INCUB, ALPHT, BETT, DELTA,
& LIFE, JLIFE, HOPT, LIFEOPT, JLIFEOPT, XCURR, LTERM, EGGNO
DIMENSION L(NMAX), TAUJ(NMAX), XJ(NMAX), H(NMAXA), E(NMAXA,5),
& LIFE(NMAXA), JLIFE(NMAXA), BATCHES(NMAXA)
COMMON /IDATA/ ALPHA, BETA, ALPHAT, BETAT, A, B, C, OMEGA, NU,
& SDAY, EGGSA, EGGSB, INCUB, ALPHT, BETT, DELTA
COMMON /O1DATA/ L, TAUJ, XJ, H, E, LIFE, JLIFE, BATCHES,
& HOPT, POPT, BOPT, LIFEOPT, JLIFEOPT
HOPT = 0.0
C WRITE(*, '(//)')

DO 30 I = NMIN, NMAX
  TEMP = 0.0
  DO 10 M = 1, I
    TEMP = TEMP + TAUJ(M)
10 CONTINUE
  JLIFE(I+1) = TEMP

  J = 0
  TEMP1 = 0.0
  TEMP2 = -TAUJ(I) / NU
  IF (TEMP2 .GT. -170.0) THEN
    XCURR = XJ(I) * OMEGA * EXP(TEMP2)
  ELSE
    XCURR = 0.0
  END IF
  LTERM = ALPHAT + BETAT*L(I)
  EGGNO = EGGSB*LTERM**3 - EGGSA

  IF (XCURR .GT. ALLDEAD) THEN
20 J = J + 1
    TEMP2 = -INCUB / NU
    IF (TEMP2 .GT. -170.0) THEN
      XCURR = XCURR * EXP(TEMP2)
    ELSE
      XCURR = 0.0
    END IF
    TEMP2 = EGGNO * XCURR
    IF (J .LE. 5) E(I+1,J) = TEMP2
    TEMP1 = TEMP1 + TEMP2
    TEMP = TEMP + INCUB
C IF (I .EQ. 14 .AND. J .LE. 5) PRINT*, J, E(I+1,J), XCURR
    IF (XCURR .GT. ALLDEAD) GO TO 20
  END IF

  H(I+1) = TEMP1
  BATCHES(I+1) = J
  LIFE(I+1) = TEMP
  IF (TEMP1 .GT. HOPT) THEN
    HOPT = TEMP1
    POPT = I + 1
    BOPT = J
    LIFEOPT = TEMP
    JLIFEOPT = JLIFE(I+1)
  END IF
C PRINT*, 'P, H, BATCHES, JLIFE & LIFE :'
C WRITE(*, '(I3,F10.1,I5,2F10.1 /)') I+1, H(I+1), BATCHES(I+1),
C & JLIFE(I+1), LIFE(I+1)
30 CONTINUE

```

```

C PRINT*, 'Optima HOPT, POPT, BOPT, JLIFEOPT, LIFEOPT : '
C WRITE(*, '(F10.1,2I5,2F10.1 /)') HOPT,POPT,BOPT,JLIFEOPT,LIFEOPT
C END

```

```

SUBROUTINE PARAM(I, MINOMEGA, MAXOMEGA, NUMIN, NUMAX)

```

```

C Writes the input parameters of the model to the default output.
C GLIB subroutines are used.
C If I=1 then the call has come from TABH - print the appropriate
C title and do not use the other 4 arguments.
C If I=2 then the call has come from PRVS - print the appropriate
C title and print out the other 4 arguments.

```

```

CHARACTER*8 TODAY, CURRTIME
INTEGER NMAX, NMAXA, BATCHES, POPT, BOPT
PARAMETER (NMAX = 15, NMAXA = NMAX + 1)
REAL ALPHA, BETA, ALPHAT, BETAT, A, B, C, L, TAUJ, XJ, H, E,
& OMEGA, NU, SDAY, EGGSA, EGGSB, INCUB, ALPHT, BETT, DELTA,
& LIFE, JLIFE, HOPT, LIFEOPT, JLIFEOPT, NUMIN, NUMAX, MINOMEGA, MAXOMEGA
DIMENSION L(NMAX), TAUJ(NMAX), XJ(NMAX), H(NMAXA), E(NMAXA,5),
& LIFE(NMAXA), JLIFE(NMAXA), BATCHES(NMAXA)
COMMON /IDATA/ ALPHA, BETA, ALPHAT, BETAT, A, B, C, OMEGA, NU,
& SDAY, EGGSA, EGGSB, INCUB, ALPHT, BETT, DELTA
COMMON /O1DATA/ L, TAUJ, XJ, H, E, LIFE, JLIFE, BATCHES,
& HOPT, POPT, BOPT, LIFEOPT, JLIFEOPT

```

```

CALL DATE(TODAY)
CALL TIME(CURRTIME)
WRITE(*,10) TODAY, CURRTIME
10 FORMAT(5(/), 10X, 'Hyas Reproductive Strategies.', //,
& 10X, 'Date : ', A8, 5X, 'Time : ', A8, '.', //)
IF (I .EQ. 1) THEN
WRITE(*,20) NMAXA
ELSE
WRITE(*,30)
END IF
20 FORMAT(10X, 'Tabulation of H (lifetime hatched egg production)', //,
& 10X, 'for all possible values of p (<= ', I2, ').', ///)
30 FORMAT(10X, 'Tabulation of the optima for a range of values', //,
& 10X, 'of the survival parameters, Omega and Nu.', ///)

WRITE(*,40) L(1)
40 FORMAT(1X, 'Parameters of the model :', //, 1X, 'Initial size =',
& F5.2, 'mm')
WRITE(*,50) ALPHA, BETA, ALPHAT, BETAT
50 FORMAT(1X, 'Moult increment : '/' Juvenile moults :',
& ' Alpha = ', F5.3, ' Beta = ', F4.2 / ' Terminal moult :',
& ' Alpha = ', F5.3, ' Beta = ', F4.2)
WRITE(*,60) A, B, C
60 FORMAT(1X, 'Instar duration : A = ', F4.1,
& ' B (size) = ', F4.2, ' C (temperature) = ', F4.2, /)
WRITE(*,70) SDAY
70 FORMAT(1X, 'Day of year on which instar 1 starts : ', F5.1)
WRITE(*,80) XJ(1)
80 FORMAT(1X, 'Initial population density = ', F3.1)
IF (I .EQ. 1) THEN
WRITE(*,90) OMEGA, NU
ELSE
WRITE(*,100) MINOMEGA, MAXOMEGA, NUMIN, NUMAX
END IF

```

```

90  FORMAT(1X, 'Survival probability : Omega = ', F5.3,
&      ' Nu = ', F6.1 /)
100 FORMAT(1X, 'Survival probability : Omega = ', F5.3,
&      ' - ', F5.3, /, 25X, 'Nu    =', F6.1, ' - ', F6.1 /)
    WRITE(*,110) EGGSA, EGGSB
110  FORMAT(1X, 'Egg production : A = ', F5.2, ' B = ', F5.3/)
    WRITE(*,120) ALPHT, BETT, DELTA
120  FORMAT(1X, 'Annual temperature : Alpha = ', F4.1,
&      ' Beta = ', F3.1, ' Delta = ', F6.2)
    END

    SUBROUTINE TABH( NMIN )

C     Tabulates H for the full range of values of P.
C     Subroutines PARAM and CONV are called.
C     Preconditions : subroutine MAINCALC has been called.

    INTEGER NMAX, NMAXA, NMIN, BATCHES, POPT, BOPT
    PARAMETER (NMAX = 15, NMAXA = NMAX + 1)
    REAL ALPHA, BETA, ALPHAT, BETAT, A, B, C, L, TAUJ, XJ, H, E,
&      OMEGA, NU, SDAY, EGGSA, EGGSB, INCUB, ALPHT, BETT, DELTA,
&      LIFE, JLIFE, HOPT, LIFEOPT, JLIFEOPT
    DIMENSION L(NMAX), TAUJ(NMAX), XJ(NMAX), H(NMAXA), E(NMAXA,5),
&      LIFE(NMAXA), JLIFE(NMAXA), BATCHES(NMAXA)
    COMMON /IDATA/ ALPHA, BETA, ALPHAT, BETAT, A, B, C, OMEGA, NU,
&      SDAY, EGGSA, EGGSB, INCUB, ALPHT, BETT, DELTA
    COMMON /O1DATA/ L, TAUJ, XJ, H, E, LIFE, JLIFE, BATCHES,
&      HOPT, POPT, BOPT, LIFEOPT, JLIFEOPT

    CALL PARAM(1, 1.0, 1.0, 1.0, 1.0)

    WRITE(*,15)
15   FORMAT(/, 10X, 'Optimal strategy for these parameters :', //)
    WRITE(*,20) NINT(HOPT)
20   FORMAT(10X, 'H                = ', I8, /, 11X, 'opt', /)
    WRITE(*,25) POPT
25   FORMAT(10X, 'p                = ', I2, /, 11X, 'opt', /)
    WRITE(*,30) BOPT
30   FORMAT(10X, 'Batches           = ', I2, /, 17X, 'opt', /)
    CALL CONV(JLIFEOPT, IY, IM, ID)
    WRITE(*,35) NINT(JLIFEOPT), IY, IM, ID
35   FORMAT(10X, 'Juvenile Life      = ', I5, ' days', /, 23X, 'opt',
&      2X, '= ', I2, ' years, ', I2, ' months, ', I2, ' days.//)
    CALL CONV(LIFEOPT, IY, IM, ID)
    WRITE(*,40) NINT(LIFEOPT), IY, IM, ID
40   FORMAT(10X, 'Life', 14X, '= ', I5, ' days', /, 14X, 'opt',
&      11X, '= ', I2, ' years, ', I2, ' months, ', I2, ' days.//)

    WRITE(*,60)
60   FORMAT(4(/, 29X, 'Lifespan, y:m:d', 9X, 'Numbers of eggs produced in'
&      ', ' successive egg batches' / 3X, 'p', 11X, 'H Batches Juvenile',
&      6X, 'Total', 7X, 'Batch 1', 6X, '2', 9X, '3', 9X, '4', 9X, '5' //)

    DO 80 I = NMIN+1, NMAXA
        CALL CONV( JLIFE(I), IY1, IM1, ID1 )
        CALL CONV( LIFE(I), IY2, IM2, ID2 )
        WRITE(*,70) I, NINT( H(I) ), BATCHES(I), IY1, IM1, ID1,
&      IY2, IM2, ID2, ( NINT( E(I,J) ), J=1,5 )
70   FORMAT(2X, I2, I12, I6, 4X, I3, ':', I2, ':', I2, I5, ':', I2, ':', I2, 1X, 5I10)
80   CONTINUE
    END

```

```

SUBROUTINE VS (NUMIN, NUMAX, NUINC, MINOMEGA, MAXOMEGA, INCOMECA, NMIN)

C      Varies the survival parameters NU and OMEGA in the
C      ranges NUMIN : NUMAX and MINOMEGA : MAXOMEGA respectively, with
C      increments NUINC and INCOMECA respectively. For each [NU,OMEGA]
C      combination, subroutines INITCALC and MAINCALC are called to
C      perform lifetime calculations. The arrays PA, BA, HA, LIFEA and
C      JLIFEA are used to hold the parameters of the optimal strategies
C      calculated for the range of values of NU and OMEGA.
C      'Local' variables : IMAX and JMAX, the maximum value that the loop
C                          identifiers I and J respectively will reach. These
C                          two are calculated at the start of this subroutine
C                          from the arguments of the subroutine. I is used to
C                          vary OMEGA. J is used to vary NU.
C      Preconditions : subroutine SETPARAM must have been called and, to
C                      prevent the upper bound of the arrays being
C                      exceeded, IMAX <= OAS and JMAX <= OAS.

      INTEGER NMAX, NMAXA, NMIN, BATCHES, POPT, BOPT, OAS, PA, BA, IMAX, JMAX
      PARAMETER (NMAX = 15, NMAXA = NMAX + 1, OAS = 20)
      REAL ALPHA, BETA, ALPHAT, BETAT, A, B, C, L, TAUJ, XJ, H, E,
&      OMEGA, NU, SDAY, EGGSA, EGGSB, INCUB, ALPHT, BETT, DELTA,
&      LIFE, JLIFE, HOPT, LIFEOPT, JLIFEOPT, HA, LIFEA, JLIFEA,
&      NUMIN, NUMAX, NUINC, MINOMEGA, MAXOMEGA, INCOMECA
      DIMENSION L(NMAX), TAUJ(NMAX), XJ(NMAX), H(NMAXA), E(NMAXA,5),
&      LIFE(NMAXA), JLIFE(NMAXA), BATCHES(NMAXA), PA(OAS,OAS),
&      HA(OAS,OAS), BA(OAS,OAS), LIFEA(OAS,OAS), JLIFEA(OAS,OAS)
      COMMON /IDATA/ ALPHA, BETA, ALPHAT, BETAT, A, B, C, OMEGA, NU,
&      SDAY, EGGSA, EGGSB, INCUB, ALPHT, BETT, DELTA
      COMMON /O1DATA/ L, TAUJ, XJ, H, E, LIFE, JLIFE, BATCHES,
&      HOPT, POPT, BOPT, LIFEOPT, JLIFEOPT
      COMMON /O2DATA/ PA, HA, BA, LIFEA, JLIFEA

      IMAX = NINT( (MAXOMEGA - MINOMEGA + INCOMECA) / INCOMECA )
      JMAX = NINT( (NUMAX - NUMIN + NUINC) / NUINC )
C      PRINT*, 'IMAX=', IMAX, 'JMAX=', JMAX

      DO 50 I = 1, IMAX
        DO 50 J = 1, JMAX
          OMEGA = MINOMEGA + (I-1)*INCOMECA
          NU = NUMIN + (J-1)*NUINC

C          PRINT*, 'I=', I, 'J=', J
C          PRINT*, 'OMEGA=', OMEGA, 'NU=', NU

          CALL INITCALC
          CALL SUBSCALC( NMIN )

          PA(I,J) = POPT
          HA(I,J) = HOPT
          BA(I,J) = BOPT
          LIFEA(I,J) = LIFEOPT
          JLIFEA(I,J) = JLIFEOPT
50      CONTINUE
      CALL PRVS(MINOMEGA, INCOMECA, IMAX, NUMIN, NUINC, JMAX)
      END

```

```

SUBROUTINE PRVS(MINOMEGA, INCOMEGA, IMAX, NUMIN, NUINC, JMAX)

C Prints out the results of subroutine VS in a format similar to
C that of P.Gould's program. PA, HA, BA, LIFEA and JLIFEA are
C tabulated, along with the appropriate values of OMEGA and NU.
C The values of OMEGA and NU are calculated (TEMP1/TEMP2 and M
C respectively) in the same way as done in subroutine VS.
C Subroutine CONV is called to convert lifetimes to yrs, mos & days.
C Subroutine PARAM is called to display the input parameters etc.
C Preconditions : none other than those required by subroutine VS.
C 'Local' variables : HI - half of IMAX. If IMAX is odd then HI is
C rounded up rather than truncated.
C M, TEMP1, TEMP2 - see above comment.
C IYx, IMx, IDx (1 <= x <= 4)-integers representing
C years, months and days (see subroutine CONV).

INTEGER NMAX,NMAXA,BATCHES,POPT,BOPT,OAS,PA,BA,IMAX,JMAX,HI
PARAMETER (NMAX = 15, NMAXA = NMAX + 1, OAS = 20)
REAL ALPHA, BETA, ALPHAT, BETAT, A, B, C, L, TAUJ, XJ, H, E,
& OMEGA, NU, SDAY, EGGSA, EGGSB, INCUB, ALPHT, BETT, DELTA,
& LIFE, JLIFE, HOPT, LIFEOPT, JLIFEOPT, HA, LIFEA, JLIFEA,
& NUMIN, NUMAX, NUINC, MINOMEGA, MAXOMEGA, INCOMEGA
DIMENSION L(NMAX), TAUJ(NMAX), XJ(NMAX), H(NMAXA), E(NMAXA,5),
& LIFE(NMAXA), JLIFE(NMAXA), BATCHES(NMAXA), PA(OAS,OAS),
& HA(OAS,OAS), BA(OAS,OAS), LIFEA(OAS,OAS), JLIFEA(OAS,OAS)
COMMON /IDATA/ ALPHA, BETA, ALPHAT, BETAT, A, B, C, OMEGA, NU,
& SDAY, EGGSA, EGGSB, INCUB, ALPHT, BETT, DELTA
COMMON /OLDATA/ L, TAUJ, XJ, H, E, LIFE, JLIFE, BATCHES,
& HOPT, POPT, BOPT, LIFEOPT, JLIFEOPT
COMMON /O2DATA/ PA, HA, BA, LIFEA, JLIFEA

MAXOMEGA = MINOMEGA + (IMAX - 1)*INCOMEGA
NUMAX = NUMIN + (JMAX - 1)*NUINC
CALL PARAM(2, MINOMEGA, MAXOMEGA, NUMIN, NUMAX)

HI = IMAX / 2
IF (IMAX - HI*2 .EQ. 1) HI = HI + 1

WRITE(*,5)
5 FORMAT(7(/))
WRITE(*,10)
10 FORMAT(2(2X,'Omega',4X,'Nu',2X,'p',9X,'H',5X,'b',5X,'Lifetime',2X,
& 'Juvenile',8X) / 2(16X,'opt',7X,2('opt',3X),'(y:m:d)',2X,
& 'Lifetime',8X) )

```

```

DO 50 I = 1, HI

PRINT*
TEMP1 = MINOMEGA + (I-1)*INCOMEGA
TEMP2 = TEMP1 + HI*INCOMEGA

DO 50 J = 1, JMAX

M = NINT( NUMIN + (J-1)*NUINC )
CALL CONV( LIFEA(I,J), IY1, IM1, ID1)
CALL CONV( JLIFEA(I,J), IY2, IM2, ID2)
IF (I .EQ. HI .AND. IMAX-HI*2 .NE. 0) THEN
  WRITE(*,20) TEMP1, M, PA(I,J), NINT( HA(I,J) ), BA(I,J),
&           IY1, IM1, ID1, IY2, IM2, ID2
  ELSE
    CALL CONV( LIFEA(I+HI,J), IY3, IM3, ID3)
    CALL CONV( JLIFEA(I+HI,J), IY4, IM4, ID4)
    WRITE(*,30) TEMP1,M,PA(I,J),NINT(HA(I,J)),BA(I,J),IY1,
&           IM1,ID1,IY2,IM2,ID2,TEMP2,M,PA(I+HI,J),NINT(HA(I+HI,J)),
&           BA(I+HI,J),IY3,IM3,ID3,IY4,IM4,ID4
  END IF
20  FORMAT(2X,F5.3,2X,I4,4X,I2,2X,I8,4X,I2,2(2X,2(I2,':'),I2) )
30  FORMAT(2(2X,F5.3,2X,I4,4X,I2,2X,I8,4X,I2,2(2X,2(I2,':'),I2),8X))
50  CONTINUE
END

```

```

SUBROUTINE TABPN(PN, MINOMEGA, INCOMEGA, NUMIN, NUINC, OAS)

```

```

C  Tabulates PN, an integer array, for the range of values of Nu
C  and Omega as determined by their minima and increments.
C  All 20*20 elements of PN are tabulated. The rows and columns of PN
C  are reversed relative to the storage of this array.
C  GLIB routines are called. OAS is assumed to be 20.

```

```

INTEGER PN, OAS
DIMENSION PN(OAS,OAS)
REAL MINOMEGA, INCOMEGA, NUMIN, NUINC
CHARACTER*8 TODAY, CURRTIME

CALL DATE(TODAY)
CALL TIME(CURRTIME)
WRITE(*,10) TODAY, CURRTIME
10  FORMAT(10X, 'Hyas Reproductive Strategies.',//,
&         10X, 'Date : ', A8, 5X, 'Time : ', A8, ' ',//)

WRITE(*,20)
20  FORMAT(10X, 'Omega (moult survival)')
WRITE(*,30) (MINOMEGA + 2.0*INCOMEGA*I, I = 0, 9)
30  FORMAT(8X, 10(F5.3, 5X) )
WRITE(*,40)
40  FORMAT(3X, 'Nu')
DO 50 I = 1, OAS
  ITEMP = NINT( NUMIN + (I-1)*NUINC )
  WRITE(*,60) ITEMP, ( PN(J,I), J = 1, 20 )
50  CONTINUE
60  FORMAT(1X, I4, 2X, 20(3X, I2) )
WRITE(*,'(//)')
END

```

```

SUBROUTINE CONVX(X, Y, OAS)

C   Converts a square two-dimensional integer array (ie. PA or BA
C   in COMMON block O2DATA), X, of dimensions OAS, into
C   a real array Y. X itself is unchanged.

INTEGER X, OAS
REAL Y
DIMENSION X(OAS,OAS), Y(OAS,OAS)

DO 50 I = 1, OAS
  DO 50 J = 1, OAS
    Y(I,J) = REAL( X(I,J) )
50 CONTINUE
END

SUBROUTINE PLVS(X, OAS, M, MINOMEGA, MAXOMEGA, NUMIN, NUMAX)

C   Plots the results of subroutine VS. A square two-dimensional
C   array X and its dimensions OAS are passed as arguments.
C   Precondition : OAS <= 20 and subroutine VS has been called.
C   If M=1 then the array being passed (to X) is Y (real version of
C   array PA, converted by subroutine CONVX).
C   If M=2 then the array being passed (to X) is Y (real version of
C   array BA, converted by subroutine CONVX).
C   If M=3 then the array being passed (to X) is HA.
C   If M=4 then the array being passed (to X) is LIFEA.
C   If M=5 then the array being passed (to X) is JLIFEA.

INTEGER OAS, ITITLE(20)
REAL X(OAS,OAS), MINOMEGA, MAXOMEGA, NUMIN, NUMAX, W(1000)

```

```

CALL GINO
CALL SAVDRA
CALL DEVPAP(200.0, 200.0, 0)
CALL WINDO2(0.0, 200.0, 0.0, 200.0)
C CALL ISOPRJ(OAS, MINOMEGA, MAXOMEGA, OAS, NUMIN, NUMAX, X, 0, 1000, W)
CALL SETSCA(0.05, 200.0, 1)
CALL SETFRA(0)
IF (M .EQ. 1) THEN
    CALL TITSTR('V*LALUES OF P OF THE OPTIMAL STRATEGY FOR A RANGE O
&F VALUES OF OMEGA AND NU.')
    CALL GRDCON(OAS, MINOMEGA, MAXOMEGA, OAS, NUMIN, NUMAX, X, 10, 0)
    ELSE IF (M .EQ. 2) THEN
        CALL TITSTR('V*LALUES OF B OF THE OPTIMAL STRATEGY FOR A RANGE
&OF VALUES OF OMEGA AND NU.')
C CALL LEVELS(10.0, 49.0)
C CALL LABCON(0, 1, 60.0, 0)
    CALL GRDCON(OAS, MINOMEGA, MAXOMEGA, OAS, NUMIN, NUMAX, X, 14, 0)
    ELSE IF (M .EQ. 3) THEN
        CALL TITSTR('O*LPTIMAL EGG PRODUCTION (H) FOR A RANGE OF VALUES
&OF OMEGA AND NU.')
        CALL GRDCON(OAS, MINOMEGA, MAXOMEGA, OAS, NUMIN, NUMAX, X, 10, 0)
    ELSE IF (M .EQ. 4) THEN
        CALL TITSTR('L*LIFETIME OF THE OPTIMAL STRATEGY FOR A RANGE OF
&VALUES OF OMEGA AND NU.')
C CALL LEVELS(4000.0, 100000.0)
C CALL LABCON(0, 1, 60.0, 0)
    CALL GRDCON(OAS, MINOMEGA, MAXOMEGA, OAS, NUMIN, NUMAX, X, 13, 0)
    ELSE IF (M .EQ. 5) THEN
        CALL TITSTR('J*LUVENILE LIFETIME OF THE OPTIMAL STRATEGY FOR A
& RANGE OF VALUES OF OMEGA AND NU.')
        CALL GRDCON(OAS, MINOMEGA, MAXOMEGA, OAS, NUMIN, NUMAX, X, 10, 0)
    END IF
CALL SOFCHA
CALL CONSPA(7.0, -15.0, 0.0, 0.0)
CALL MOVTO2(70.0, -2.0)
CALL CHASTR('O*LMEGA (MOULT SURVIVAL)')
CALL MOVTO2(-2.0, 70.0)
CALL CHASWI(1)
CALL CHAANG(90.0)
CALL CHASTR('N*LU (INTERMOULT SURVIVAL)')
CALL DEVEND
CALL GINEND
END

```

SUBROUTINE CONV(X, IY, IM, ID)

C Converts a real number X (a number of days) into its component
C integer parts of years (IY), months (IM) and days (ID). X itself
C is unchanged. One month is taken to be 30.4375 days. One year
C is taken to be 365.25 days.

```

IY = INT( X/365.25 )
REM = MOD( X, 365.25 )
IM = INT( REM/30.4375 )
ID = NINT( REM - IM*30.4375 )
END

```