THE POPULATION BIOLOGY OF LIGIA OCEANICA (L.) (CRUSTACEA : ONISCOIDEA).

by

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ABSTRACT

The dynamics and life history of an isolated population of Ligia oceanica (L.) inhabiting a sea-wall exposed to moderate wave action have been studied over a period of three years. Sex ratio, size at maturity, growth, breeding phenology, size and age structure, population density and size, female breeding size, fecundity regression and brood-pouch mortality have been determined. From these data population natality, and schedules of survivorship, fecundity and reproductive value are calculated. Although the supralittoral zone of rocky shores is generally regarded as a severe and stressful habitat, the dynamics of the population exhibit only minor differences between years, and no direct influence of wave exposure can be determined.

This population is compared with another nearby but isolated population occupying an harbour wall completely protected from wave action. These populations are presumed to suffer different levels of density-independent mortality due to the wave exposure characteristics of the sites. The sheltered site population shows no significant differences between the two years of study. Interpopulation differences in age and size structure, growth rate, population breeding phenology and breeding sizes are slight. However the sheltered population shows increased adult survival and longevity, decreased weight specific fecundity and reproductive allocation, and increased brood-pouch mortality. Because winter survival is high, when mortality due to wave action is expected to be severe, this factor is rejected as an important determinant of the life history. The reduced survival at the exposed site can be interpreted as a consequence of the increased reproductive allocation by individuals at this site.

The majority of females are semelparous, but within both populations two distinct waves of breeding activity occurred each year. Larger, faster growing individuals breed at the end of their first year, LATE in the season, and have high weight specific fecundities and low absolute and weight specific egg sizes. Smaller, slower growing individuals delay reproduction and breed in their second year, EARLY in the season. Although gaining greatly in size through growth the effect on fecundity is offset by a decrease in weight specific fecundity and parallel increases in absolute and weight specific egg size.

The following trade-offs are recognised for individual female Ligia : between growth and reproduction (within breeding groups), growth and reproduction (between breeding groups), reproduction and survival (between breeding groups), weight specific egg size and weight specific fecundity (between breeding groups), and between absolute egg size and fecundity (within breeding groups). Two possible life history strategies are recognised. (i) An ability of a female parent to alter egg size seasonally may optimise total offspring fitness in the different environments they experience. (ii) An ability of small, mature females to delay reproduction until the following year may also increase their fitness. By assuming that offspring survival is related to egg size it is possible to model this tactic. The population breeding phenology is seen as a direct consequence of the life history and has the indirect effect of stabilizing the population. The ability of individual females to vary their life history traits depending on individual circumstances (size and season) may represent a flexible approach to the environment which is not envisioned in the more formal models of life history evolution.

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ABBREVIATIONS

Abbreviations of test statistics follow Sokal & Rohlf (1969, 1981) unless stated otherwise.

Energy flow terminology follows I.B.P. nomenclature (Petrusewicz & MacFadyen, 1970).

S.I. units have been used throughout.

The following abbreviations have been used in the text :

R.H.B.	Robin Hood's Bay
DW	Dry weight
AFDW	Ash-free dry weight
ANOVA	Analysis of variance
ANCOVA	Analysis of covariance

Other abbreviations are defined where used in the text.

The sea-slater <u>Ligia oceanica</u> (Linnaeus, 1767), male, about 22mm head to telson length. This specimen illustrates the marking technique described in Chapter 2. Small drops of cyanoacrylate ester are applied from a syringe needle to the dorsal segments, followed by small drops of cellulose paint. Four marks are illustrated : red, yellow, purple and orange. This animal has recently moulted the posterior part of its exoskeleton.

GREENAWAY

I know so well this turfy mile,
   These clumps of sea-pink withered brown,
The breezy cliff, the awkward stile,
   The sandy path that takes me down.

To crackling layers of broken slate
   Where black and flat sea-woodlice crawl
And isolated rock pools wait
   Wash from the highest tide of all.

I know the roughly blasted track
   That skirts a small and smelly bay
And over squelching bladderwrack
   Leads to the beach at Greenaway.

Down on the shingle safe at last
   I hear the slowly dragging roar
As mighty rollers mount to cast
   Small coal and seaweed on the shore,

And spurting far as it can reach
   The shooting surf comes hissing round
To heave a line along the beach
   Of cow~~a~~ries waiting to be found.

Tide after tide by night and day
   The breakers battle with the land
And rounded smooth along the bay
   The faithful rocks protecting stand.

But in a dream the other night
   I saw this coastline from the sea
And felt the breakers plunging white
   Their weight of water over me.

There were the stile, the turf, the shore,
   The safety line of shingle beach
With every stroke I struck the more
   The backwash sucked me out of reach.

Back into what a water-world
   Of waving weed and waiting claws?
Of writhing tentacles uncurled
   To drag me to what dreadful jaws?

Sir John Betjeman
A few late Chrysanthemums (1954)

CHAPTER 1

LIFE HISTORIES AND WOODLICE

1. INTRODUCTION

A species life history is made up of a large number of traits which are linked, more or less immediately, to the reproductive success and fitness of the organism. The sorts of trait we can consider include degree of iteroparity, longevity, age at first breeding, reproductive effort, fecundity, egg size, parental care, growth rate, body size, breeding seasonality, resistance to starvation and survivorship. These traits can be summarised by age-specific schedules of fecundity and survival probabilities. The influential paper by Pianka (1970) was especially important because it drew attention to the idea that such traits might represent a coevolved adaptation or strategic response to a particular factor or group of factors. Stearns (1976, 1977, 1980) has reviewed the theories of life history evolution and made general criticisms of their assumptions and standing as scientific theories. Charlesworth (1980) has also summarised many of these theories and stressed the genetical aspects. Rose (1983) has reviewed the "fundamental presuppositions" that life history theorists have made, implicitly or explicitly, in formulating their ideas, and the evidence for and against these presuppositions.

In this chapter I give a very general introduction to the various classes of theory of life history evolution which can be tested with, or compared to, field and laboratory data. The population dynamics of woodlice, and the relation of these animals to life history theory, is also reviewed briefly.

2. LIFE HISTORY STRATEGIES

i. r- and K-selection and related matters

Of the variety of theories of life history evolution the most popular and generally known is that of r- and K-selection. It is frequently the only theory given any substantial discussion in ecology texts (eg Krebs, 1978; May, 1981; Begon & Mortimer, 1981). As originally formulated by MacArthur (1962) and MacArthur & Wilson (1967) it described the fitness of genotypes under different degrees of crowding, specifically the conditions to be found on islands following colonisation. They argued that where population density was low, immediately following colonisation, the fittest genotypes would be those which maximised "r", the intrinsic rate of increase. When conditions become resource limited, that is when the population has approached "K", the carrying capacity of the environment, genotypes which are most efficient at converting the limited available resources into successful offspring will be favoured. Under conditions of population growth r-selection will operate, while under constant density or equilibrium conditions, K-selection will operate, where "r" and "K" are parameters derived from the familiar logistic equation of population growth (Pearl & Reed, 1920). Pianka (1970) pointed out that a continuum would exist between r- and K-selected species, dependent on the proportion of time the populations spent under resource abundant and resource limited environmental conditions. He also listed those ecological and life history attributes likely to be characteristic of species under r- and K-selection. Roughgarden (1977) has termed these predicted attributes the "lore" of r- and K-selection, emphasising their lack of rigorous derivation (Caswell, 1982a).

The concept was broadened by the admirable attempt to link the processes which regulate population numbers with the evolution of life histories. This extension of the original theory envisaged that populations regulated by high levels of density-dependent mortality should be K-selected while those which show poor regulation, due to high levels of density-independent mortality, should be r-selected (Roughgarden, 1971; Gadgil & Solbrig, 1972; Pianka, 1970, 1972). Hence a connection was made between the type of mortality experienced and the position of the species on the r-K continuum. This has, I believe, become the basic understanding of the terms r- and K-selection amongst ecologists (see also Stearns, 1976, 1977; Parry, 1981).

While the theoretical genetics of density-independent and density-dependent selection for life histories is well established (Roughgarden, 1971; Charlesworth, 1971, 1980, 1984), the ecological basis of the arguments underlying r- and K-selection theory have been severely criticised. Wilbur, Tinkle & Collins (1974) pointed out that the nature of the density-dependent control of the population is important. The theory only holds if, under density-dependence, resources are limited. If density-dependent predation acts to maintain the population at a level below significant over-exploitation of resources, then r-selection should still result.

The theory of MacArthur & Wilson (1967) was framed in terms of discrete generations lacking age stucture. The most forcible criticisms of the theory emphasise the importance of age-structure on the outcome of selection (Wilbur et al. 1974; Mertz, 1975; Charlesworth, 1980). Many considerations of life history evolution (eg Charnov & Schaffer, 1973; Schaffer, 1974b; Stearns, 1976; Michod, 1979) have stressed that the life history resulting from selection depends on the age-specificity of the mortality. The relative levels of density-independent or density-dependent mortality are seen as irrelevant for the evolution of the species' life history. What is important is the distribution of mortality, of whatever source, with age (Schaffer, 1974b; Charlesworth, 1980).

r- and K-selection theory has also been criticised for not incorporating explicitly the nature of constraints or trade-offs between life history variables (eg Stearns, 1976), which are the basis of so many models of the evolution of various aspects of life histories (Calow, 1979; Law, 1979a,b; Rose, 1983). Pianka (1970) does mention the concept but, because the life history may depend critically on the form of the functional relationship of the life history trade-offs (Stearns, 1976, 1977; Law, 1979a), its omission is serious.

Although MacArthur & Wilson (1967) used the logistic model of population growth, the outcome of selection is probably not too sensitive to the functional form of the density-dependence (Charlesworth, 1971). However Begon (1984) has pointed out the possibility that while a population may be severely resource limited, and density regulated, those individuals which reproduce successfully might all enjoy abundant resources through good fortune in a spatially and temporally heterogeneous environment. In these circumstances the effect of density-dependence on life history evolution would be slight.

An additional failing of the theory is that it takes no account of stochastic variations in offspring recruitment which have been shown to have very different effects on the fittest life history (Murphy, 1968; Schaffer, 1974a) to those suggested by r- and K-selection theory (Stearns, 1976, 1977).

Green (1980) has pointed out the importance of one of the corollaries of r- and K-selection in determining the outcome of selection. This proposes that K-selected species should have stable, equilibrium populations, whereas r-selected species should have non-equilibrium populations. This may also be invalid. Non-equilibrium populations which spend the majority of time in decline, with occasional rapid increases, should have individuals with even more K-selected life histories than those in equilibrium populations (Caswell, 1982a). Only in populations which spend most of their time growing, but which suffer occasional catastrophic mortality, should r-selected attributes be apparent (Green, 1980; Caswell, 1982a).

In a related argument Istock, Vavra & Zimmer (1976) have suggested that the ability of a population to track the available resources may also be important. Density-dependence is rarely perfect due to rapid and unpredictable fluctuations in resource abundance, demographic delays, or the delayed response of predators. Even under strong density-dependence populations may experience periods of resource abundance and shortage which are likely to have complex affects on the component life history traits (Istock, Vavra & Zimmer, 1976; Istock, Zisfein & Vavra, 1976; Istock, 1981). This is especially probable in seasonal environments where reproduction is likely to occur in a period of resource abundance following mortality, perhaps density-dependent, during less favourable seasons.

For all these reasons the theory of r- and K-selection has been rejected by many prominent ecologists (Schaffer, 1979; Charlesworth, 1980; Stearns, 1983a). However the criticisms detailed above have not prevented authors from extending the theory, or at least the terms, further. One of the correlates of the r-K continuum is with the environment (Cody, 1966; Pianka, 1970; Stearns, 1976). Environments which are either severe or unpredictable are thought to impose a greater load of density-independent mortality, and hence the theory has been extended to include a consideration of the severity, stability and predictability of the environment as possible selective components (Parry, 1981). Southwood et al. (1974) proposed that the durability of the habitat (defined as the ratio of the generation time to the duration of the favourable period) was directly related to the selection of r- and K- life histories. Where this ratio is small (significantly less than unity) each generation can be affected by the resource exploitation of previous generations, and K- selection should operate. Where this ratio approaches unity populations can severely overexploit their available resources without affecting subsequent generations, and r-selection should operate.

These ideas have been further elaborated by several authors who identify a third evolutionary force, "stress" (Grime, 1977) or "adversity" (Southwood, 1977; Greenslade, 1983) selection, a term first used by Whittaker (1975). These authors recognise that certain physical environments may be more stressful than others, and that species inhabiting them should devote more resources to maintenance, and hence less to reproduction, than similar species in more equable habitats where competition may be more important. In stressful habitats species take advantage of periods of favourable conditions where reproductive success is likely. Adversity selected species have the same characteristics as K-selected species but the selective force is physical rather than biological. Habitats which are both stressful and unpredictable are seen as being biologically untenable (Greenslade, 1983).

These developments of the original r- and K- theory take little account of the criticisms detailed above. Southwood et al. (1974) define habitat durability relative to generation time as a selective force, yet the generation time of a population is the outcome of selection on such characteristics as survivorship, age at first reproduction and degree of iteroparity, which are the traits whose evolution we are trying to explain. I see adversity selection as an attempt to reconcile the r- and K- and bet-hedging (see below) theories of life history evolution without addressing the problems inherent with both theories (see also Horn, 1978).

Although r-, K- and adversity selected may be useful tags to attach to a combination of life history traits we observe in a species we should perhaps be careful to use them as no more than labels until we have a better understanding of the underlying selective processes. In reviewing the empirical evidence Stubbs (1977) found no simple relationship betwen r- and K- species, as defined by their life history traits, and the intensity of density-dependence experienced. Indeed, the density-dependence was found to act in a different, age-specific fashion within each group.

ii. Bet-hedging and stochastic models

r- and K- selection and the optimality models described in the next section are completely deterministic : various schedules of age-specific extrinsic mortality (ie that not due to the trade-off with reproduction) have only minor effects on the timing and distribution of reproductive effort (Gadgil & Bossert, 1970; Schaffer, 1974b). They are quite different to those models which Stearns (1976) termed "bet-hedging".

Murphy (1968) first examined the consequences of variations in pre-breeding survivorship on the fitness of perennial life histories. He showed that where recruitment success of an individuals offspring into the breeding population is variable then increased iteroparity should be favoured. Schaffer (1974a) and Schaffer & Gadgil (1975) reached similar conclusions, while Calow (1973) in a related argument considered the effects of perturbations in food supply on growth and reproduction in systems with semelparous and iteroparous phenologies. Bell (1980) emphasized that it is the ratio of adult to juvenile variability in survival that is important. In particular Schaffer (1974a) incorporated the trade-off between reproductive effort and survival in a model to examine variations in both adult survivorship and reproductive success. For an iteroparous species variations in post-breeding survival favours a greater reproductive effort and reduced iteroparity, while variations in recruitment success favours reduced reproductive effort and greater iteroparity. For semelparous species variations in reproductive success favours a polymorphic population in which only a fraction of individuals in the population breed in any one season. The mosquito Wyeomyia smithii might represent an example of such a strategy (see Istock, 1981).

Stearns (1976), in his excellent review, contrasted those life history traits he would expect of species inhabiting stable and fluctuating environments as a result of r- and K-selection (leaving aside any criticisms of defining the action of selection in these environments) and bet-hedging theories of life history evolution. He found that the predicted traits were exactly reversed in the two cases. Those traits he listed for the bet-hedging hypothesis could be called the "lore" of bet-hedging, for they are not derived from the work of Murphy (1968) and Schaffer (1974a), who focus on the mortality experienced, the degree of iteroparity and reproductive effort. In particular such features as fecundity and maturity are not considered in their models. Stearns views of high fecundity associated with a bet-hedging strategy seem to stem from rather different ideas presented by Mountford (1973).

In a recent extension of these ideas Lacey et al. (1983) have suggested that an organism may increase its fitness by incorporating a degree of variability in some other life history traits, such as investment per offspring.

Problems with the bet-hedging approach centre on the genetics of selection in age-structured populations experiencing frequent periods of environmental change (Charlesworth, 1980). In addition Hastings & Caswell (1979) have emphasized the problems of adequately defining fitness in stochastic models of this type. They show that the effect of variable survival depends on the fitness criteria used, and that under certain assumptions the predictions of Schaffer (1974a) can be reversed.

iii. Reproductive effort and optimality models

Cole (1954) demonstrated that a large evolutionary advantage could be realised at little cost by an iteroparous species becoming semelparous and he posed the perplexing problem of why iteroparity is of such widespread occurrence. Murphy (1968) pointed to one possible explanation. However Charnov & Schaffer (1973) generalised Cole's result to include different levels of juvenile and adult mortality, and stressed the importance of the age-specificity of the mortality in determining the optimal life history. They showed that the evolution of semelparity will be favoured if

P/Y or more extra offspring can be added to the brood at a cost of no future expectation of offspring, where P/Y is the ratio of parental to offspring survival rate. They argued that since P/Y is generally large the evolution of the perennial phenology is much more likely. Hence these authors emphasized two important points, the age-specificity of the mortality imposed by the environment and the significance of costs associated with different levels of reproduction. I disagree with Bell (1980) that these models imply the existence of no costs associated with greater levels of reproduction. More recently and generally Rose (1983) has remarked on the importance of trade-offs between variables as being the only theoretical basis of life history evolution supported by the available evidence.

The costs of reproduction have been formalised in the concept of reproductive effort (but see Bell, 1980), which has become so important in evolutionary population ecology. The term was first used by Williams (1966a,b), though the idea can be traced to Fisher (1930). Organisms are viewed as having limited resources at their disposal which have to be allocated between competing processes. Those resources devoted to reproduction comprise the reproductive effort. Assuming a constant resource budget (Hirshfield & Tinkle, 1975) any increased allocation to reproduction entails a reduced allocation to other processes on which survival depends. Thus greater reproductive effort may increase present reproductive value but at the expense of lowered residual reproductive value through decreased survivorship and/or reduced fecundity (Williams, 1966a; Gadgil & Bossert, 1970; Calow, 1979).

The trade-off between current reproductive effort and future reproduction has been the basis of a number of models of life history evolution (eg Cody, 1966; Gadgil & Bossert, 1970; Schaffer, 1974a; Schaffer & Gadgil, 1975). Particularly important have been those models which have used a trade-off between reproductive effort and future reproduction in models of age-structured populations (Charlesworth, 1980). In these models reproductive value (Fisher, 1930), or more properly Schaffer's modified reproductive value, has been maximised for each age class in growing populations (Schaffer, 1974b, 1983; Taylor et al. 1974; Schaffer & Rosenzweig, 1977; Caswell, 1982b) and has been extended for the case of density-dependence (Charlesworth & León, 1976; León, 1976; Michod, 1979). Although the equivalence of maximising reproductive value with fitness (as population growth rate or increase in gene frequency) has been criticised (Caswell, 1980), this was based on a misunderstanding (Yodzis, 1981; Schaffer, 1981).

These optimisation models predict the evolution of iteroparity or semelparity dependent on the nature of the functions relating fecundity and survival to reproductive effort. Unfortunately for species with very limited degrees of iteroparity, such as woodlice, it is generally not possible to measure the form of these functions. Indeed they have not been measured for any species. Schaffer & Rosenzweig (1977) have shown that, depending on the nature of these functions, there may be more than one life history strategy each of which is locally, if not globally, maximal for semelparous species.

For iteroparous species the effort devoted to reproduction at each occasion but the last should be sub-maximal. Gadgil & Bossert (1970) suggested that reproductive effort should increase with age in iteroparous species, but others (Charlesworth & León, 1976) have shown that the exact relationship with age again depends on the assumptions made. Thus for two species whose individuals have identical resource budgets that which is semelparous should have a higher reproductive effort than the iteroparous counterpart. (Abrams (1983) has examined a model of life history strategies where individuals may increase their energy budgets at the expense of decreased survivorship and to the detriment of the remainder of the population.) For species where the prospect of an individuals survival to reproduce again in the future is grim, reproductive effort should be maximal and suicidal. Hence the cause of mortality is shifted from one extrinsic to the individual to being intrinsic to it (Michod, 1979). It seems clear from the above considerations that where juvenile survival is either poor and/or variable, relative to adult survival, iteroparity should be favoured and be accompanied by lower levels of reproductive effort. Mortality of newly released woodlice is generally regarded to be high (eg Sutton, 1972). It seems likely that mortality and its variance will always be closely correlated making the distinction between selection of life histories due to these two components difficult.

While most models of optimal life histories examine the relationships between age, survivorship schedule, age at maturity and reproductive effort (Charlesworth, 1980), it seems unlikely that a single trade-off between reproduction and survival is sufficient to account for all patterns of life histories. In particular it is unreasonable to assume that trade-offs with reproductive effort per offspring are not an important component of fitness through an effect on juvenile survival (Smith & Fretwell, 1974; Brockelman, 1975). Sibly & Calow (1983) have made a start on this problem by considering the life histories resulting from the trade-offs between pairs of five life history variables, including effort per egg.

Other suggested influences on species life histories include the possible gains in fitness to be derived from an ability to respond flexibly to unexpected conditions (eg Hirshfield & Tinkle, 1975; Nichols et al. 1976; Goodman; 1979; Boyce, 1979). The theroretical basis of these ideas, particularly the genetics of the selection, are incompletely understood.

3. WOODLOUSE LIFE HISTORIES AND POPULATION DYNAMICS

Since Heeley (1941) presented basic data on aspects of the life histories of certain species in the laboratory there have been many more detailed studies of the population biology of isopods. Of these the studies on the terrestrial woodlice are much more precise, reflecting the difficulties of sampling the more vagile marine species. However there have been good studies on the marine isopods Cirolana harfordi (Johnson, 1976a,b) and C. imposita (Shafir & Field, 1980a,b).

Interest in woodlice has centred on describing their population dynamics and speculating on possible methods of regulation of their populations. The terrestrial pillbug Armadillidium vulgare has received most attention. The population dynamics of this species have been studied by Paris & Pitelka (1962) and Paris (1963), Davis (1978), Al-Dabbagh & Block (1981), Miller & Cameron (1983) and M. Hassall (pers. comm.). This species is the only one whose reproductive strategy has been considered, in the excellent papers by Lawlor (1976a,b) and Brody, Edgar & Lawlor (1983). Al-Dabbagh & Block (1981) compared the life history characteristics of two, and Miller & Cameron (1983) three, populations of this species.

The population dynamics and life history of Trichoniscus pusillus (sensu lato) has also received much study by Sutton (1968), Standen (1970, 1973) and Phillipson (1983). Philoscia muscorum has been studied by Sutton (1968) and Sunderland, Hassall & Sutton (1976). McQueen & Carnio (1974) and McQueen (1976a,b) made a thorough study of Porcellio spinicornis, and McQueen (1976c) Tracheoniscus rathkei. The population biology of the following species has also received some attention : Ligidium japonica (Saito, 1965, 1969), L. hypnorum (Stachurski, 1968, 1972), Porcellio scaber (Davis, 1970), P. laevis (Nair, 1984), and the desert dwelling Hemilepistus reaumuri (Shachak, 1980).

The maritime slaters of the genus *Ligia* have received substantial attention. Species occur in the supralittoral zone on shores worldwide and the temperate species appear to occupy very similar habitats (see Jackson, 1922). The ecology of *L. oceanica* was first studied by Nicholls (1931a,b), and more recently the population biology has been considered further by Jöns (1965) in Germany, and Mocquard, Picaud & Besse (1974) and Besse, Picaud & Mocquard (1975) in France. However there has been no detailed study of the population dynamics of this species. The population biology and ecology of *L. pallasii* on the Canadian west coast has been studied by Carefoot (1973a,b, 1979), while Koop & Field (1980, 1981) have detailed the population biology and energetics of the southern African *L. dilatata*.

i. Population regulation

While most authors have stressed the stability of the populations they have studied (eg Paris & Pitelka, 1962; Sutton, 1968; Sunderland *et al*. 1976; McQueen, 1976a,b,c) mild controversy has simmered over the mode of regulation enjoyed by these populations. Many authors have emphasised the importance of climate. Paris (1963) suggested that weather acted in a density-dependent manner through competition for suitable refuges, and Stachurski (1968) presented further evidence for the importance of shelter sites. Sutton (1968) found that drought prevented reproduction during one summer, but by sheltering deep in the soil, coupled with enhanced breeding and survival, the population structure was immediately re-established. McQueen & Carnio (1974) and McQueen (1976a,b) suggested, on the basis of simulation models based mostly on laboratory data, that population numbers are determined solely by the effect of temperature on growth, reproduction and survival, and that yearly average temperature is sufficiently constant for population persistence. A similar approach on another species (McQueen, 1976c) did not support this hypothesis as a general mechanism of woodlouse population regulation.

Food availability has been suggested as a factor regulating populations of Ligidium hypnorum (Stachurski, 1972) and Ligia dilatata (Koop & Field, 1980). Koop & Field (1980) found that individual growth was greatest during the cooler winter months when the availability of their food was high. Since fecundity depends on the size achieved, any factor which determines growth can affect future population size. However Paris (1963) found no effect on the population structure of Armadillidium vulgare from the addition of their preferred food, and concluded that food availability was unimportant to these populations. However many authors have shown that food quality may also be an important factor in determining growth (Merriam, 1971; Rushton & Hassall, 1983).

Sunderland et al. (1976) described a phenomenon they termed "cohort-splitting", whereby animals born in any one year grow at two distinct rates and, as a result, breed at different times. They suggested that cohort-splitting should contribute to the stability of woodlouse populations. That this and similar types of phenomena can result in a degree of population stability was first suggested by Murdoch (1966), and has been suggested for other woodlouse species (Phillipson, 1983; Al-Dabbagh & Block, 1981).

Predation has not been proposed as a factor regulating woodlouse populations. Although a wide range of invertebrate predators may feed on woodlice in the field (Sunderland & Sutton, 1980), predation has not been shown to be an important source of mortality of healthy woodlice.

In determining the mode of regulation enjoyed by a population, and the manner of its operation, we gain an idea of the types of selection acting on individuals. There is apparently no general mechanism of woodlouse population regulation, and so no obvious common factor presents itself here, apart from the apparent stability of their populations, to select their life histories.

ii. Life histories

Although the costs associated with reproduction are a fundamental feature of life history evolution (Rose, 1983), only Lawlor (1976a,b) has attempted to determine these for a woodlouse, even though many authors have examined species life history traits (eg Al-Dabbagh & Block, 1981; Miller & Cameron, 1983; Rushton & Hassall, 1983). Lawlor (1976a,b) studied the reproductive strategy of *Armadillidium vulgare* and noted that woodlice which reproduce do not grow as much as those which do not (Hubbell, 1971). As a consequence of this trade-off between reproduction and growth, he showed that isopods should breed earlier and twice in a summer, or later and only once, dependent on their size. Recently it has been shown that survival is also size related in this species (Brody *et al*. 1983), so that retarded growth and survival are both costs of reproduction for *A. vulgare*. The occurrence of substantial post-reproductive mortality of woodlice has been commented upon by a number of field workers (Sutton, 1968; Sunderland *et al*. 1976; Al-Dabbagh & Block, 1981).

A. vulgare is the only species which is convincingly iteroparous (Paris & Pitelka, 1962; Lawlor, 1976a,b), though not in all populations studied (eg Weeting Heath, Al-Dabbagh & Block, 1981). Although many species are capable of breeding more than once under laboratory conditions (eg Heeley, 1941), the evidence of second broods in field populations is difficult to determine. The picture is confused by the complex pattern of breeding shown by many woodlouse populations(eg Standen, 1973; Carefoot, 1973b; Besse *et al*. 1975; Sunderland *et al*. 1976; Davis, 1978; Phillipson, 1983). Within these populations there are frequently two peaks of reproduction due to animals of different ages. Unfortunately too little attention has been paid to distinguishing a second wave of breeding within a population from second broods produced by individuals within that population. Where this distinction has been recognised (eg Besse *et al*. 1975; McQueen, 1976a,c; Phillipson, 1983) the proportion of individuals which manage to produce second broods appears to be only a few percent. Even in the enormous marine species Glyptonotus antarcticus only 1-2% breed twice (White, 1970). I term such species "essentially semelparous". However the small numbers successfully producing second broods may be important in determining the species life history. Sutton (1968) and Sutton et al. (1984) have suggested that the ability of individuals to produce second broods during periods of favourable conditions may allow woodlice populations to respond quickly to such conditions. That species life histories should not be inflexible, but able to respond to unexpected conditions, has been suggested by some authors (eg Hirshfield & Tinkle, 1975; Nichols et al. 1976).

Stearns (1976, 1977) and Clutton-Brock & Harvey (1979) have emphasized the importance of intra-specific and inter-specific comparison in determining what features are adaptive. The lack of data, especially on reproductive effort, for woodlice (apart from that of Lawlor, 1976a) makes inter-specific comparison of woodlouse life histories as adaptations difficult (but see Sutton et al. 1984). Stearns (1976) recommended that, ideally, comparisons should be on a controlled, inter-population basis with defined expectations, but in a later review (Stearns, 1980) noted that such studies had been less successful at detecting strategies than broader, inter-specific comparisons at higher taxonomic levels. However there have recently been some more rewarding intra-specific studies (eg Schaffer & Elson, 1975; Leggett & Carscadden, 1978; Law et al. 1977; Law, 1979b; Ballinger, 1979; Constantz, 1979; Alon & Stancyk, 1982; Berven, 1982; Stearns, 1983a,b) and, given the lack of adequate comparable data on other isopod species, is the approach taken here.

Two populations of Ligia oceanica (Linnaeus, 1767) experiencing similar environmental conditions but differing in a defined way have been studied. The response of the populations to this factor, and the life history traits displayed by individual females, are examined for evidence of any tactical response to individual circumstances. It is hoped in this way to at least arbitrate between some of the premises on which some theories of life history evolution are based, as well as providing basic data on this, the largest species of British woodlouse.

CHAPTER 2

POPULATION DYNAMICS AT AN EXPOSED SITE AT ROBIN HOOD'S BAY

1. INTRODUCTION

Ligia oceanica is one of the characteristic animals of the upper littoral or supralittoral zone of rocky shores, and members of this genus occur in this zone worldwide (see Jackson, 1922). The upper littoral is generally regarded as having an extreme physical environment (Lewis, 1964). Periods of tidal immersion are more variable higher up the shore, and periods of warm and sunny weather coinciding with neap tides can result in hyperosmotic sea water or total aridity. In contrast torrential rain can lead to inundation by fresh water. Hence desiccation and osmotic stress can be sudden and extreme. In addition the rock surface of the shore can experience strong wave and wind exposure. Such conditions might be expected to have a substantial affect on the population dynamics of species inhabiting this zone by exerting a high level of density independent mortality.

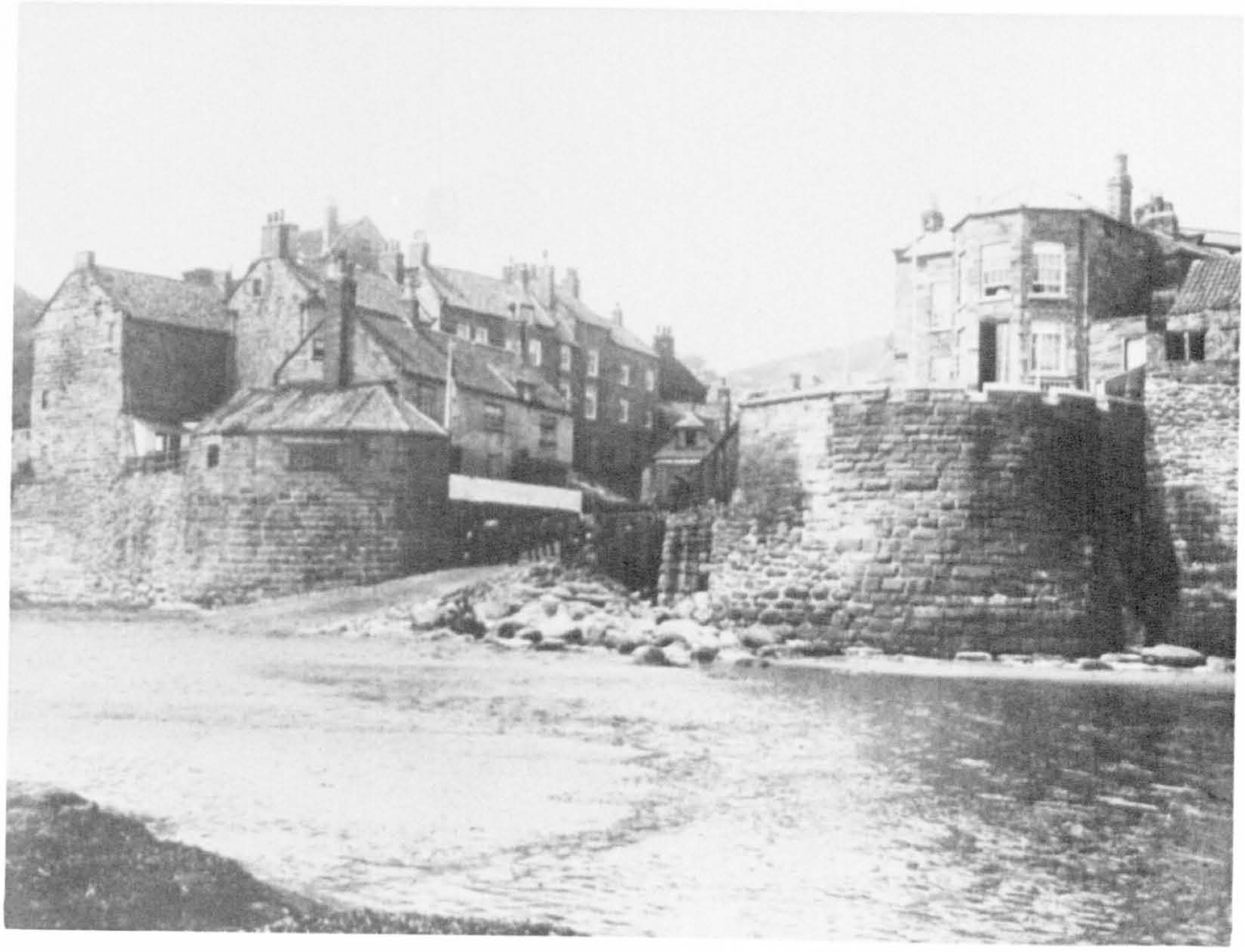
Although the value of studies lasting only three years, such as this, is limited (Lewis, 1976), these limitations are less severe if the species being studied is short lived. Hence it should be possible to gain an impression of the type of dynamics experienced by populations subject to such extreme conditions.

PLATE 3

Robin Hood's Bay photographed in 1886 by Francis Frith, showing the nature of the sea wall protecting the Bay Hotel has changed little in recent times.

PLATE 2

Robin Hood's Bay photographed in 1981 by the author, showing the sampling site on the Bay Hotel wall. The site occupies the lower two metres of the wall. The presence of a stream isolates the population from an adjacent small population on the wall of the former Wellcome Marine Laboratory across the slipway.



2. SITE DESCRIPTION

The sampling site at Robin Hood's Bay on the east Yorkshire coast (G.R. NZ 953 049) is a sea wall, shown in Plate 2 and diagrammatically in Fig 1. The wall is made up of large irregular stone blocks with mortar in-between. Where the mortar has been eroded cracks between the blocks lead to deep crevices in which Ligia reside during the day, safe from predation and wave action. The wall is 24.7 m long and tapered so that the point most distant from the sea is 2.4 m high, and that nearest 8.2 m high, giving a total planar area of 123.8 m^2. The mean height above chart datum is about 7 m, and the majority of the habitat lies above M.H.W.S. (5.4 m). The site is exposed to fairly severe wave action (Lewis scale 2-3, Lewis, 1964).

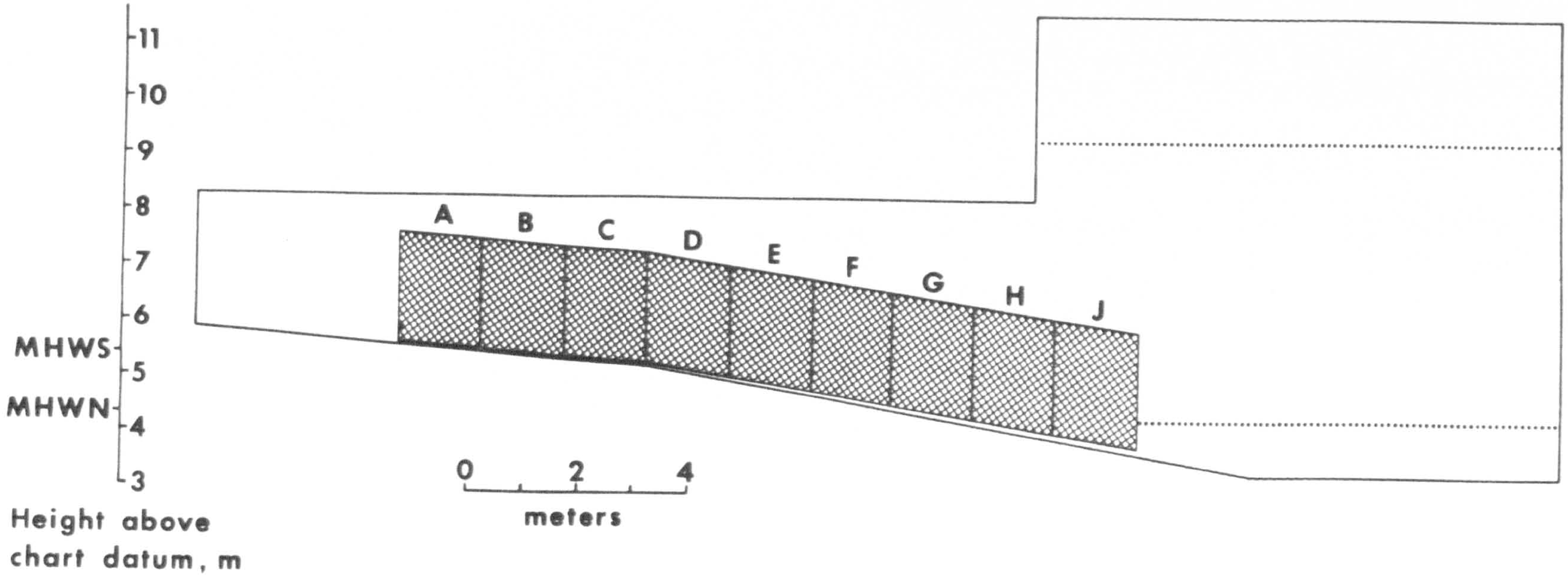
The sea wall is bounded on all sides by unsuitable habitat. Above lies the Bay Hotel, a free house, while below a stream runs along the base of the wall preventing any migration to or from an adjacent population across the slipway. To the north lies a very extensive concrete sea wall devoid of crevices and upon which Ligia have never been observed. To the southwest the wall disappears into a culvert from which the stream emerges. Hence the population is closed to immigration and emigration.

Occasional hazardous surveys by ladder at night showed that Ligia do not occur all over the wall. Particularly the higher and lower parts are not used. The approximate distribution of Ligia is shown by the dotted lines in Fig 1. The total area of utilised habitat is 95.7 m^2 of planar surface.

From April 1981 temperature was recorded continually by means of a thermocouple embedded in rock at mid-shore level, adjacent to the sampling site. The mean weekly minimum temperature of the rock when exposed by the tide is shown in Fig 2. This might best equate with the temperatures experienced by Ligia on a rock surface at night.

FIGURE 1

Diagrammatic plan of the Bay Hotel wall sampling site at Robin Hood's Bay. See also Plate 2.



Diagrammatic plan of the Bay Hotel wall sampling site at Robin Hood's Bay

FIGURE 2

Mean weekly minimum night-time rock temperature at Robin Hood's Bay at mid-shore level.


TEMP, °C
15
10
5
0
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
1981
1982

Photographs taken by Francis Frith in 1886 show the sea wall to be essentially unchanged, except for the addition of some mortar (compare Plates 2 and 3). The *Ligia* population is probably long established on this man-made site and has had a substantial period in which to become adapted to the local conditions. The east coast of Yorkshire is comprised largely of glacial drift overlying Jurassic shales which are eroding rapidly (Agar, 1960). This is not suitable habitat for *Ligia* which is confined to isolated sea and harbour walls in this area.

3. POPULATION DENSITY AND STRUCTURE

i. Sampling Methods

The area sampled was 2 m x 13.5 m situated at the base of the sea-wall. This was divided into 108 planar quadrats approximately 0.5 m x 0.5 m square, the corners of each quadrat being permanently marked by a small dot of shore paint. The actual surface area of any quadrat varied, depending on the irregular nature of the wall's surface. The sampling area was divided vertically into 9 blocks of 12 quadrats (see Fig 1) so that stratified random samples could be taken. On each sampling occasion 3 quadrats were selected at random from each block of 12, giving a total of 27 samples.

Sampling was done at night, when the animals emerge to feed, commencing about one hour after sunset but to some extent dependent on the tides. Ligia seemed not to react to the low intensity torch used. All animals within a quadrat were collected except for an unknown proportion remaining within the crevices (see section 4.iv). Juveniles less than 3-4 months of age were too small to be collected until autumn (see section 6.ii). The animals in each sample were stored overnight in 75 cm^3 containers at 10°C on filter paper moistened with sea water. This allowed time for the animals to reach a standard water balance prior to weighing. The water content of Ligia can fluctuate dramatically dependent upon recent conditions (Edney, 1951,1954; Numanoi, 1934). The following day individuals were weighed to 0.1 mg and sexed. Reproductive and moulting states were noted for each, as were injuries : all were returned to their quadrat of capture that evening. Hence sampling was non-destructive : extremely important when dealing with a small population. Only rarely (<1%) did animals die in the laboratory.

The sampling interval was approximately monthly from July 1979 to October 1982. However samples were taken more frequently during the summer months, while during the winter sampling was often prevented by low temperatures and strong winds, under which conditions Ligia do not emerge from their refuges.

For size-frequency analysis it was often necessary to combine data from samples collected on two, or occasionally three, adjacent nights to obtain the large number of animals desirable for statistical analysis.

ii. Results

a) Spatial Distribution

Like the majority of other organisms studied (Southwood, 1978a) isopods are frequently aggregated (Allee, 1926; Friedlander, 1965). Likewise the distribution of Ligia has been found to be contagious. Using the Poisson Index of dispersion (Seber, 1973; Southwood, 1978a) :

$$I_D = s^2.(n-1)/\bar{x}$$

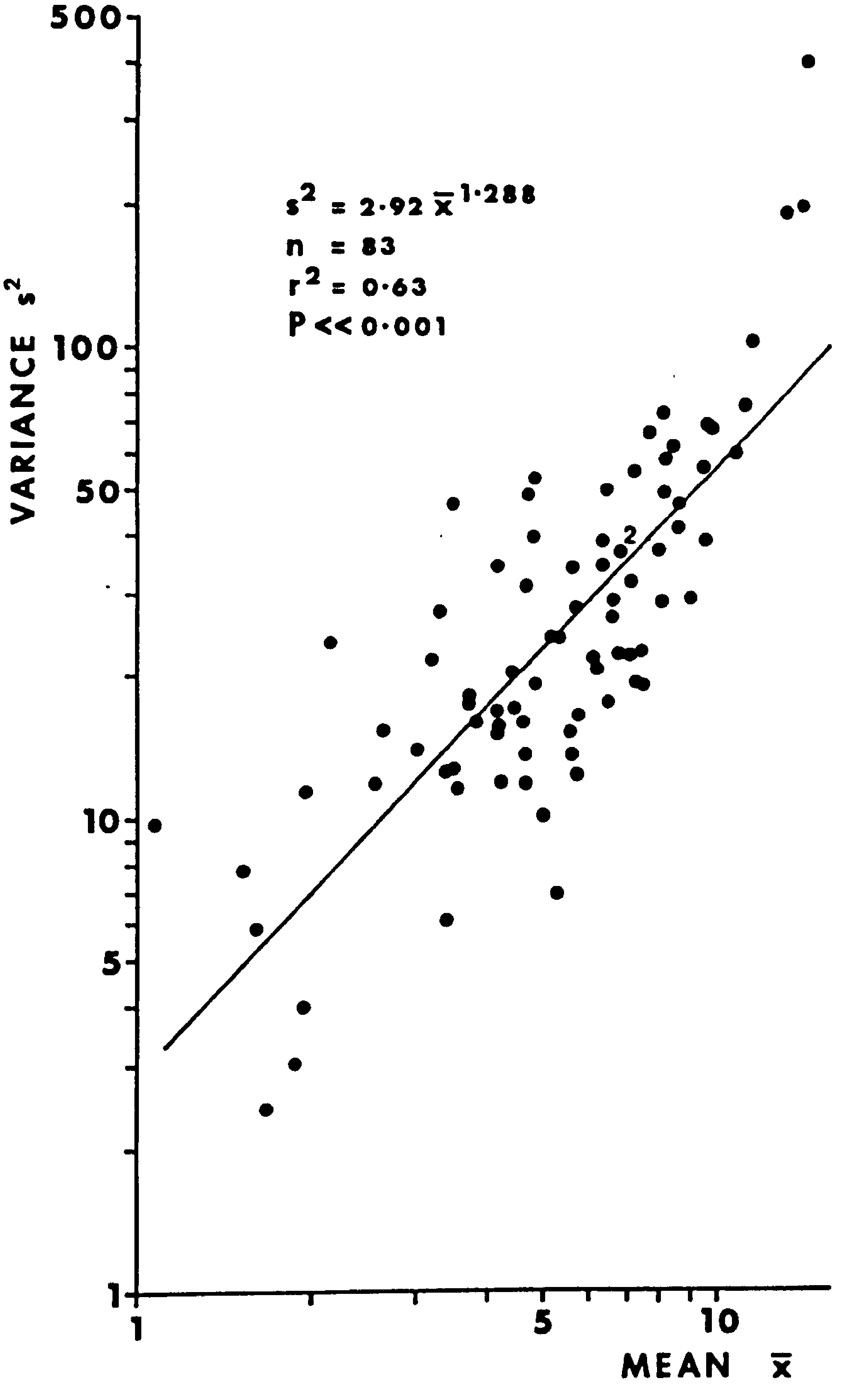
where n = number of samples, s^2 = variance and $\bar{x}$ = mean. Of 83 sampling occasions all but one gave a value for I_D very much greater than that of χ^2 for $P = 0.05$ with n-1 degrees of freedom, indicating a significant departure from a Poisson distribution.

Applying Taylor's Power Law (Taylor, 1971; Taylor, Woiwod & Perry, 1978) to the data gave a value for b of 1.29 (Fig 3). The slope of the line is regarded as an index of the aggregation characteristic of the species (Southwood, 1978a). However, whatever statistic is used to measure the degree of aggregation or contagion the result reflects one or more of the following :

a) The inherent tendency of the species to aggregate (Taylor et al., 1978)
b) The heterogeneous nature of the habitat, with some areas being more suitable than others (Allee, 1926; Farr, 1978).
c) The quadrat size (Seber, 1973).

FIGURE 3

Taylor's power law plot of variance of mean against mean number of isopods per 0.5m x 0.5m square quadrat.


$s^2 = 2{\cdot}92\,\bar{x}^{1{\cdot}288}$
n = 83
$r^2 = 0{\cdot}63$
P << 0·001
2
VARIANCE s^2
500
100
50
10
5
1
1
5
10
MEAN $\bar{x}$

Of these quadrat size is unimportant if, as is the case, the mean number of animals per quadrat is greater than one (Kathirgamatamby, 1953). Terrestrial isopods are not well adapted physiologically for life on land and behavioural adaptations to reduce desiccation, including aggregation, are well known (Edney, 1954, 1968; Perttunen, 1961; Warburg, 1968). In a series of laboratory experiments (Farr, 1978) demonstrated that *Ligia exotica* do aggregate in response to conspecifics, and that this behaviour might be influenced by a chemical factor associated with them.

In an attempt to show whether some quadrats were more favourable to *Ligia* than others the number of animals caught in a particular quadrat, x , was expressed as a proportion of the total caught on that occasion, $\sum^{n} x$, to remove the effects of changes in population density. Because some samples comprised less than the usual 27 replicates these proportions were standardised by multiplying by the number of replicates, n :

$$x_Q = x\ .n/\sum^{n} x$$

and a single classification ANOVA performed on the data. The average number of samples per quadrat was 18.85 (range 10-31). The null hypothesis being tested is that there is no difference between the quadrats in the mean number of animals caught. This would be the case if the animals aggregate at random with respect to the habitat covered by the quadrats. The results are shown in Table 1. The data was tested for homogeneity of variances using Bartlett's test. The data were highly heteroscedastic : square root and logarithmic transformations substantially reduced this, but the data remained significantly heteroscedastic. Sokal and Rohlf (1981) suggest that moderate heterogeneity of variances may not be too serious for the overall test of significance, so the significant differences between the quadrat means may be accepted. However the data has been analysed using the more conservative, non-parametric Kruskal-Wallis test. The result of this test was also highly significant ($H = 634.9$; d.f. = 107; $P \ll 0.001$).

TABLE 1. ANOVA of the mean number of animals collected in particular quadrats during the study. Numbers caught in each quadrat were $LOG_{10}(x+1)$ transformed and then corrected for changes in population density by dividing by the total number caught on that occasion.

SOURCE OF VARIATION		D.F.	S.S.	M.S.	F
Between quadrats	:	107	23.72	0.222	8.89 ***
Within quadrats	:	1928	48.07	0.025	
TOTAL	:	2035	71.79		

Bartlett's test : H = 195.4, P<< 0.001

This result is not unexpected as the quadrats vary in their total surface areas and this will contribute to the significant differences between the quadrats. This result suggests that the environment is not spatially homogeneous, with some areas being more favoured by *Ligia* than others.

b) Sex Ratio and Maturity

Male woodlice can be recognised by the presence of the appendix masculina, an extension of the first and second pleopods. Unlike the majority of terrestrial woodlice the sex of female *Ligia* can be determined throughout life from maturity by the presence of oostegites on the ventral surface of the first five perionites. The oostegites undergo developmental changes which reflect the reproductive state of the female (Mocquard *et al*., 1974). These external sexual characteristics develop gradually over a series of moults, and probably precede full maturity. Animals lacking external sexual characteristics have been termed immatures.

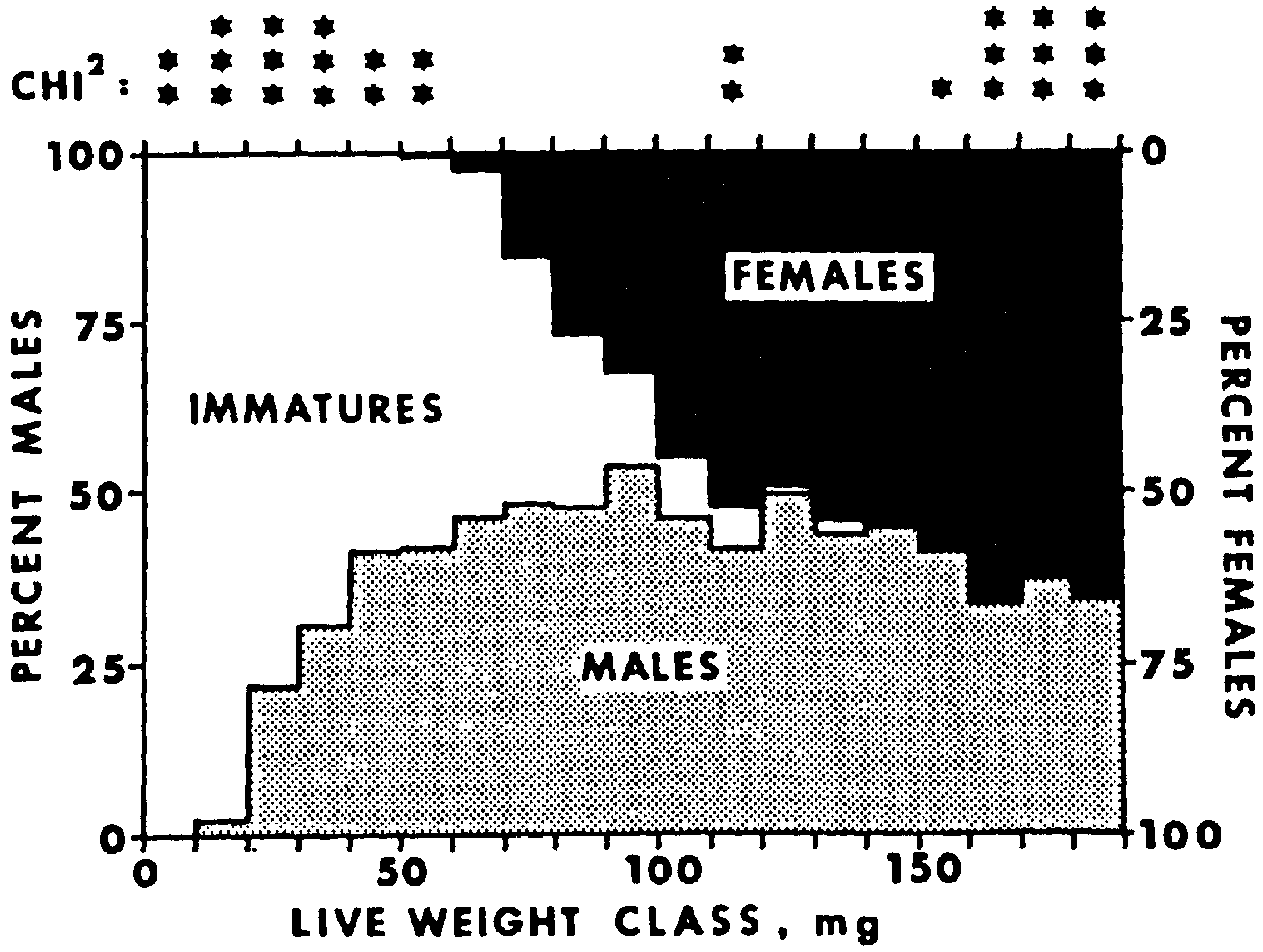
In order to determine the sex ratio and onset of maturity in the Robin Hood's Bay population all animals less than 190 mg live weight have been divided into 10 mg size classes and the number of males, females and immatures expressed as a percentage of the total in each size class (Fig 4). It can be seen that males develop external characteristics at a smaller live weight than females. The ratio males:females+immatures has been tested against an expected sex ratio of 1:1 for each size class using χ^2 (see Fig 4). At 60-70 mg live weight the sex ratio is not significantly different from 1:1 and the majority of males have developed external sexual characteristics. At live weights greater than 150 mg the sex ratio declines due to differential survival of the sexes (see section 7). Although the primary sex ratio cannot be known (Fiala, 1980), from theoretical considerations (Fisher, 1930) it is reasonable to assume that it is 1:1 at the time when the young are released, i.e. when female investment stops. Making this assumption it is possible to assess the probability of an immature of known weight being male or female. The propor-

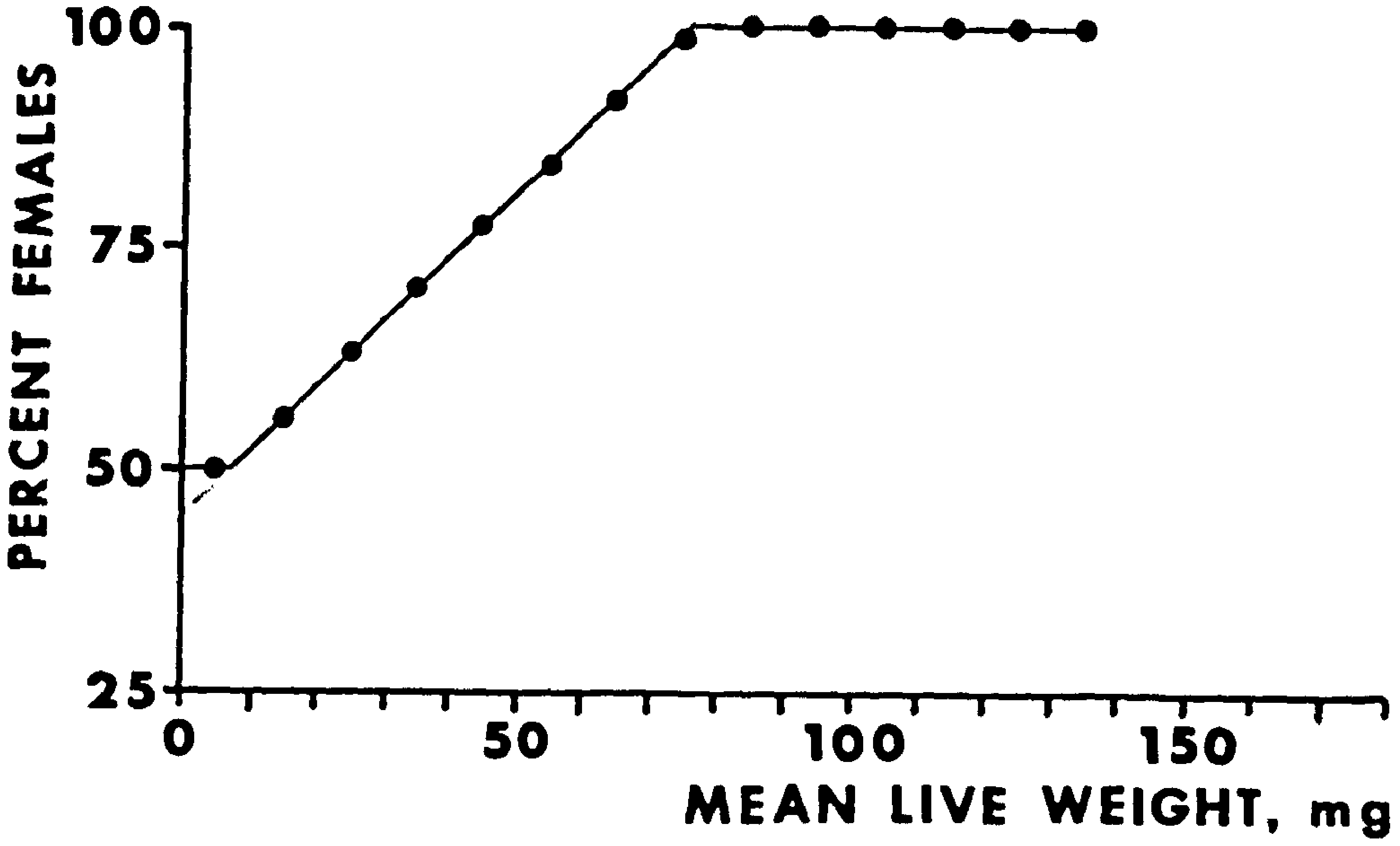
FIGURE 4

Percentage of males, females and immatures in each size class using all samples collected at Robin Hood's Bay. χ^2 indicates significant departures of the ratio males : females + immatures from an expected ratio of 1:1.

FIGURE 5

Percentage of immatures at Robin Hood's Bay which are probably female as a function of immature live weight, assuming an initial sex-ratio of 1:1.


CHI² :
100
75
50
25
0
PERCENT MALES
IMMATURES
FEMALES
MALES
0
25
50
75
100
PERCENT FEMALES
0
50
100
150
LIVE WEIGHT CLASS, mg


100
75
50
25
PERCENT FEMALES
0
50
100
150
MEAN LIVE WEIGHT, mg

tion of immatures which are probably female in each size class has been calculated as :

$$(I-(0.5T-M))/I$$

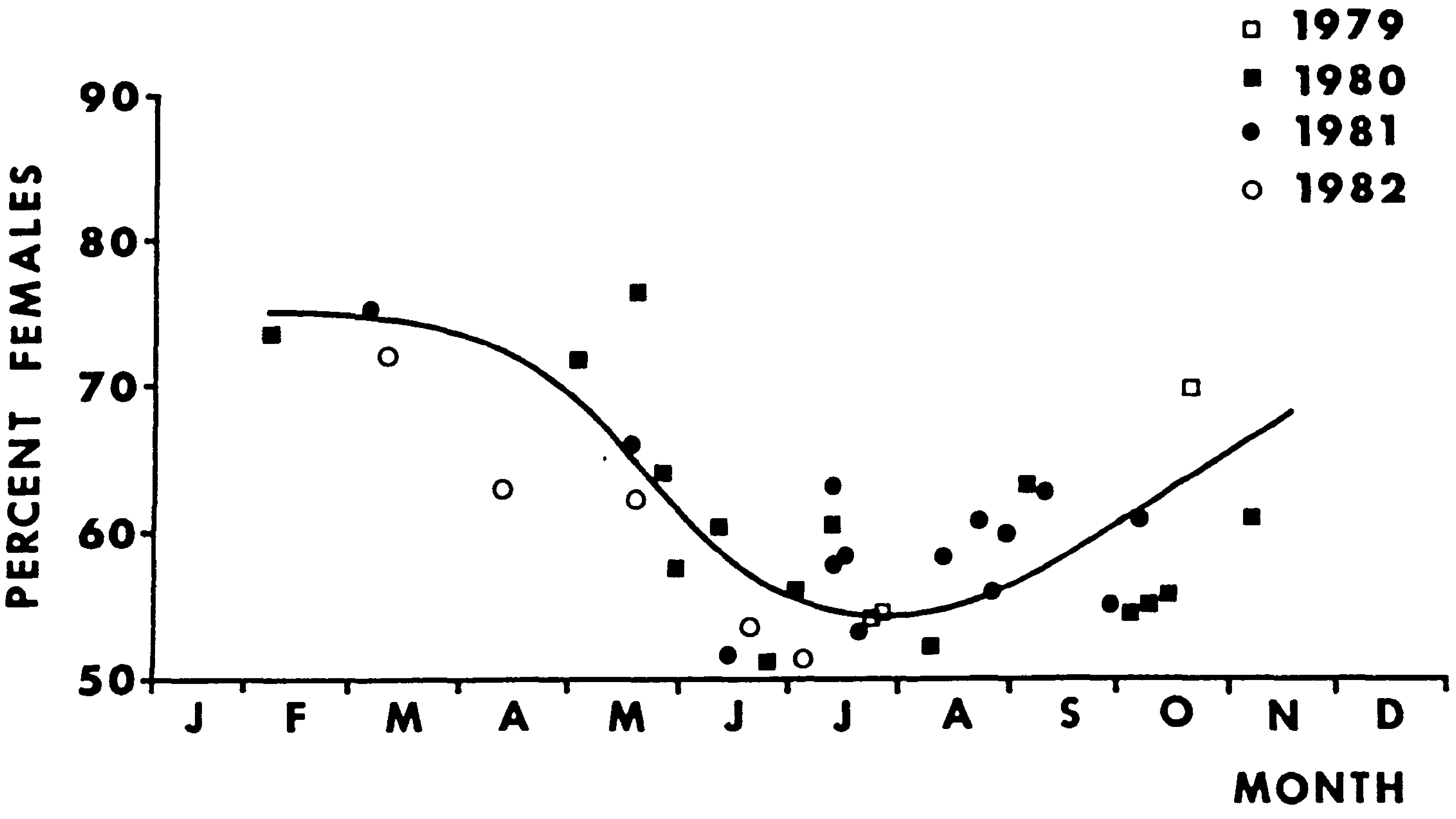
where I = no. of immatures, M = no. of males, T = total no. in size class. The relationship between mean live weight and percentage of immatures which are probably female could be described by the linear equation $y = 0.72x + 44.89$ ($n = 9$; $r^2 = 0.88$; $P < 0.001$) which has been used in a model (Fig 5) to assess the probability of an immature being male or female in the subsequent size frequency and growth analyses.

The sex ratios of all samples used for size-frequency analyses have been tested against an expected ratio of 1:1 using χ^2. Only mature animals greater than 200 mg live weight were included. Of 36 samples tested 22 showed a significant departure from 1:1 at the 5% level or higher. All 36 samples were biased towards females. When sex-ratio was plotted against time of year a seasonal trend was apparent (Fig 6). The sex-ratio declines during spring as young animals are recruited into the adult population, thereafter the sex-ratio becomes more biased towards females as the effects of differential survivorship become more pronounced.

The sex ratio of a population at any time is dependent upon the primary sex ratio as altered by differential maturity and differential survivorship of the sexes. Frequently it is the primary sex ratio that is of interest, for example in assessing the relative proportions of the sexual and parthenogenetic forms of the woodlouse Trichoniscus pusillus (Fussey & Sutton, 1981; Frankel et al., 1981). Unless due account is taken of differential maturity and survivorship single samples may be woefully inadequate in determining the primary sex ratio.

FIGURE 6

Seasonal variation in adult population sex-ratio at Robin Hood's Bay.


□ 1979
■ 1980
● 1981
○ 1982
PERCENT FEMALES
90
80
70
60
50
J
F
M
A
M
J
J
A
S
O
N
D
MONTH

c) Population Age and Size Structure

The results of the size frequency analysis are shown in Figs 7 and 8. Immatures have been divided into males or females on the basis of the relationship in Fig 5. The size of the size class intervals was decided after applying Scott's (1979) formula for optimal class intervals on a representative sample of individual age class distributions. The number in each size class is shown as a percentage of the total number sampled on each occasion.

The individual size frequency histograms have been divided into different age classes using a number of criteria. Each new year class remains discrete, that is it does not overlap with the previous year class, for the first 12 months of its life. In about June of each year the age classes start to become indistinct when separated only on the basis of live weight. However the age of individual females within the population could be determined not only from their live weights but also from their reproductive condition and by the developmental stage of their oostegites (Nicholls, 1931a; Gebelin, 1939; Mocquard et al., 1974; Willows, 1984). When females release their broods they effectively lose weight, but could be distinguished from younger females of the same weight by their larger linear dimensions. This method of age determination was preferred to the available graphical (Harding, 1949; Cassie, 1954) and statistical (Hasselblad, 1966; Schnute & Fournier, 1980) methods because it has more biological reality, and avoids making many assumptions such as the normality of the distributions. The male size distributions have been split by eye and are therefore much less reliable once a year class has exceeded 12 months of age.

The majority of the size frequency distributions show only two age classes, the exceptions being those taken in September and October which show three. Births occur in June and July but these recruits are not taken in samples until September. Hence maximum longevity (June to October) was determined to be about 30 months.

FIGURE 7

Size structure of <u>Ligia oceanica</u> population at Robin Hood's Bay from July 1979 to April 1981. The percentage of each sample in each size class is shown for males (left hand side) and females (right hand side) in each histogram. Alternate year classes are indicated by alternate black and white areas. Overlapping female year classes can be distinguished by the use of reproductive criteria (see text).

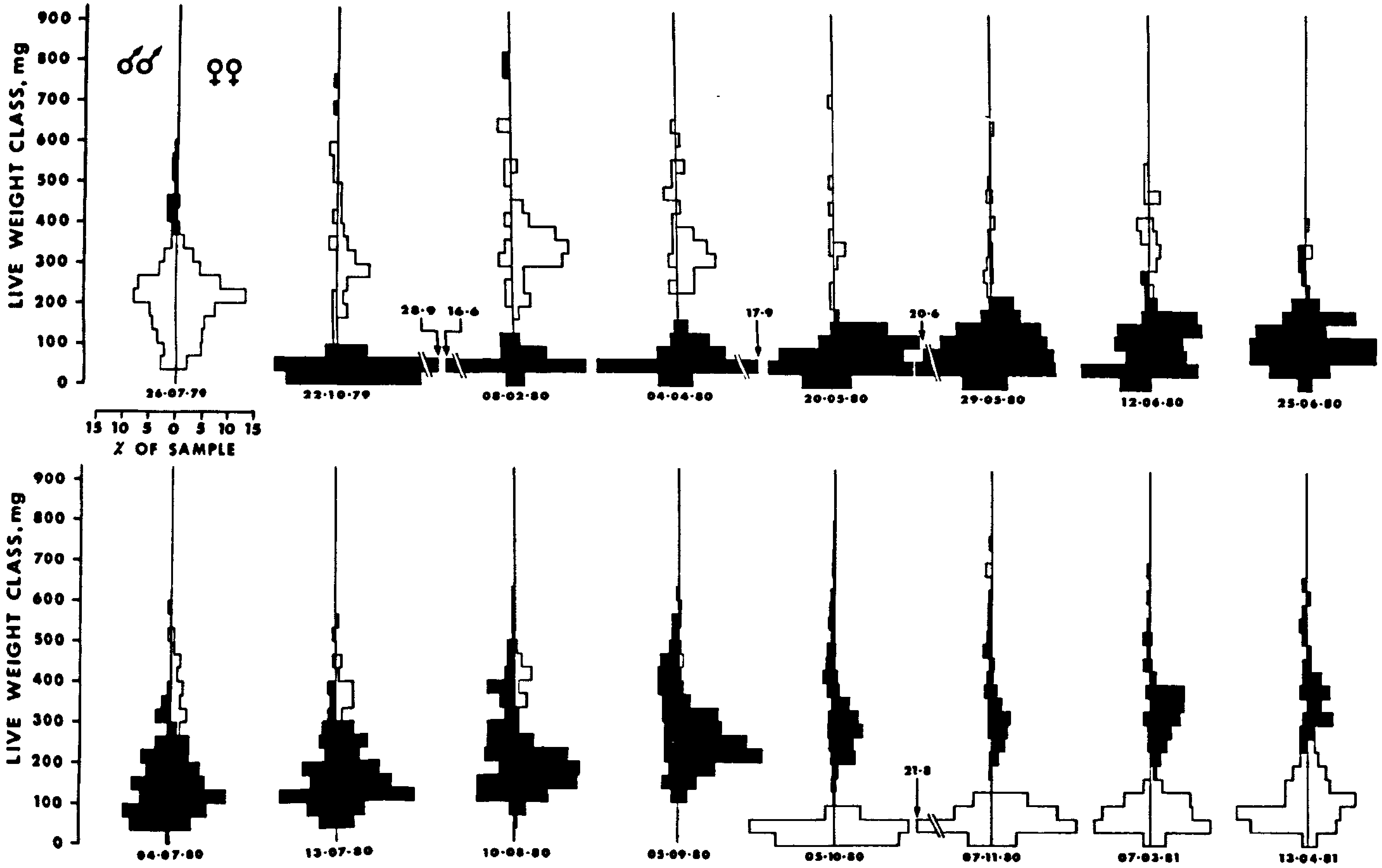
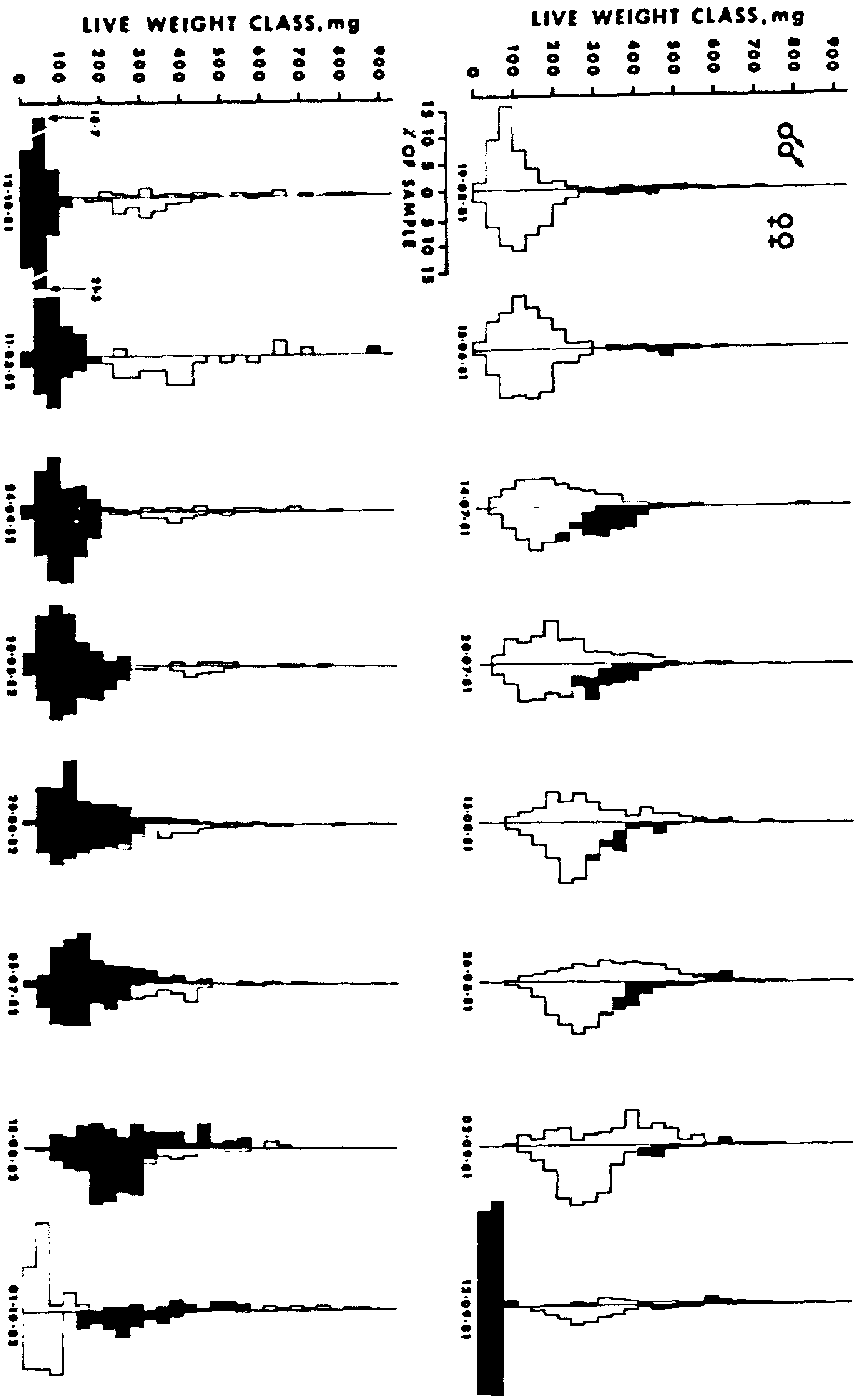

LIVE WEIGHT CLASS, mg
900
800
700
600
500
400
300
200
100
0
♂♂
♀♀
15 10 5 0 5 10 15
% OF SAMPLE
26-07-79
22-10-79
28-9
16-6
08-02-80
04-04-80
17-9
20-05-80
20-6
29-05-80
12-06-80
25-06-80
LIVE WEIGHT CLASS, mg
04-07-80
13-07-80
10-08-80
03-09-80
05-10-80
21-8
07-11-80
07-03-81
13-04-81

FIGURE 8

Size structure of Ligia oceanica population at Robin Hood's Bay from May 1981 to October 1982. The percentage of each sample in each size class is shown for males (left hand side) and females (right hand side) in each histogram. Alternate year classes are indicated by alternate black and white areas. Overlapping female year classes can be distinguished by the use of reproductive criteria (see text).


LIVE WEIGHT CLASS, mg
0
100
200
300
400
500
600
700
800
900
♂♂
♀♀
15 10 5 0 5 10 15
% OF SAMPLE
10·05·81
15·06·81
14·07·81
20·07·81
11·08·81
26·08·81
02·09·81
12·09·81
LIVE WEIGHT CLASS, mg
0
100
200
300
400
500
600
700
800
900
10·7
21·3
12·10·81
11·02·82
24·04·82
20·05·82
20·06·82
08·07·82
10·08·82
01·10·82

After the first 12 months of sampling the number of individuals in each sample was increased by combining two or three adjacent nights' samples. This explains why the first 12 months histograms look 'coarse'. However a remarkable feature of the data is the similarity in the size and age structure of the population from year to year. Compare any months sample between years in Figs 7 & 8. Clearly the size structure of the population was similar from year to year.

The decrease in weight of the 1979 year class females apparent between May and June 1981, and a similar decrease in weight of the 1980 year class females between May and June 1982 was due to the release of offspring by these females in June of those years.

d) Adult population density

Population density estimates, as mean numbers per 0.25 m^2 quadrat ± 95% C.I., between May and October for the four years 1979 to 1982 are shown in Fig 9. In 1979 only five estimates of population density were made, four in late July and one in October. Each year's recruits, sampled first in September, are not shown in Fig 9 (see section 6.ii). The standard errors are large due to the aggregation characteristic of the population. In the following analyses the data have been $\mathrm{Log}_{10}(x+1)$ transformed to reduce the variance heterogeneity (see section 3.ii.a).

Within each of the four years of study there were significant differences between the sampled population densities (Table 2). Examination of Fig 9 shows a clear trend within each year with adult population density decreasing steadily throughout each summer.

In order to examine year to year changes in population densities at R.H.B. samples spanning the end of July in each year have been subjected to ANOVA. The end of July was chosen as being the only period for which data for 1979 are available. The population densities for this period, together with the transformed values, are shown in Table 3

FIGURE 9

Changes in adult population density at Robin Hood's Bay (as numbers per 0.5m x 0.5m quadrat ± 95% C.I.) during the summers of 1979 and 1980 (top), 1981 (middle) and 1982 (bottom).

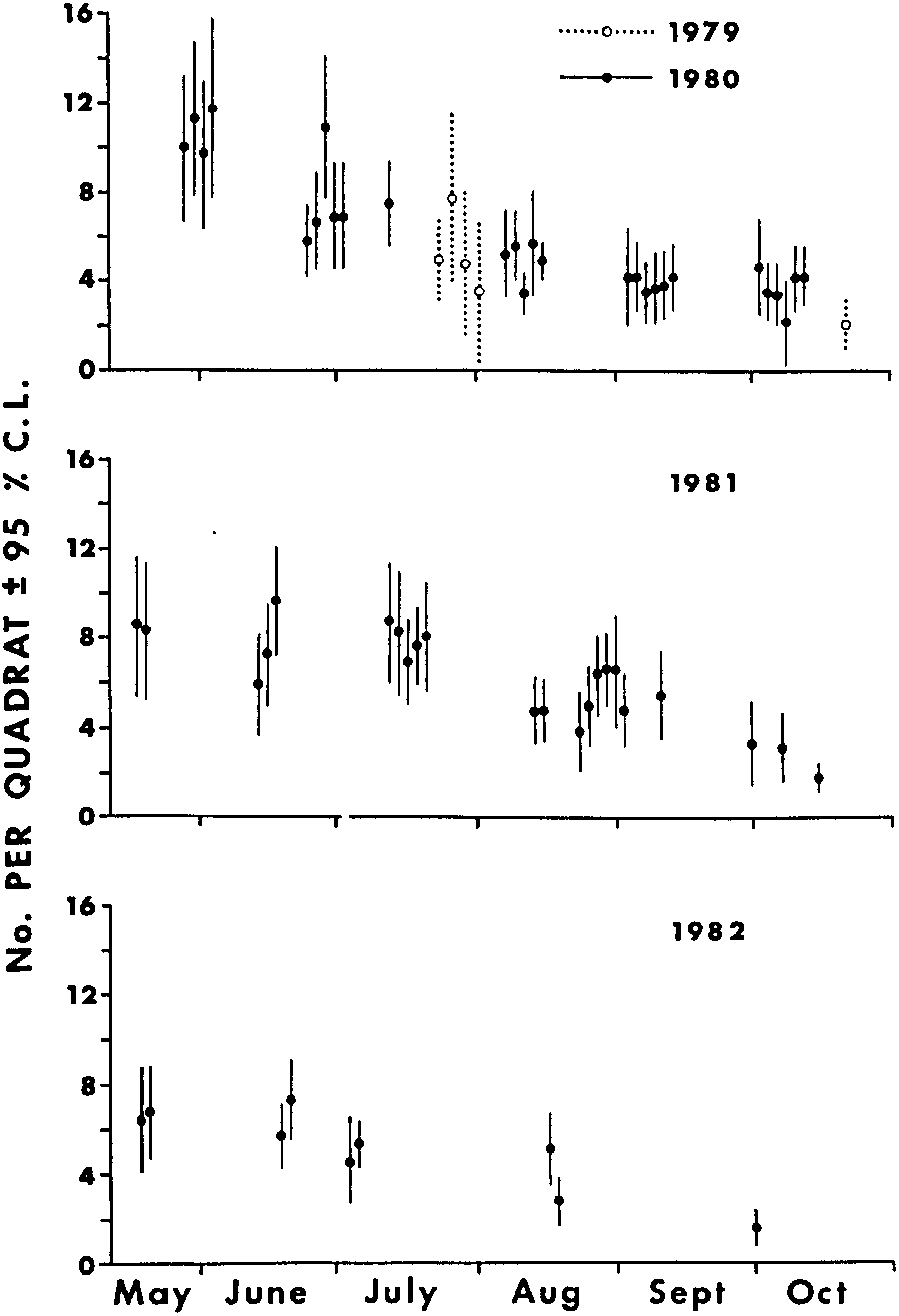

No. PER QUADRAT ± 95 % C.L.
1979
1980
1981
1982
0
4
8
12
16
May
June
July
Aug
Sept
Oct

TABLE 2. ANOVA table of the changes in population density within the years 1979 to 1982. The data was $LOG_{10}(x+1)$ transformed for the analysis.

YEAR	SOURCE OF VARIATION	D.F.	S.S.	M.S.	F
1979	Between samples	4	2.32	0.579	3.90 **
	Within samples	93	13.79	0.148	
	TOTAL	97	16.11		
	Bartlett's test	H = 3.84, n.s.			
1980	Between samples	26	19.61	0.754	5.71 ***
	Within samples	702	92.68	0.132	
	TOTAL	728	112.29		
	Bartlett's test	H = 20.73, n.s.			
1981	Between samples	21	14.15	0.674	5.52 ***
	Within samples	572	69.82	0.122	
	TOTAL	593	83.97		
	Bartlett's test	H = 23.22, n.s.			
1982	Between samples	7	2.50	0.358	3.77 ***
	Within samples	208	19.71	0.095	
	TOTAL	215	22.21		
	Bartlett's test	H = 12.34, n.s.			

TABLE 3. Mean July population densities at R.H.B. Values are numbers per 0.25 m^2 quadrat ± 95% confidence intervals.

DATE OF ESTIMATE	n	POPULATION DENSITY	
		UNTRANSFORMED	$LOG_{10}(x+1)$ BACKTRANSFORMED
29 July 1979	77	5.26 ± 1.56	2.95 $^{-0.78}_{+0.97}$
28 July 1980	54	6.35 ± 1.35	4.91 $^{-1.03}_{+1.25}$
28 July 1981	108	6.24 ± 0.90	4.80 $^{-0.75}_{+0.86}$
27 July 1982	108	4.41 ± 0.69	3.32 $^{-0.55}_{+0.63}$

TABLE 4. ANOVA table of the July population densities for the four years 1979 to 1982. The data was $LOG_{10}(x+1)$ transformed for the analysis.

SOURCE OF VARIATION		D.F.	S.S.	M.S.	F
Between years	:	3	1.94	0.645	5.75 ***
Within years	:	343	38.48	0.112	
TOTAL	:	346	40.42		

Bartlett's test : H = 12.26, $P \ll 0.01$

S.N.K. test. Those values asterisked differ at $P < 0.05$ or less.

YEAR	1980	1981	1982	1979
1981	0.008			
1982	0.136 *	0.128 *		
1979	0.175 *	0.167 *	0.039	

1980 1981 1982 1979

and the results of the ANOVA in Table 4. Significant ($P < 0.001$) differences were found between years in the mean July densities. Application of the a posteriori S.N.K. procedure (Sokal & Rohlf, 1969) indicated significant differences between the years 1980 & 1979, 1980 & 1982, 1981 & 1979, 1981 & 1982, and no significant difference between 1980 & 1981, 1979 & 1982. The years ranked in population density 1980 > 1981 > 1982 > 1979. However the differences were not great :the coefficient of variation of the mean July densities was only 25%, and the maximum (1980) density only 1.66 times the minimum (1979).

e) Breeding phenology

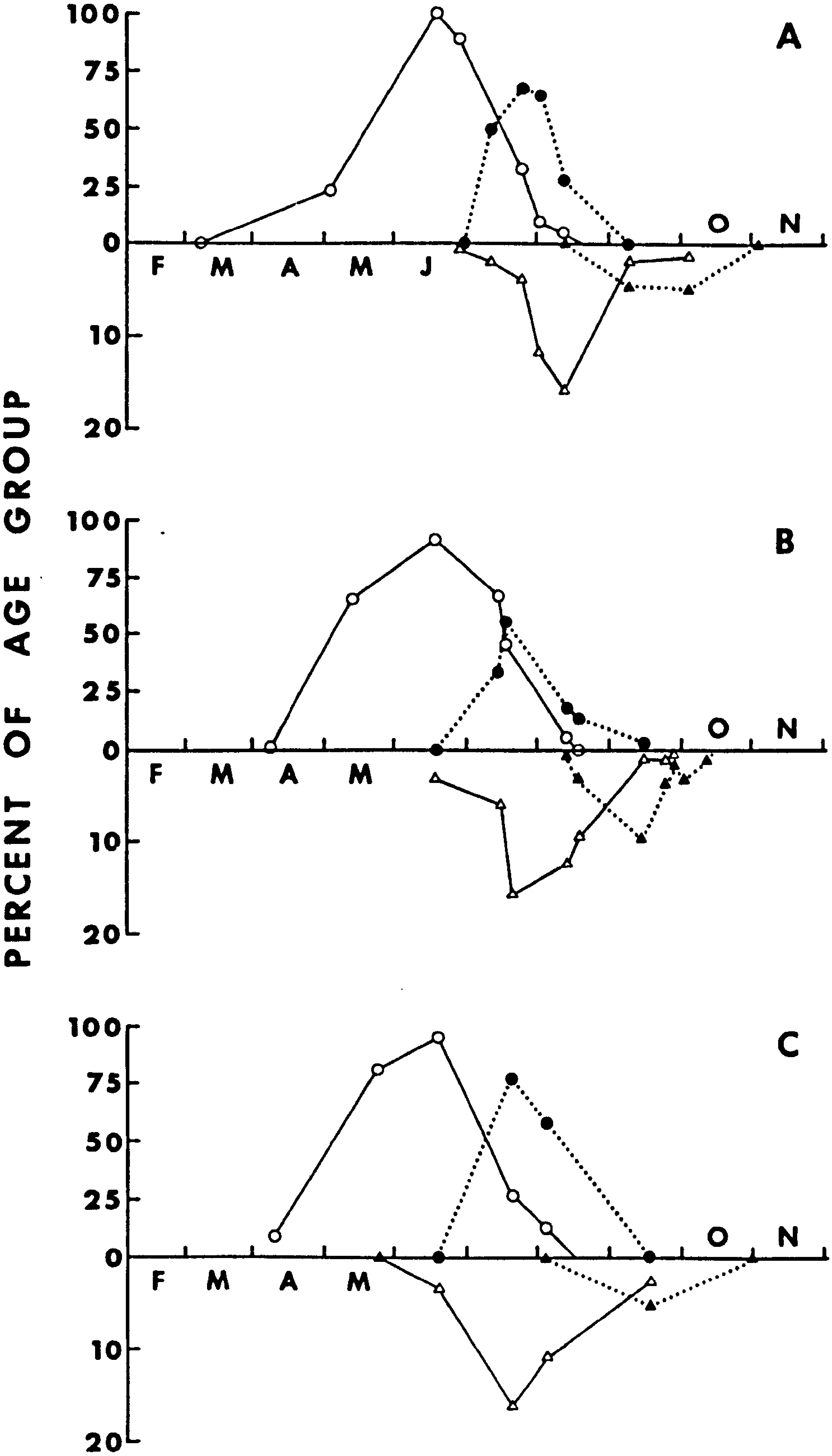
Females carrying broods were found from March to September, however a complex breeding phenology was apparent. In Fig 10 the number of breeding females is expressed as a percentage of the total number of females in that year class for each sample. Data for 1980, 1981 and 1982 are presented. The first wave of reproduction was due to animals which were entering their second summer, at an age of about 18 months. These animals started producing broods in March and, in each of the three years, 100% of the females of this age had produced broods by May, the peak in brood carrying occurring in mid-May. Thereafter the percentage of animals carrying broods declined as the progeny were released. Corresponding with this was an increase in the number of post-parturient females, that is animals with empty brood pouches which had yet to moult to the non-breeding condition. In each of the three years studied the peak release date was about the second week in June.

The second wave of breeding was due to animals in their first summer, aged about 12 months. They started producing broods in late May and peak numbers were taken in late June and early July. Only 16.1 ± 1.8% (95% C.I.) of the females of this year class produced broods at this time. The peak in brood carrying was again followed by a smaller peak in the number of post-parturient animals. The reason this peak was consistently less than the peak in brood

FIGURE 10

Breeding phenology of the population at Robin Hood's Bay. Ordinate gives the percentage of females in each age class in each sample which were gravid or post-parturient (ie having released their offspring but not undergone the following moult) for the years : a. 1980, b. 1981 and c. 1982.

○———○ EARLY gravid
●·········● EARLY post-parturient
△———△ LATE gravid
▲·········▲ LATE post-parturient


PERCENT OF AGE GROUP
A
B
C
100
75
50
25
0
10
20
F
M
A
M
J
O
N

carrying is due to the much shorter time females spend in the post-parturient state (2-3 weeks, see Fig 10).

I have termed these two breeding groups EARLY and LATE respectively. There was some degree of overlap between the two groups in brood carrying. However individuals could be assigned to a particular group or year class not only by analysis of the size frequency histograms, but also on the developmental stage of the neonates within the brood pouch. By the time LATE breeding females produced their broods of golden yellow eggs, those carried by EARLY breeding females had become dark green and showed signs of development (eye spots and segmentation), or had developed into neonates. In addition a very small number of very large animals produced broods in August/September. These could only be animals which had produced broods earlier in the year and were producing second broods. The numbers were too small to be included in Fig 10.

A remarkable feature of the data was the constancy of the timing of breeding of the two year classes in the three years of the study, and the sizes of animals carrying these broods. Results of two way ANOVA on the live weights of females carrying EARLY and LATE broods in the three years are shown in Table 5. Because of the computational difficulties of 2 way ANOVA with unequal sample sizes (Sokal & Rohlf, 1981) forty values for live weights have been selected at random for each group. Not unexpectedly the means were highly correlated with the variance ($r^2 = 0.93$, $P < 0.001$), and the data significantly heteroscedastic (Bartlett's Test). Logarithmic transformation reduced this heterogeneity of variance. The ANOVA demonstrated the obvious : highly significant differences in the live weights of animals breeding EARLY and LATE, but also revealed no significant differences between years and no significant interaction.

TABLE 5. Two way ANOVA table of the live weights of females carrying EARLY and LATE broods in the three years 1980 to 1982 at R.H.B. The data was $LOG_{10}(x)$ transformed.

SOURCE OF VARIATION		D.F.	S.S.	M.S.	F
Between EARLY & LATE	:	1	3.394	3.3942	551.00 ***
Between years	:	2	0.026	0.0131	2.12 n.s.
Interaction	:	2	0.000	0.0002	0.02 n.s.
Error	:	234	1.441	0.0062	
TOTAL	:	239	4.862		

Bartlett's test : $H = 11.45$, $P < 0.05$.

4. POPULATION SIZE

The size of the R.H.B. population could be estimated from the estimates of population density. However to check the reliability of these estimates multiple mark release recapture (M.R.R.) studies were undertaken to provide alternative independent estimates of population size, survivorship and also growth rate. The R.H.B. population was judged to be ideal for this kind of study, being small and closed to immigration and emigration. Because each year's recruits were never included in samples there was effectively no recruitment into the adult population being measured. Loss of marks from the population was due to death and moulting only. The M.R.R. models of Fisher & Ford (1947) and Jolly-Seber (Jolly, 1965; Seber, 1965, 1973) were judged appropriate for the study.

i. Sampling methods

The sampling procedure was essentially that explained previously (see section 3.i). The population was sampled every other night for a period of nine or eleven days, dependent on daylength and tides. The sampled animals were marked and returned 24 hours later to their quadrat of capture. Hence the marked animals had 24 hours to disperse through the population before the next sample.

Marking proved to be difficult with none of the usual methods (Southwood, 1978a,b) being effective. Ultimately a small drop of cyanoacrylate ester ("superglue") applied to the perion, followed by an equally small drop of cellulose paint, was found to provide a permanent and visible mark. By using combinations of colour, position and numbers of marks, day- and quadrat-specific marks could be encoded. Animals <90 mg live weight were too small to be marked. Those showing signs of imminent moult were not marked.

In all six M.R.R. studies were undertaken, four in 1980 and two in 1981. In 1981 the marked animals were coded for quadrat of capture (and release) in order to assess dispersal distances. In three studies all the animals caught were weighed and sexed in order to assess whether recapture probabilities were size or sex related.

ii. Testing the assumptions

The precision and bias of the results of data analysed using a mark and recapture model depend on the amount of data collected and the extent to which the assumptions of the model are fulfilled by the field population. The only certainty is that the assumptions will not hold perfectly, but it is our responsibility to attempt to evaluate to what extent they are met (Begon, 1979, 1983). This is the aim of this section, with particular reference to the Fisher-Ford model. In this case the following assumptions are made :

a) That loss of marks was due to moulting and death only.
b) That capture and marking does not affect an individual's subsequent chance of recapture.
c) That capture and marking does not affect an individual's chance of dying.
d) That all individuals in the population have an equal chance of capture. In this case, where the animals are sampled at random within a fixed sub-area of the total habitat of the population, this includes the assumption :
e) that individuals disperse at random throughout the whole population between each release and recapture.
f) That all individuals are equally likely to survive, i.e. survivorship is unrelated to age, sex or size.
g) That survivorship of marks is constant over the period of each study.
h) That sampling periods are instantaneous, or at least short in relation to the total time period of the study.

Arnason & Mills (1981) examined theoretically the effect of loss of marks, in this case due to moulting, on the Jolly-Seber model. Not surprisingly they found that the estimate of population size, $\hat{N}$, is unaffected while that of survivorship, $\hat{\phi}$, is biased downwards.

In particular if the capture probabilities vary amongst animals then the models will be far from accurate (Roff, 1973b; Bishop & Sheppard, 1973). The majority of the tests used below are described in Begon (1979) and Seber (1973). Some have been criticised by Roff (1973b) as being insensitive.

a) Loss of marks

Batches of animals from Whitby were marked and maintained in the laboratory. The only loss of marks was due to moulting (about 4%).

b) Initial marking mortality

In laboratory cultures there was no difference in mortality between unmarked (control) and marked groups of animals over the experimental period.

In addition the field data was analysed to see whether marking is detrimental to some animals. Should this be the case then animals marked for the first time on Day_i will be under-represented in subsequent samples. The results are shown in Table 6. There was only one significant result ($P < 0.05$) for the seven studies, and the overall $\chi^2 = 25.71$, d.f. = 24, $P \approx 0.35$. There seems to be little evidence for initial marking mortality.

c) Age of marks

This test examines whether the survival of marks is independent of the age of the marks, i.e. the length of time they have been released in the population. The results are shown in Table 7. Overall $\chi^2 = 13.68$, d.f. = 24, $P > 0.95$. I conclude that survivorship is independent of the age of the marks.

TABLE 6. Test of the assumption of initial marking mortality.

DATE OF STUDY	X^2	D.F.	P
1 June 1980	1.22	3	≈ 0.75
30 June 1980	1.01	3	≈ 0.80
13 August 1980	9.64	3	< 0.05 *
10 September 1980	4.75	4	≈ 0.30
9 October 1980	4.20	4	≈ 0.40
18 July 1981	0.75	3	≈ 0.85
31 August 1981	4.14	4	≈ 0.40
TOTAL	25.71	24	≈ 0.35

TABLE 7. Test of the assumption that the age of marks has no effect on the probability of recapture.

DATE OF STUDY	X^2	D.F.	P
1 June 1980	0.72	3	≈ 0.85
30 June 1980	3.19	3	≈ 0.40
13 August 1980	0.77	3	≈ 0.85
10 September 1980	2.73	4	≈ 0.60
9 October 1980	4.01	4	≈ 0.40
18 July 1981	0.69	3	≈ 0.90
31 August 1981	1.57	4	≈ 0.80
TOTAL	13.68	24	>0.95

TABLE 8. Test of the assumption of constant survival.

DATE OF STUDY	X^2	D.F.	P
1 June 1980	2.07	2	≈ 0.35
30 June 1980	1.55	2	≈ 0.50
13 August 1980	0.73	2	≈ 0.70
10 September 1980	2.29	3	≈ 0.50
9 October 1980	0.92	3	≈ 0.80
18 July 1981	0.32	2	≈ 0.90
31 August 1981	3.53	3	≈ 0.30
TOTAL	11.41	17	≈ 0.80

TABLE 9. Test of the assumption that recapture probabilities do not vary between the sexes.

DATE OF STUDY	X^2	D.F.	P
9 October 1980	7.94	5	≈ 0.15
18 July 1981	6.56	4	≈ 0.15
31 August 1981	4.30	5	≈ 0.50
TOTAL	18.80	14	≈ 0.15

TABLE 10. Test of the assumption that the probability of recapture does not vary with size.

DATE OF STUDY	X^2	D.F.	P
9 October 1980	11.47	23	> 0.95
18 July 1981	13.10	15	≈ 0.60
31 August 1981	32.61	23	≈ 0.10
TOTAL	57.18	61	≈ 0.60

d) Constant survival

Here I test the observed number of mark days survived on each recapture day against the expected number assuming a constant survival rate. The results are shown in Table 8. Overall $\chi^2 = 11.41$, d.f. = 17, $P \approx 0.8$. I conclude that survivorship, within each study period, was not significantly different from the average.

e) Bias in sex ratio

By testing the sex ratio of all those animals released on Day_i and subsequently recaptured against the sex ratio of all the animals marked and released on Day_i we can test the assumption that these two subgroups are equally catchable by assuming that their survival rates are constant. The results are shown in Table 9. Overall $\chi^2 = 18.80$, d.f. = 14, $P \approx 0.15$. I conclude that the sex ratios of the recaptured animals did not differ significantly from that of those released.

f) Size bias

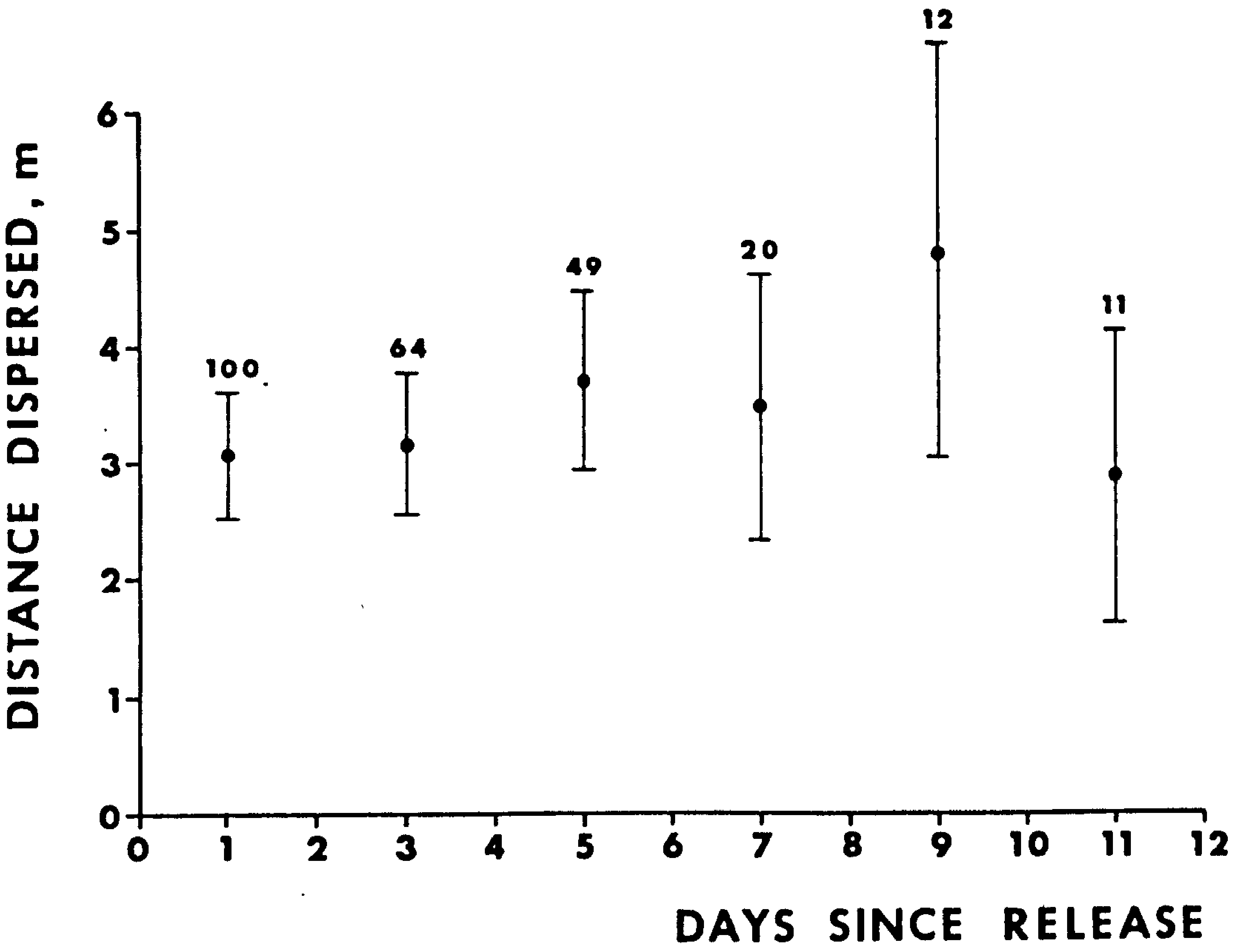
It seemed possible that larger (= older) animals might be more susceptible to recapture than smaller (= younger) animals. To test for this the size frequency distribution of all the animals caught during a study was used to generate expected frequencies for the sizes of those animals recaptured, assuming that growth would be negligible over the period of study. The results are shown in Table 10. Overall $\chi^2 = 57.18$, d.f. = 61, $P = 0.6$. I conclude that there was no evidence of size bias in the recaptures.

g) Dispersal

Population size will be seriously underestimated if the marked animals do not disperse throughout the population in the one night available. The distance dispersed by individuals was determined by measuring the direct distance between the mid-point of the quadrat of release and the mid-

FIGURE 11

Distance dispersed (± 95% C.I.) by marked *Ligia oceanica*, measured as the distance between quadrats of release and recapture, against the time interval between release and recapture.


DISTANCE DISPERSED, m
0
1
2
3
4
5
6
0
1
2
3
4
5
6
7
8
9
10
11
12
DAYS SINCE RELEASE
100
64
49
20
12
11

point of that of recapture. Because animals will tend to disperse out of the sampling area these estimates will tend to be underestimates, and possibly of limited use. The greater the actual distance dispersed the greater the underestimate. The results are shown in Fig 11. One way ANOVA showed no significant differences between the mean distances dispersed over one to eleven days (F = 1.34; d.f. = 1,250; n.s.). The overall distance dispersed was 3.3 ± 0.3 m (95% C.I.).

Visual surveys of the most distant regions of the habitat revealed large numbers of marked animals dispersed all over the sampling site. Such evidence of dispersal throughout the population is reassuring.

iii. Results

The results of the M.R.R. analyses, incorporating Bailey's (1952) modification for bias, are shown in Table 11. The average estimate of population size, $\hat{N}$, is shown for each study period together with the 95% C.I. of these estimates. The estimated survival rates, $\hat{\phi}$, and their C.I. are shown in Table 12. Although the Jolly-Seber model will furnish estimates of the standard errors of $\hat{N}$ and $\hat{\phi}$ these are "little more than a bad joke" (Gilbert, 1973), an opinion borne out by the analyses of Manly (1971) and Roff (1973a). Hence I have used all the estimates of population size or survival for each study to estimate the standard errors. Also shown in Table 11 are the estimates of population size based on the mean estimates of population density obtained over each period of study multiplied by the area of the sampling site over which Ligia was found.

In general the Jolly-Seber method gave slightly lower estimates of $\hat{N}$ than the Fisher-Ford model, but with substantially greater C.I. Those estimates based directly on population density gave the smallest C.I., but the agreement between these estimates and those based on the M.R.R. was good. The average population size was estimated to be about 2400. Early in the summer, about June, it appeared to be about 3000, falling to about 1500 by September/October.

TABLE 11. Estimates of the population size of *Ligia oceanica* at Robin Hood's Bay.

DATE OF STUDY	DENSITY x AREA			FISHER-FORD MODEL			JOLLY-SEBER MODEL		
	$\hat{N}$	95% C.I.	n	$\hat{N}$	95% C.I.	n	$\hat{N}$	95% C.I.	n
1 June 1980	3669	± 533	135	2986	± 682	4	2952	± 1390	3
30 June 1980	2896	± 358	135	3259	± 724	4	3000	± 2741	3
13 August 1980	1900	± 319	135	1769	± 677	4	1569	± 1773	3
10 September 1980	1514	± 257	162	2383	± 1091	5	2290	± 1316	4
9 October 1980	1422	± 250	162	2171	± 606	5	2228	± 851	4
18 July 1981	3006	± 387	135	2604	± 585	4	2554	± 1487	3
31 August 1981	2075	± 278	162	2091	± 392	5	1832	± 896	4

TABLE 12. Survival estimates (numbers.day^{-1}) from the Fisher-Ford and Jolly-Seber multiple mark and recapture models.

DATE OF STUDY	FISHER-FORD MODEL	JOLLY-SEBER MODEL ± 95% C.I.
1 June 1980	0.921	0.954 ± 0.949
30 June 1980	0.912	0.837 ± 0.789
13 August 1980	0.875	0.963 ± 1.439
10 September 1980	0.901	0.863 ± 0.821
9 October 1980	1.000 #	1.025 ± 0.758
18 July 1981	0.941	0.939 ± 0.391
31 August 1981	0.939	0.823 ± 0.506

Calculated value actually 1.005. As this is not possible in a closed population a value for suvivorship of 1.000 was used in the calculation of population size for this study.

All the estimates of survival rate (nos.day^{-1}) were high, but would be biased downwards due to the loss of marks by moulting. The values are in agreement with those obtained directly (see section 7).

iv. Discussion

Bishop & Sheppard (1973) evaluated the accuracy of $\hat{N}$ derived from the Fisher-Ford and Jolly-Seber models under a variety of conditions which, happily, closely match those in the present study. Sampling intensity can be estimated (Roff, 1973a) by :

$$\text{Sampling intensity} = \sum_{i=1}^{i=n} m_i / \sum_{i=1}^{i=n} M_i$$

where m_i = no. marks recaptured on day_i and M_i = marks at risk on day_i. This gives estimates (± 95% C.I.) of 6.6 ± 1.5% for the Fisher-Ford method and 7.0 ± 2.3% for the Jolly-Seber method. Given the estimated values of $\bar{N}$ and $\bar{\phi}$ this would give an accuracy (that is a 95% probability of N being close to $\bar{N}$) of about 25% according to Begon (1979), compared with observed coefficients of variation of $\hat{N}$ of 28% for the Fisher-Ford and 65% for Jolly-Seber model. The Jolly-Seber method is known to be less efficient than the Fisher-Ford when data are scanty or sampling occasions few (Manly, 1970; Bishop & Sheppard, 1973; Begon, 1979). Robson & Regier (1964) also present a model by which the accuracy of mark and recapture estimates of population size can be predicted from the numbers of animals marked and the numbers caught. Again the predicted accuracy of each estimate of $\bar{N}$ is about 25%. They suggest 10% as being that required by careful research into population dynamics. However given the close correspondence of the seven estimates of population size over the two years, the lack of evidence for any contraventions of the underlying assumptions of the M.R.R. models, and the close agreement with the estimates based on surface density x area, it may be concluded that the adult population of <u>Ligia</u> at R.H.B. was indeed small and falls from about 3000 to 1500 between June and September. In addition it seems unlikely that many animals remain in their crevice refuges during periods of darkness. If this were the case then the estimates of population size based on the estimates of population density would be lower than those derived from the M.R.R. censuses. Such is not the case.

5. FECUNDITY

i. Methods

A consequence of the small size of the R.H.B. population was that no data on fecundity could be collected without risk of severely affecting the population dynamics. Hence data were only collected in 1982 when all females carrying broods collected in samples were weighed and the eggs dissected from their brood pouches and counted. Where eggs showed signs of development the number of undeveloped eggs was counted to estimate brood pouch mortality. There was no variation apparent in the developmental stage of the eggs, as is generally the case for isopods (Green, 1965), though exceptions are known (e.g. Eltringham & Hockley, 1961; Holdich, 1968).

In the calculation of the fecundity regressions only data on animals carrying eggs which showed no signs of development have been included. This minimises two sources of error :

a) The loss of eggs from the brood pouch. This is known in marine isopods (Holdich, 1968) and amphipods (Fish & Mills, 1979).
b) Growth of the female following the deposition of the eggs in the brood pouch.

ii. Results

a) Fecundity regressions

Females were classified as either EARLY (1980 year class) or LATE (1981 year class) and the data are shown in Fig 12. Egg number was linearly related to female size, as is usually the case, in both groups of animals (Table 13). Surprisingly the EARLY and LATE groups appeared to have distinctly different relationships : LATE breeding animals carrying more eggs than would an EARLY female of identical weight. Analysis of covariance (ANCOVA) showed that the

FIGURE 12

Female size fecundity regression for EARLY (□) and LATE (■) breeding females at Robin Hood's Bay in 1982. The fecundity regressions are :

EARLY : $y = 0.16x + 21.31$.
LATE : $y = 0.27x + 7.99$.

where y is egg number and x is female live weight in mgs. (▲ : VERY LATE).

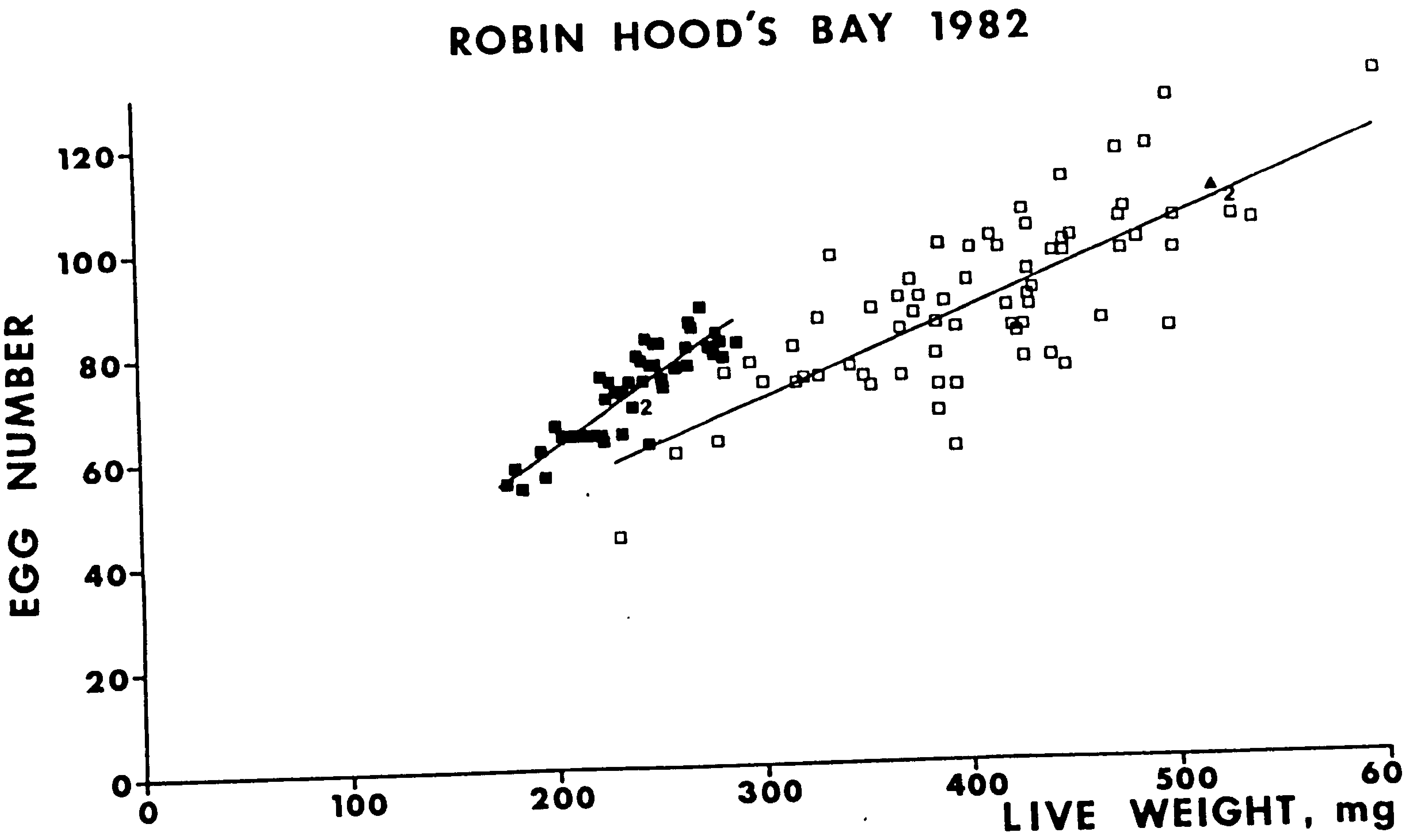

ROBIN HOOD'S BAY 1982
EGG NUMBER
0
20
40
60
80
100
120
0
100
200
300
400
500
600
LIVE WEIGHT, mg
2
2

TABLE 13. Analysis of covariance (ANCOVA) of the regressions of fecundity on live weight for EARLY and LATE groups of females at Robin Hood's Bay.

SOURCE OF VARIATION	D.F.	S.S.	M.S.	F
Due to EARLY regression	1	9201.2	9201.2	87.09 ***
Error (deviations from slope)	66	6973.4	105.7	
EARLY group TOTAL	67	1674.6		
Due to LATE regression	1	2639.0	2639.0	160.43 ***
Error (deviations from slope)	42	690.9	16.5	
LATE group TOTAL	43	3329.9		
Between groups	1	6489.2	6489.2	36.60 ***
Within groups	110	19504.5	177.3	
Common slope within groups	1	11467.2	11467.2	155.51 ***
Error (deviations from common slope)	109	8037.4	73.7	
Difference between slopes	1	373.1	373.1	5.26 *
Error (deviations from slope within each group)	108	7664.3	71.0	
TOTAL (groups + within)	111	25993.7		
Common slope within study	1	16261.7	16261.7	
Error (deviations from common slope)	110	9732.0	88.5	
Among intercepts	1	1694.6	1694.6	22.98 ***
Error (deviations from common slope)	109	8037.4	73.7	

slopes of the fecundity regressions of the two breeding groups were significantly different ($F = 5.26$; d.f. = 1,108; $P < 0.025$). The full results of the analysis are shown in Table 13. The effect of this difference is to reduce the discrepancy in fecundity due to the size difference between females in the two groups. However the EARLY breeding females still produce more eggs per individual than do the LATE breeders ($F = 36.60$; d.f. = 1,110; $P \ll 0.001$).

Although egg numbers are generally related to female size in Crustacea (e.g. Jensen, 1958a) some authors have been unable to find such a relationship within the genus Ligia : e.g. Pandian (1972) on L. oceanica and Carefoot (1973b) on L. pallasii, while others have : e.g. McGill (1978) on L. occidentalis and Koop & Field (1980) on L. dilatata. Failure to find a relationship may be due to :

a) A lack of discrimination of seasonal differences between breeding groups.
b) Not standardising for brood developmental stage.
c) A small range of female sizes.

A notable feature of these fecundity regressions for L. oceanica is the large amount of residual variation not explained by the regression : this will be examined later.

b) Brood pouch mortality

Average brood pouch mortality was low : 1.86 ± 1.32% (95% C.I., $n = 45$). There was no significant difference between EARLY and LATE breeding groups ($t = 0.30$, d.f. = 44, n.s.). The percentage values were ARCSINE $\sqrt{x}$ transformed for the analysis. There was no evidence of embryo loss from the brood pouch except in rare specimens with malformed oostegites. There was no evidence of increased mortality in large specimens.

There is little published data on brood pouch mortality in Ligia, but what there is suggests that it is low (Pandian, 1972; Koop & Field, 1980). Carefoot (1973b) gives a value of <5% for Ligia pallasii. Brood pouch mortality in terrestrial isopods is generally low : 0.8%, 3.6% and 4.6% are recorded for Philoscia muscorum (Sutton, 1968; Sunderland, Hassall & Sutton, 1976); 7.4% and 6% in Armadillidium vulgare (Paris & Pitelka, 1962, Al-Dabbagh & Block, 1981). Lawlor (1976) found that brood pouch mortality increased from 2.39% in animals aged one year to 3.27% in three year old females of A. vulgare. Davis (1978) found brood pouch mortalities of 2.77% and 5.66% in early and late breeding groups of P. scaber.

Except in Idotea baltica (Strong, 1978), brood pouch mortality has been found to be much greater in marine isopods : Jones & Naylor (1971) record about 50% in Jaera spp., while Sjöberg (1970) notes up to 60% in this group; Jones (1974) records 26.5% for J. normanndii. Holdich (1968) found 36.4% for Dynamene bidentata. In part this higher mortality is due to unequal developmental rates within a brood and/or loss from the brood pouch during development, neither of which seem to occur in terrestrial isopods.

6. NATALITY AND RECRUIT DENSITY

i. Estimation of natality

Natality has been estimated for the three years 1980 to 1982. The female population has been divided into those breeding EARLY, those breeding LATE, and a very small number of EARLY breeders which carry a second brood (VERY LATE). The mean size of those females carrying broods in each year was calculated for each group. From this figure the average fecundity of an individual female was calculated from the regression of fecundity on live weight established in 1982 (Fig 12). Thus I assume that the nature of this relationship does not change between years.

The average density of females of each group was assessed for a time period spanning the date of release of their young into the population. The proportion of each year class breeding at each time was assessed from Fig 10. This was the maximum proportion of animals in reproductive condition, including both animals with broods and post-parturient animals in some cases. The contribution by each breeding group to the egg standing crop is then given by :

Density x Proportion Breeding x Fecundity

From this the number of births m^{-2} could be derived by correcting for brood pouch mortality.

For the VERY LATE group of breeding animals, which were very few in number, slightly different values had to be used. To assess the size of breeding animals the average size of females of this age, whether breeding or not, was used. The fecundity was calculated from the regression for EARLY breeding animals.

The standard errors of the estimated quantities have been used to derive standard errors for the computed quantities following Gilbert (1973) :

Table 14. Calculation of natality.

	1980			1981			1982		
	EARLY	LATE	V. LATE	EARLY	LATE	V. LATE	EARLY	LATE	V. LATE
DATE OF DENSITY ESTIMATE	14 June	1 Aug.	5 Sept.	16 June	30 July	5 Sept.	5 June —	27 July	18 Aug.
No. FEMALES m^{-2} ±S.E. (n)	1.48 ±0.46 (54)	10.37 ±1.12 (81)	0.52 ±0.18 (54)	1.73 ±0.34 (81)	10.28 ±0.75 (135)	1.33 ±0.32 (81)	2.30 ±0.35 (108)	8.04 ±0.78 (108)	1.04 ±0.35 (54)
L.W. PREGNANT FEMALES mg ±S.E. (n)	426.6 ±13.9 (40)	243.9 ±4.2 (64)	476.4 ±26.7 (7)	412.4 ±9.0 (64)	237.5 ±3.9 (78)	445.9 ±6.9 (9)	415.2 ±9.6 (91)	232.8 ±3.6 (99)	404.4 ±18.3 (13)
WGT. SPEC. FECUND. per INDIVIDUAL ±S.E.	90.9±10.7	73.6±4.2	99.0±11.6	88.5±10.5	71.9±4.2	94.0±10.4	89.0±10.5	70.6±4.2	87.2±11.0
% YEAR CLASS BREEDING ±S.E. (n)	100 (15)	15.7 ±3.6 (102)	14.3 ±13.2 (7)	100 (35)	15.7 ±3.4 (115)	33.3 ±9.1 (27)	100 (38)	16.6 ±2.3 (253)	14.3 ±9.4 (14)
EGG STANDING CROP m^{-2} ±S.E.	134.6±46.1	119.8±31.1	7.3±7.3	153.0±34.9	115.8±27.3	41.7±15.9	204.3±39.4	94.2±17.1	12.9±9.7
BIRTHS m^{-2} ±S.E.	132.1±44.2	117.6±30.6	7.2±7.2	150.2±34.2	113.7±26.8	41.0±15.6	200.5±38.6	92.5±16.8	12.7±9.5
TOTAL NATALITY m^{-2} ± S.E.	257 ± 54			305 ± 46			306 ± 43		

If $\bar{z} = \bar{x} + \bar{y}$ then $SE_{\bar{z}} = \sqrt{SE_{\bar{x}}^2 + SE_{\bar{y}}^2}$

and if $\bar{z} = \bar{x} \cdot \bar{y}$ then $SE_{\bar{z}} = \bar{x}.\bar{y}.\sqrt{\left(\frac{SE_{\bar{x}}}{\bar{x}}\right)^2 + \left(\frac{SE_{\bar{y}}}{\bar{y}}\right)^2}$

The results are shown in Table 14.

The natality estimates for the three years 1980 to 1982 were all remarkably similar, with that for 1980 being slightly lower than those for 1981 and 1982. Not only was the total natality in each year similar, but the relative contributions of the EARLY (56%), LATE (37%) and VERY LATE (7%) breeding animals to the total natality were also very similar between years.

Closer examination shows that the most significant factor resulting in variation in natality by a breeding group was variation in population density. Population density was also the least accurate of the estimates made. It should be noted that in calculating the natality the estimates of population density have not been $LOG_{10}(x+1)$ transformed. Hence they contain variation due to the aggregation characteristic of the population in addition to variation in population density. It is the only the latter which will affect natality estimates.

ii. Recruit density

Newly released Ligia are both very small and extremely numerous. At R.H.B. they could be found mostly at the base of the sea-wall in amongst growth of Enteromorpha spp., where they might be better able to avoid desiccation. As reported elsewhere (e.g. Nicholls, 1931a) they are less nocturnal in their habits at this stage. By October they could be sampled using the quadrat method described earlier but, because of the increased search time per quadrat, only twelve random quadrats could be sampled on each occasion. The estimated densities are shown in Table 15. Although by this time some recruits were quite large and conspicuous, the smaller animals could easily be overlooked. This, together with declining temperatures and therefore declining activity at this time of year, makes the estimates in Table 15 likely to be underestimates.

These estimates, together with those for the adult animals, have been used in the constuction of life tables and survivorship curves.

TABLE 15. First estimates of recruit density. Values are numbers per 0.25 m^2 quadrat ± 95% C.I.

YEAR	DATE	DENSITY
1980	11 September	9.08 ± 3.43
	13 September	17.58 ± 8.97
	15 September	14.50 ± 12.69
	6 October	6.17 ± 2.95
	8 October	8.08 ± 3.40
	11 October	8.58 ± 4.07
1981	13 September	13.42 ± 8.85
	9 October	7.25 ± 4.70

7. SURVIVORSHIP AND LIFE TABLES

Only one year class (1979) was followed throughout its life, and for this I do not have an estimate of natality (ie. numbers at t = 0), and so it cannot be used to construct a time-specific life table. Given these limitations I felt justified in using all the data available to construct average survivorship curves and life tables (Deevey, 1947) for the population. This is reasonable given the stable age distribution of the population throughout the study and the very limited changes in population density between years. Hence the life tables are both time- and age-specific, the two types being identical when the assumed conditions are met. Using the estimates of natality (Table 14) I have been able to calculate the number of recruits per unit area for the three years. Using the mean figure as a starting point, and assuming that all the recruits are born on July 1st of each year, with a sex ratio of 1:1, life tables for males and females have been constructed by using the estimates of population density of each age class at the time of each sample.

The life tables are shown in Tables 16 and 17, and are constructed on a 30 day time interval. The data are represented graphically as survivorship curves in Fig 13. Initial life expectancy is poor, only 79 days for females and less for males. However if young animals survive their first three months then life expectancy is high : well over a year for females. Male life expectancy is generally lower than that of females until very late in life when, aged about 24 months, it is slightly higher. Maximum longevity in both sexes was about 30 months. The presence of a few large males in autumn indicates a slightly greater longevity in this sex. Occasionally these animals would persist into early spring.

Surprisingly, perhaps, survivorship was always higher overwinter than during the summer. This is probably explained by general inactivity during cold weather when the animals remain within their crevices except on occasional warm nights. Ligia oceanica are known to be able to withstand

TABLE 16. Life table for females at R.H.B.

DAYS$_x$	l_x	d_x	L_x	T_x	e_x	$30e_x$	$100q_x$
0	1000	571	715	2636	2.64	79	57
30	429	231	314	1936	4.48	134	54
60	198	82	157	1606	8.11	243	41
90	116	17	108	1449	12.49	375	15
120	99	2	98	1342	13.55	407	2
150	97	1	97	1244	12.82	385	1
180	96	1	96	1147	11.95	358	1
210	95	1	95	1052	11.07	332	1
240	94	1	94	957	10.18	305	1
270	93	2	92	864	9.29	279	2
300	91	4	89	772	8.48	254	4
330	87	7	84	683	7.85	235	8
360	80	6	77	599	7.49	225	8
390	74	7	71	522	7.05	212	10
420	67	6	64	449	6.69	201	9
450	61	6	58	385	6.30	189	10
480	55	5	53	327	5.94	178	9
510	50	5	48	274	5.48	164	10
540	45	5	43	227	5.03	151	11
570	40	4	38	184	4.60	138	10
600	36	4	34	146	4.06	122	11
630	32	4	30	112	3.50	105	13
660	28	4	26	82	2.93	88	14
690	23	5	21	57	2.46	74	22
720	18	5	15	36	2.00	60	28
750	12	6	10	21	1.75	53	50
780	8	4	6	11	1.38	42	50
810	4	4	3	5	1.25	38	100
840	2	2	2	2	1.00	30	100
870	1	1	1	1	0.50	15	100
900	0	0	0	0	0.00	0	100

where x = age

l_x = number alive at start of interval x

d_x = number dying in interval x

L_x = number alive between age x and x+1

$T_x = \sum_{x}^{k} l_x$

e_x = age-specific expectation of life in units of 30 days.

$30e_x$ = age-specific expectation of life in days.

$100q_x$ = mortality rate per hundred alive at beginning of age interval x

k = last age group.

TABLE 17. Life table for males at R.H.B.

DAYS$_x$	l_x	d_x	L_x	T_x	e_x	$30e_x$	$100q_x$
0	1000	558	721	2312	2.31	69	56
30	442	236	324	1591	3.60	108	53
60	206	82	165	1267	6.15	185	40
90	124	34	107	1102	8.89	267	27
120	90	7	87	995	11.06	332	8
150	83	2	82	909	10.95	328	2
180	81	1	81	827	10.20	306	1
210	80	0	80	746	9.33	280	0
240	80	0	80	666	8.33	250	0
270	80	1	80	586	7.33	220	1
300	79	0	79	507	6.41	192	0
330	79	4	77	428	5.41	162	5
360	75	9	71	351	4.67	140	12
390	66	13	60	280	4.24	127	20
420	53	11	48	221	4.16	125	21
450	42	9	38	173	4.12	124	21
480	33	7	30	136	4.11	123	21
510	26	6	23	106	4.08	122	23
540	20	4	18	83	4.15	125	20
570	16	3	15	65	4.06	122	19
600	13	3	12	51	3.89	117	23
630	10	2	9	39	3.90	117	20
660	8	2	7	30	3.75	113	25
690	6	1	6	23	3.83	115	17
720	5	1	5	18	3.50	105	20
750	4	1	4	13	3.25	98	25
780	3	1	3	10	3.17	95	33
810	2	0	2	7	3.50	105	0
840	2	0	2	5	2.50	75	0
870	2	1	2	3	1.50	45	50
900	1	0	1	2	1.50	45	0
930	1	1	1	1	0.50	15	100
960	0	0	0	0	0.00	0	100

where x = age

l_x = number alive at start of interval x

d_x = number dying in interval x

L_x = number alive between age x and $x+1$

$T_x = \sum_{x}^{k} l_x$

e_x = age-specific expectation of life in units of 30 days.

$30e_x$ = age-specific expectation of life in days.

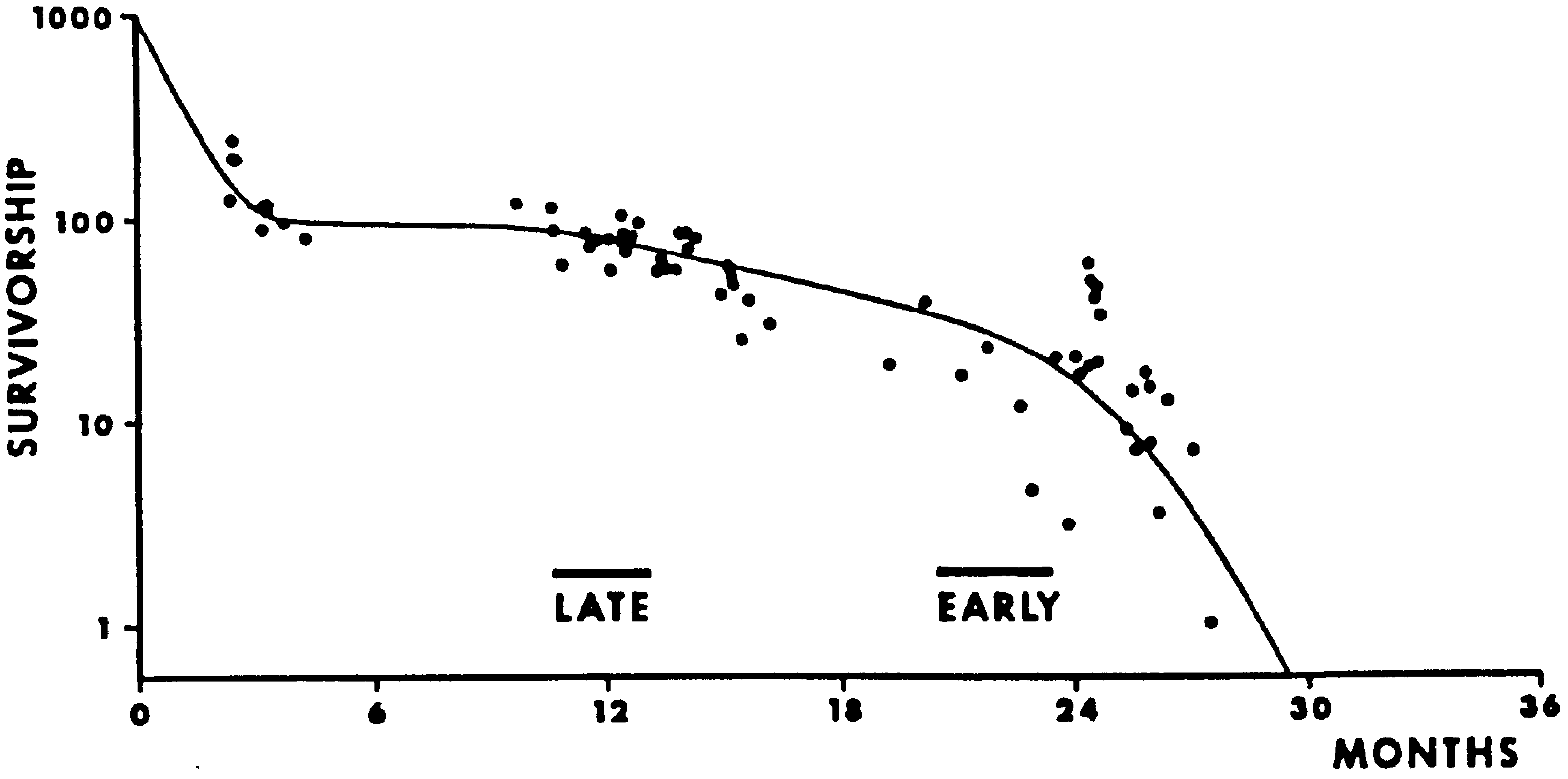
$100q_x$ = mortality rate per hundred alive at beginning of age interval x

k = last age group.

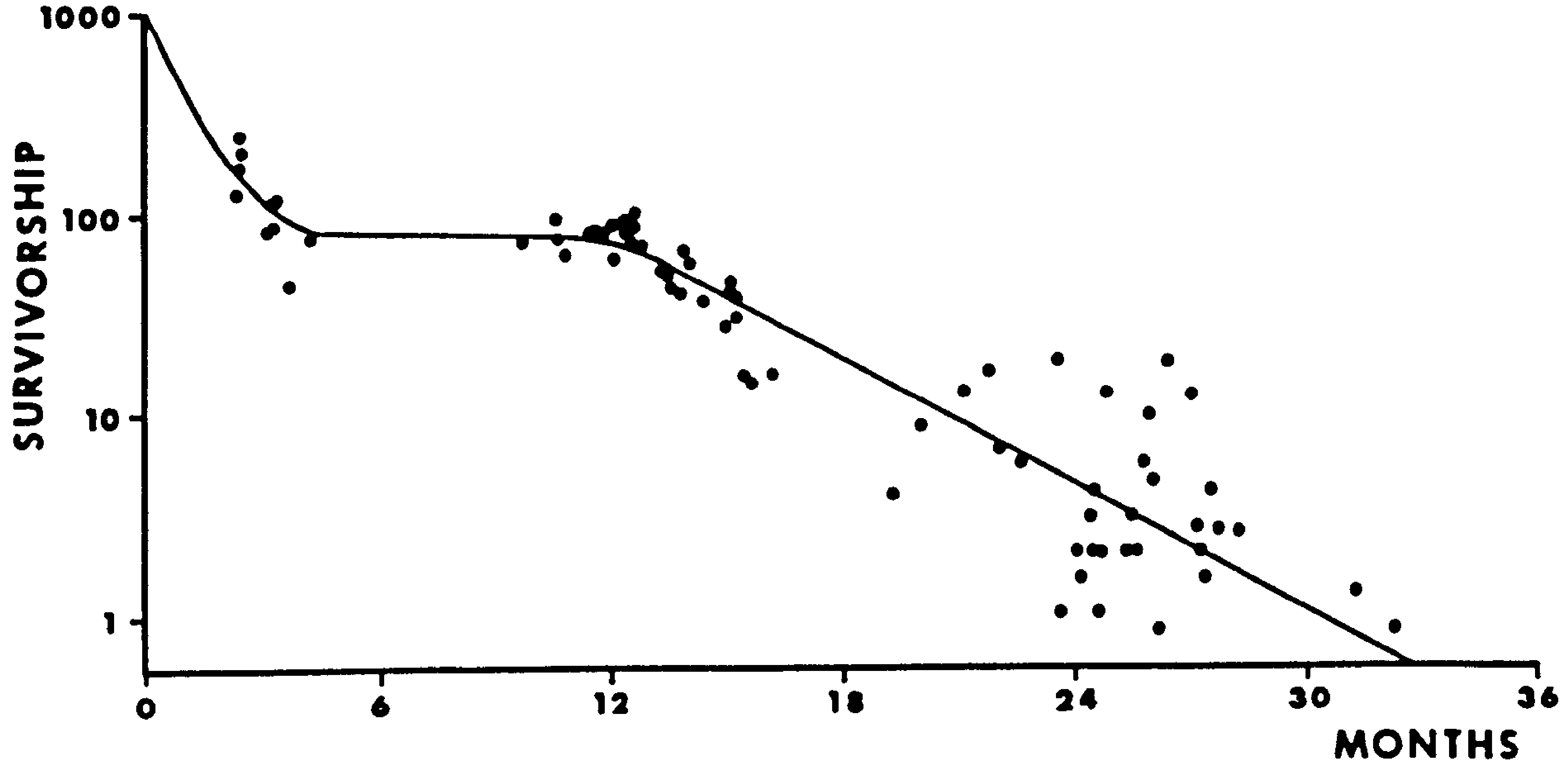
FIGURE 13

Survivorship curves for females and males at Robin Hood's Bay. The periods when LATE and EARLY breeding females are carrying broods are indicated.

FEMALES



MALES



prolonged periods of starvation and are better able to do so in the winter than during the summer even at the same experimental temperature (Storch & Lehnert-Moritz, 1980). These authors found that histological changes in the hepatopancreas brought about by ten weeks starvation could be reversed within a week by feeding on Mytilus edulis, perhaps a somewhat unlikely food resource in the field.

Causes of mortality for Ligia were difficult to define. Various authors (e.g. Sutton, 1968; Sunderland et al., 1976; Al-Dabbagh & Block, 1981) have suggested that woodlice are particularly prone to death following release of the brood, perhaps as a result of stress imposed by the post-parturient moult. The survivorship curve suggested that increased mortality did indeed follow the release of young by the older EARLY females. To examine post-reproductive mortality in Ligia a number of females recently post-parturient or about to release their broods were collected from a population at Whitby. These were maintained in the laboratory and their survivorship and stage in the moult cycle recorded daily. A control group, consisted of a random collection of animals but excluding post-parturient females, was also maintained. All the post-reproductive females belonged to the EARLY group (i.e. were aged about 24 months). The daily survival rates were ARCSINE $\sqrt{x}$ transformed : the mean values for both groups were high but significantly different ($t = 4.55$, d.f. = 41, $P \ll 0.001$) :

GROUP	n	DAILY SURVIVAL RATE	UPPER 95% CONFIDENCE LIMIT	LOWER 95% CONFIDENCE LIMIT
Control	24	1.000	1.000	0.999
Post-Reproductive	19	0.980	0.993	0.960

There was no evidence of increased mortality during the peak moulting period of the post-reproductive animals, so the difference in survivorship might only reflect the difference in age of the two groups of animals. Although the post-parturient moult does not, of itself, result in increased mortality, individuals might be more susceptible to adverse climatic conditions at this time. The sharp increase in mortality observed after 24 months of age might be post-reproductive mortality of this sort, or might reflect the onset of senescence.

Of other causes of mortality of *Ligia* predation has received some attention. Mink, *Mustela vison*, can consume *Ligia* in some quantities (N. Dunstone, pers. comm.), but are not known at R.H.B. I have observed rats, *Rattus norvegicus*, taking *Ligia* on rocky shores in Anglesey. Rock pipits, *Anthus spiroletta*, are known to feed on *Idotea* spp. (Gibb, 1956) and may possibly take *Ligia*. Nicholls (1931a) reported that crabs, *Carcinus maenas*, can take *Ligia*, but it is not believed that the one crab resident on the R.H.B. sampling site could make significant inroads into the population, especially given its apparent lack of talent in catching them. Although small mammals and birds may be significant predators on rocky shores, *Ligia* living on sea-walls appear to be immune.

Occasionally animals would be collected suffering from desiccation, especially during neap tides in August. Such animals typically have a contracted appearance and dry cuticular surface. Other abiotic factors possibly contributing to mortality are heavy seas, which could wash animals off the wall, and strong winds which could blow them off.

There was no single, dominant and identifiable cause of mortality. Predation could be ruled out, and probably a range of climatic factors contribute together to cause the observed mortality pattern.

8. FERTILITY AND REPRODUCTIVE VALUE

Fertility tables (Birch, 1948) have been calculated for each year class, but only those for the 1979 and 1980 year classes are complete. The number of survivors (l_x) was calculated by dividing the density of reproductive females by the average total yearly natality, and is justified only if the population age structure and size was constant from year to year. The age structure was constant but there were slight variations in population density between years. The fecundity schedule (m_x) has been calculated using the size specific fecundities derived from the fecundity regression for 1982. The net reproductive rate (R_o), the field value for the intrinsic rate of increase (r_f) and the generation time (T) have been calculated in the usual manner (Birch, 1948) as :

$$R_o = \sum_{x=0}^{\infty} l_x . m_x$$

$$\sum_{x=0}^{\infty} e^{-r_f . x} \; l_x . m_x = 1$$

$$R_o = e^{r_f . T}$$

and the results shown in Table 18.

The values for R_o are slightly greater than 1.0, and those of r_f slightly greater than 0.0, and reflect the greater than average population densities recorded in 1980 and 1981, when these two year classes were responsible for much of the reproduction by the population. Population densities in July (Table 3) are determined primarily by the previous summer's recruits, two year old animals being only a small proportion of the total. Because of the division of reproduction by a single year class into two main periods in successive years, and because the contributions of EARLY and LATE animals to R_o are about equal, no one year class alone can be responsible for a greater or lower than average yearly recruitment. Recruitment depends on the reproductive performance of two groups of animals belonging to different year classes. As Sunderland, Hassall & Sutton (1976)

TABLE 18. Fecundity schedule for the Robin Hood's Bay population.

BREEDING GROUP	1979			1980			1981			1982		
	l_x	m_x	$l_x \cdot m_x$	l_x	m_x	$l_x \cdot m_x$	l_x	m_x	$l_x \cdot m_x$	l_x	m_x	$l_x \cdot m_x$
LATE	----	-----	----	0.072	5.67	0.41	0.071	5.54	0.39	0.056	5.75	0.32
EARLY	0.01	44.61	0.45	0.012	43.43	0.52	0.016	43.67	0.70	-----	----	----
V. LATE	0.004	6.95	0.03	0.009	15.36	0.14	0.007	6.12	0.04	-----	----	----
R_o						1.07			1.13			
r_f						0.003			0.007			
T (years)						1.57			1.60			

concluded from their study of *Philoscia muscorum*, a division of reproduction by a year class between different years can contribute a degree of stability to the population dynamics of such species, even though individuals are semelparous. This cannot be the evolutionary cause of the phenomenon as it would require the operation of group selection (Maynard Smith, 1976).

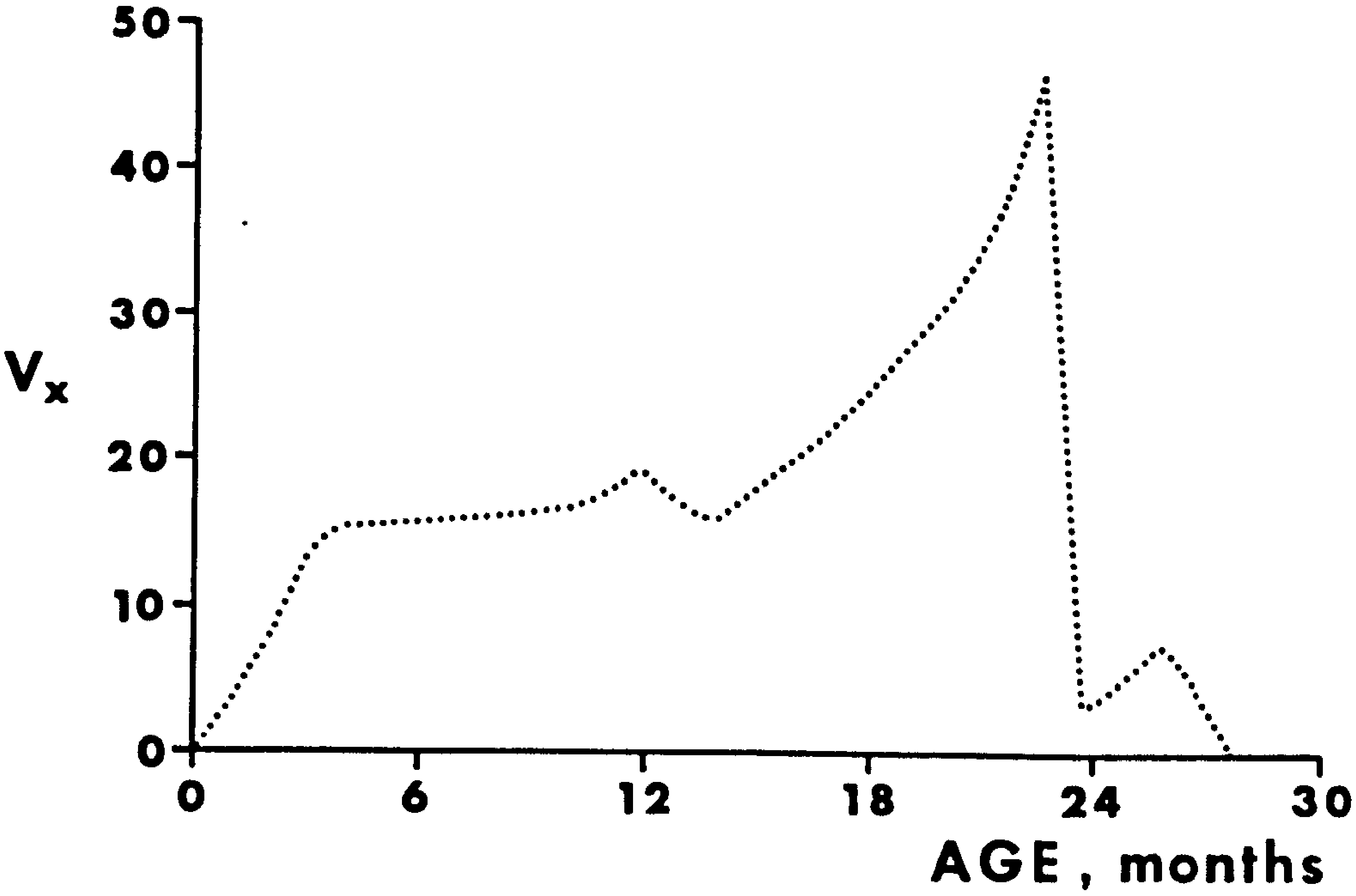
Fisher's age specific reproductive value (V_x) (Fisher, 1930; Stearns, 1976) has been calculated as :

$$V_{x'} = \frac{1}{l_{x'}} \cdot \sum_{x=x'}^{\infty} l_x \cdot m_x$$

using values of l_x from Table 16 and the average weight specific fecundities of the different breeding groups for m_x. The result is shown in Fig 14. Initially V_x increased as juveniles experienced initial mortality and then remained at a fairly steady level until the LATE breeding animals (≈16% of the total) released their offspring. V_x then increased sharply as the number of survivors decreased, and peaked just before the EARLY breeding animals released their offspring. The reproductive value of those animals producing a second brood near the end of their lives is very small. Although the EARLY and LATE groups contribute more or less equally to the net reproductive rate, individuals producing EARLY broods late in life have a much higher value of V_x. This is because all individuals which survive produce EARLY broods and offspring at this age and have, overall, a higher absolute fecundity per individual than the smaller proportion of individuals which reproduce earlier in life. The EARLY reproducing animals, at maximal V_x, should be those most sensitive to natural selection (Fisher, 1930; Stearns, 1976).

FIGURE 14

Fisher's (1930) reproductive value (V_x) as a function of age for Ligia oceanica at Robin Hood's Bay.


50
40
30
20
10
0
V_x
0
6
12
18
24
30
AGE , months

9. DISCUSSION

Ligia at R.H.B. is remarkable for the stability of its population between years. This stability is achieved through a constancy of all the components contributing to the population dynamics, namely the percentage of each year class breeding EARLY and LATE within each year, the time of breeding, the size and densities of gravid females, and the survivorship. Although fecundity was only determined for one year, data from the population at Whitby suggests that fecundity does not change between years either.

Particularly striking were the similarities between years in breeding phenology and size of females producing EARLY and LATE broods. This reflects almost identical growth rates during the months preceeding the onset of reproduction and suggests that some process is limiting or regulating growth. Temperature (Sutton, 1972) and food availability and quality (Merriam, 1971; Rushton & Hassall, 1983) are both important in determining woodlouse growth rates. Temperature acts mainly by affecting the metabolic activity level of animals, though it may also affect the productivity of the habitat. While we do not have in situ measurements of temperature it seems unlikely that the yearly temperature regimes were so similar during the study as to explain totally the highly consistent reproductive patterns which were observed. The possibility that the population is limited by the availability of a resource, probably food but possibly shelter sites (crevices), is more attractive. Koop & Field (1980) found that for the South African Ligia dilatata growth is actually slower during the warmer summer months. Rapid growth was correlated with the deposition of kelp (the major food item of this species) on the shore in winter. Hence they concluded that it was the availability of allochthonous detritus that limited growth rates, not temperature.

To test this hypothesis the field population would have to be manipulated experimentally by reducing the level of the population. If the population is resource limited the remaining animals should respond by either increased growth rates and/or increased survivorship, both of which would result in increased natality per capita. However, if temperature is responsible for the observed stability of the population, as suggested for populations of *Porcellio spinicornis* Say (McQueen & Carnio, 1974; McQueen, 1976a,b), then there should be little affect when compared with previous years. This manipulation has been performed on the population of *L. oceanica* at R.H.B. by removing about half the gravid females of each breeding group in 1982. The Whitby population provides a control. The effects, if any, on the population will not be known until 1983 and 1984.

The breeding phenology of *Ligia* at R.H.B. is complex and interesting. Each year class is made up of two subgroups; one born early in the year in June, and one born later in July/August. Unfortunately these animals cannot be distinguished in field samples, and so their individual mortality patterns cannot be determined. About 16% of the surviving females of this year class will reproduce in their first summer (≈12 months old). Since only the largest females of the year class produce broods at this time they were presumably born early in the previous summer and have experienced a greater number of degree days of growth. This also suggests that there is a minimum size which must be achieved before reproduction can occur. After overwintering the remaining animals of this year class reproduce the following spring, and release their broods in June (≈24 months old). A very few of these animals survive to produce a second brood very late in the summer. It is not known whether those animals which reproduce in their first summer themselves survive to reproduce a second time in June, but only a few could be involved. This pattern of reproduction is shown diagrammatically in Fig 15a. Reproduction in *Ligia* is essentially semelparous.

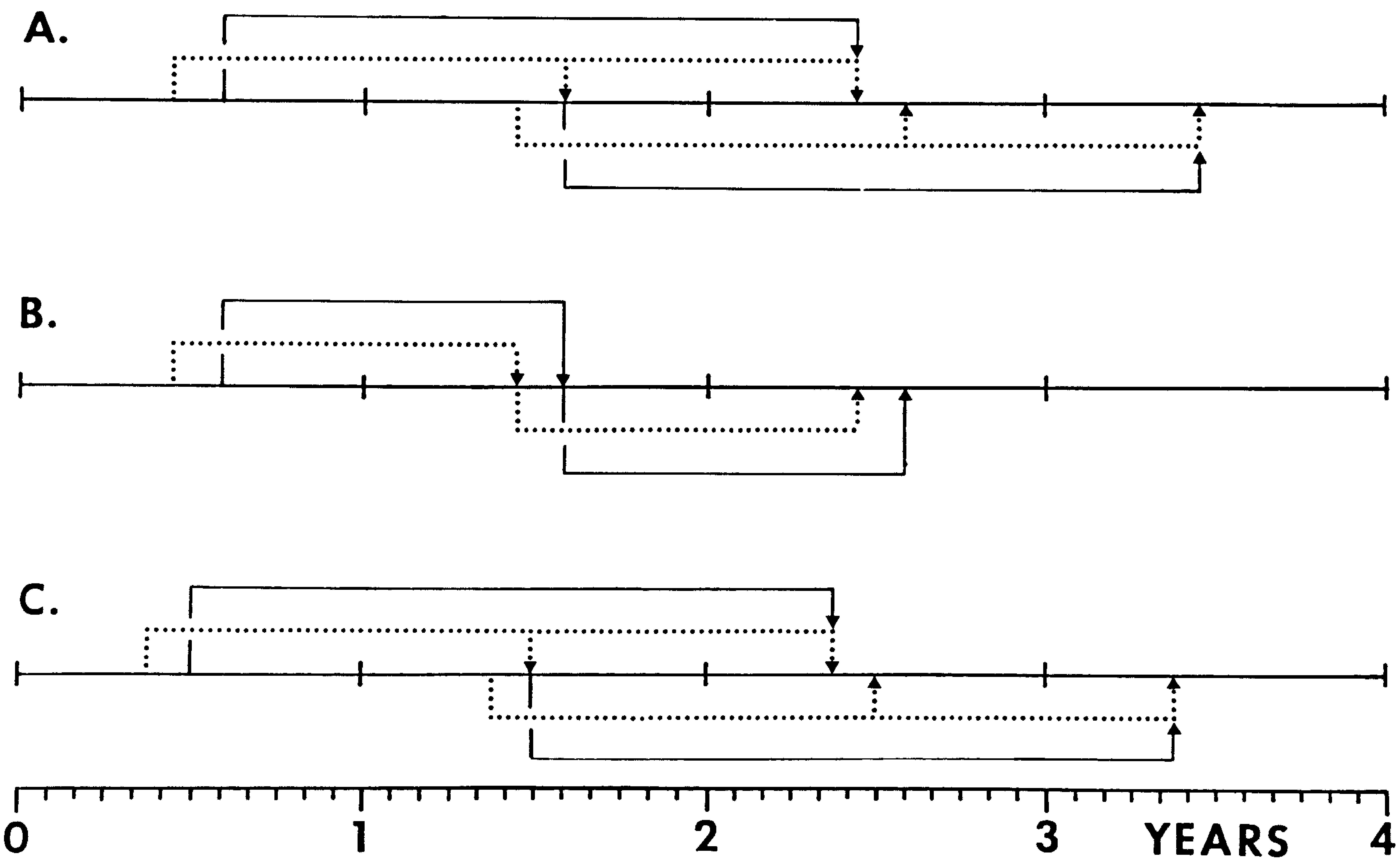
Two independent studies on populations of *L. oceanica*, in the Western Baltic (Jöns, 1965) and near La Rochelle on the Charente-Maritime (Mocquard *et al.*, 1974; Besse *et al.*, 1975), have both described two phases of brood production

FIGURE 15

Diagrammatic representation of the breeding phenologies of *Ligia* populations.

a. *Ligia oceanica* at Robin Hood's Bay (this study)
b. *Ligia oceanica* at La Rochelle (Besse et al. 1975)
c. *Ligia pallasii* at Vancouver (Carefoot, 1973b).

………………… offspring born to EARLY breeding females
———————— offspring born to LATE breeding females


A.
B.
C.
0
1
2
3
YEARS
4

and recruitment. Both recorded the time of year when births occur as June and July/August, exactly the same times of year as those determined in this study. This suggests an invariant seasonality in the reproductive biology of L. oceanica which we would not expect over such a wide latitudinal range.

However the situation in the French population is actually somewhat different to that at R.H.B. At La Rochelle each breeding group is made up of animals aged 12 months, and all those animals born EARLY reproduce EARLY, and those born LATE breed LATE (see Fig 15b). The maximum longevity of females in the French population was only 15-18 months, compared to 30-36 months at R.H.B., and the majority of animals died after the production of a single brood (Besse et al., 1975). From their data (Mocquard et al., 1974) I have calculated the mean sizes of gravid females reproducing EARLY and LATE as 205.8 mg (n = 425) and 168.6 mg (n = 214) respectively, compared with 416.6 mg (n = 195) and 237.3 mg (n = 241) at R.H.B. Not only are the females within each breeding group in the French population considerably smaller, but the average weight of females reproducing LATE, in July/August, on the French coast is less than the minimum size of gravid females ever recorded at R.H.B.

The time of year at which Ligia produces its broods appears to be constant and independent of latitude. This being the case then the observed differences in sizes and ages at reproduction can be interpreted as a consequence of different rates of growth at different localities. Animals in the French population grow much faster than those at R.H.B., and grow sufficiently quickly to enable all animals to reach reproductive size before the onset of the favourable reproductive season in their first summer. Ligia seem to reproduce at the first opportunity that size, as determined by growth rates, and season allow. For the French population this is 12 months after birth for both groups of recruits. In the less hospitable climate of R.H.B. lower growth rates result in only a few animals achieving the minimum size at which reproduction can occur in their first summer. This leads overall to an increase in the age at first reproduction. However it does not explain why more animals in their first summer at R.H.B. do not reproduce. Although the majority are immature and below the size at which reproduction can occur, some are above the minimum sizes observed at La Rochelle. These animals are presumably physiologically capable of producing broods yet do not do so. Perhaps the environmental cue to reproduction occurs too early in the development of these animals at R.H.B.

Jöns (1975) studied his population over a single summer and determined the two phases of recruitment by the analysis of length frequency histograms. The first group of recruits achieved sexual maturity by the end of their first summer and, as in the French population (Mocquard _et_ _al_., 1974), had a faster growth rate than the second wave of recruits. The latter did not achieve sexual maturity until the following spring. From his data it is impossible to distinguish whether or not the two groups of recruits are born to animals of similar size and age as those at R.H.B., or those at La Rochelle, if either. At R.H.B. only a proportion (mostly males) of animals born during a summer are mature by autumn, and if his estimate of longevity (15-18 months) is correct, then the Baltic population would seem to have more in common with that in France than that at R.H.B.

Do other species within the genus _Ligia_ exhibit this pattern of reproduction? Carefoot (1973b) in his study of _L. pallasii_ on the Pacific coast of Canada found that 70% of females entering the winter of their second year would become gravid by midwinter (about 18 months old), but the eggs showed no signs of development until May when juveniles were first released. Furthermore he states :

> "Those females not holding a winter brood of eggs and reaching reproductive maturity by the spring of their first year (10-14 months of age depending on whether they were of early or late recruitment stock of the previous year), produce their first brood of young at this time."

Broods produced in spring will result in offspring being released in early summer. Again two distinct reproductive periods are evident, with broods being produced in winter and spring, rather than spring and summer as in L. oceanica. Clearly the breeding phenology of L. pallasii is very similar to that of L. oceanica at R.H.B., and is summarised in Fig 15c. Jackson (1922) noted the morphological similarities of the two species and considered them to be closely related. This similarity extends to their ecology. Both are north temperate, living in crevices in cliffs and on rocky shores, and, like L. oceanica, L. pallasii is herbivorous, feeding mostly on encrusting diatoms and green seaweeds (Carefoot, 1973a). Furthermore, both live up to two years, and are of similar size with similar growth rates in addition to possessing similar breeding phenologies.

In the population of Ligia dilatata studied by Koop & Field (1980) there was no evidence of two breeding groups. L. dilatata breeds first at 12 months of age, and only 2-5% of animals live to 24 months of age and a second breeding season. They concluded that L. dilatata usually only breed once. The survivorship curve for this species is similar to that for L. oceanica at R.H.B., with a constant low rate of mortality up to the time at which females reproduce. Following this a faster mortality rate was experienced by the year class. Koop & Field (1980) do not discuss initial juvenile survivorship over the first six months of life, but it is clear from their data that mortality is substantial.

The upper intertidal zone is frequently regarded as a severe habitat (eg. Carefoot, 1973a; Lewis, 1964) and populations of species inhabiting this region might be expected to suffer high levels of density independent mortality and be unstable. Such is clearly not the case for this species at least. The R.H.B. population of Ligia has remained very constant over three years, and shows interesting similarities with other populations of this and other species. Although the supralittoral may indeed be a severe environment Ligia is well adapted to it and these adaptations can be divided into the behavioural and physiological.

Ligia is well able to withstand physiological stress. Large, rapid and prolonged increases in osmotic pressure due to water loss by desiccation are tolerated (Parry, 1953). Animals also show significant levels of osmoregulation when placed in dilute sea water and this helps to reduce the decrease in internal blood osmotic pressure (Parry, 1953; Todd, 1953; Wilson, 1970). Ligia can survive in 100-50% aerated sea water indefinitely (Parry, 1953), while their ability to resist prolonged starvation (Storch & Lehnert-Moritz, 1980) has already been noted. Although Ligia rapidly loses water by transpiration when maintained at relative humidities less than 100% its large size reduces its susceptibility to desiccation (Edney, 1951).

The success of woodlice in occupying the terrestrial habitat is generally ascribed to behavioural mechanisms to avoid the worst excesses of the environment (Edney, 1954, 1968; Warburg, 1968). By occupying deep, moist crevices during the day and in the winter variations in temperature are lessened and desiccation avoided (Edney, 1953; Glynne-Williams & Hobart, 1952), while they remain protected from strong winds, wave action and vertebrate predators. Additional behavioural adaptations include temperature regulation by cuticular respiration (Edney, 1951, 1953, 1954, 1968), reduced water loss by aggregation (Farr, 1978), water uptake by anal drinking (Spencer & Edney, 1954) and migration. Local seasonal migrations of L. oceanica up the shore in September have been described by a keeper on the Fastnet Light (O'Connor, 1945).

For the majority of terrstrial woodlice a lack of water can pose major physiological (Edney & Spencer, 1955) and ecological (Sutton, 1968) problems, while for Ligia its supply is as regular as the tides. The environment Ligia experiences may be harsh and seasonal, but the evidence suggests that Ligia is unaffected. This is supported by this study of the population dynamics, showing a constant population size between years, an overall constancy in the component parts of the species population ecology and very low levels of mortality, especially overwinter, experienced by adults prior to reproduction. Crevices between rocks in the supralittoral surely represent one of the more permanent structural resources within the environment especially when defined, as they must be, in terms of the lifespan of the animal (Southwood *et al*., 1974; Southwood, 1977). The constant and predictable nature of conditions within supralittoral crevices over space and time, given gross seasonal and latitudinal variations in climate and biota, probably helps explain why different populations and species of *Ligia* have such similar ecologies.

Ligia populations have characteristics of both K-strategists (in the terminology of Pianka, 1970, 1972) and stress (Grime, 1977) or adversity (Southwood, 1977; Greenslade, 1983) adapted species. That *Ligia* might be adversity adapted is supported by their physiology. *Ligia* resist osmotic stress by osmoregulation (Parry, 1953; Todd, 1953; Wilson, 1970), and this is much more expensive in energetic terms than the alternative strategy of osmoconformity (Potts, 1954; Potts & Parry, 1963). In the harsh osmotic environment of the supralittoral osmoregulation presumably confers a benefit in terms of individual survivorship and hence reproductive success that offsets the energetic cost.

Ligia would also fit the definition of a K-strategist of Southwood *et al*., (1974) and Southwood (1977) in that it occupies a habitat of long, if seasonal, stability and durability and has those characteristics of a K-selected species as defined by Pianka (1970, 1972). However iteroparity is a characteristic of K-selected species (Pianka, 1970, 1972; Stearns, 1976) yet *Ligia* is semelparous. An alternative model of life history evolution, that of "bet-hedging" (Murphy, 1968; Schaffer, 1974a; Stearns, 1976) predicts that species should be iteroparous only if juvenile survivorship, and therefore recruitment, is unpredictable. Such is not the case for *Ligia oceanica* which, although experiencing high levels of juvenile mortality (≈ 90%), had constant recruitment during the period of this study. Furthermore the size structure of the population suggests that it had been so in the recent past.

Although semelparous, the complex breeding phenology of Ligia at R.H.B. means that even if all recruitment should fail in one year there would be limited natality the following year due to surviving females reproducing EARLY that spring. Such would not be the case for the French population of Mocquard et al., (1974) and Besse et al., (1975), which would only persist if the progeny of one breeding group were to fail to reach maturity in a given year. Hence for a semelparous species the complex breeding phenology of L. oceanica confers a degree of bet-hedging on the population. However this cannot be the evolutionary cause unless we are to raise the spectre of group selection. The effect of temperature on growth rates, shortening the time taken to reach reproductive size, is the proximal explanation. Possible evolutionary explanations will be considered in Chapter 6.

CHAPTER 3

POPULATION DYNAMICS AT A SHELTERED SITE AT WHITBY, AND COMPARISON TO ROBIN HOOD'S BAY.

1. INTRODUCTION

Ligia oceanica is found in highly exposed situations and also in harbours and sea-lochs completely sheltered from wave action. Increased wave exposure can be expected to exert increased levels of density independent mortality. The theory of r- and K-selection, as proposed by MacArthur & Wilson (1967), predicts that those genotypes which maximise "r" should be favoured by high levels of density independent mortality, while under high levels of density dependent mortality genotypes adapted to high carrying capacities should be favoured. Menge (1974) examined the effect of different levels of wave action on the ecology and life history characteristics of two starfish species from this point of view. Recently Stearns (1983a) has looked for differences in life history traits among populations of mosquitofish (Gambusia affinis) inhabiting reservoirs with stable and fluctuating water levels. He also argued, a priori, that differences in habitat should lead to predictable differences in life history traits between the populations. In addition he examined the genetic basis of these differences (Stearns, 1983b).

I decided to study the influence of exposure on the ecology of Ligia by comparing the population at R.H.B. with a sheltered population in Whitby harbour. Separated by only about 10 km of coast, the two sites were chosen to have as similar gross climates (temperature, rainfall, daylength, etc.), habitat structure and food resources as possible, while the isolation of the two populations and the lack of a dispersal stage in the life history of Ligia allows the possibility of local genetic differentiation.

Exposure is known to be important in determining the distributions of many littoral organisms through a variety of mechanisms (Lewis, 1964), and may be expected to affect the population dynamics of such species. Menge (1974) demonstrated such an effect on two competing starfish, *Leptasterias hexactis* and *Pisaster ochraceus*. Roberts & Hughes (1980) found differences in the population ecology of *Littorina rudis* at sheltered and exposed sites in North Wales. More indirect is the response of the dogwhelk *Nucella lapillus* which counters increased crab predation at more sheltered localities by increasing the strength of shell relative to body mass. This strategy should incur an energetic penalty compared to dogwhelks at exposed sites where predation is much less (Hughes & Elner, 1979; Currey & Hughes, 1982).

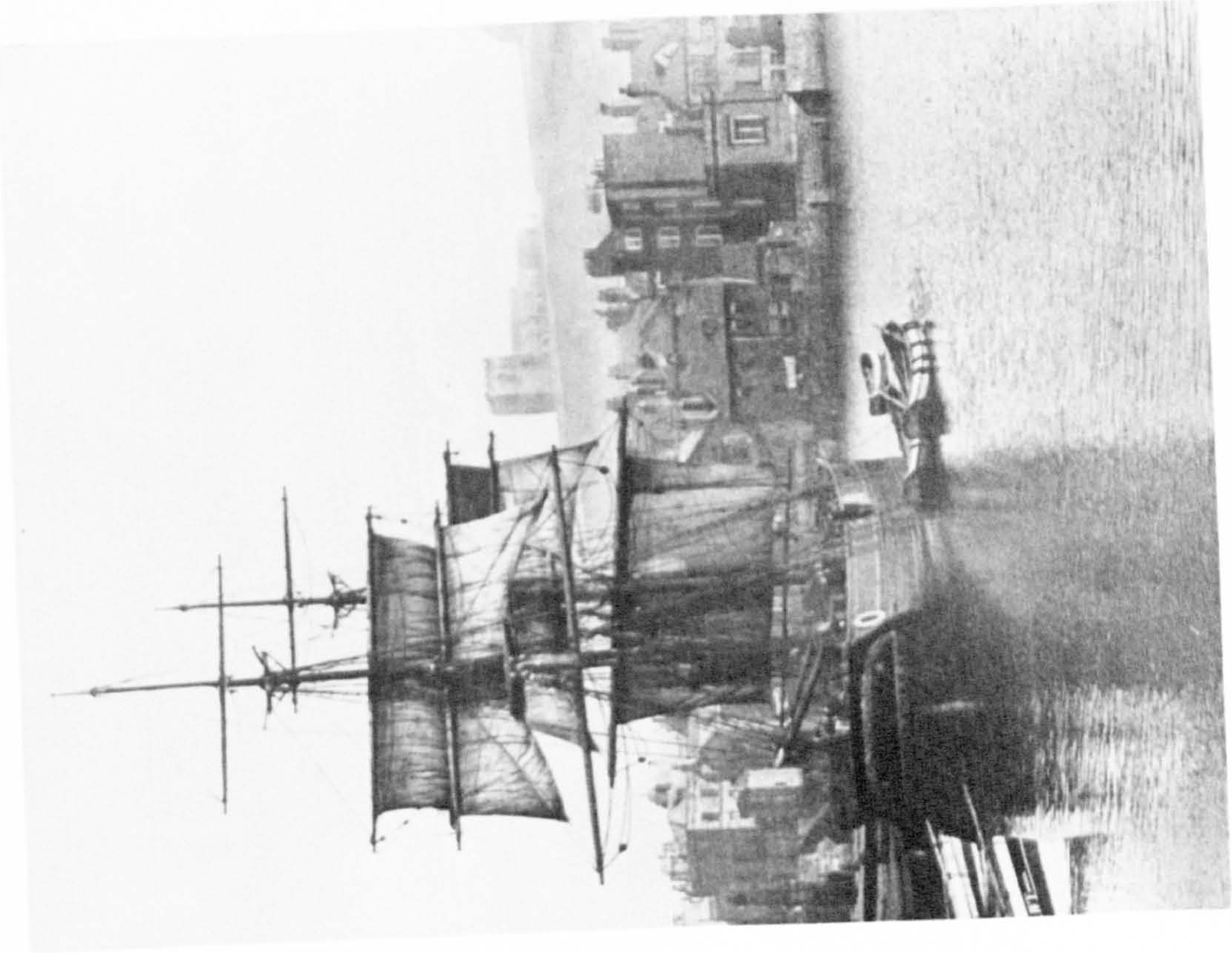
There have been few studies of the variation in population dynamics and life history characteristics between populations of the same species. Apart from those mentioned above, there have been notable studies on insects (Whittaker, 1971; Gilbert, 1980; Istock, 1981; Randall, 1982), snails (Hughes & Roberts, 1981; Begon & Mortimer, 1981), fish (Schaffer & Elson, 1975; Leggett & Carscadden, 1978; Constantz, 1979; Stearns & Sage, 1980), frogs (Berven, 1982), lizards (Ballinger, 1979) and plants (Gadgil & Solbrig, 1972; Law *et al*. 1977; Law, 1979a). Such studies have frequently revealed differences between populations throughout a latitudinal or altitudinal range. Amongst the Crustacea Strong (1972) has studied the life history traits of the amphipod *Hyalella azteca* in laboratory cultures derived from three distinct populations, while Alon & Stancyk (1982) have examined the life history traits of two populations of the shrimp *Palaemonetes pugio*. There have been two intraspecific studies of an isopod (*Armadillidium vulgare*) by Al-Dabbagh & Block (1981) and Miller & Cameron (1983).

PLATE 4

Whitby harbour photographed about 1890 by the famous local photographer Frank Meadow Sutcliffe. The harbour wall sampling site can be seen directly beyond the ships bow.

PLATE 5

Whitby harbour photographed in 1981, showing the harbour wall just after high water. The harbour wall sampling site appears very similar in condition to that shown in Plate 4.



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2. SITE DESCRIPTION AND SAMPLING METHODS

The harbour at Whitby provides suitable habitat for a very substantial population of Ligia. All animals were collected from a wall on the eastern side of the upper harbour (G.R. NZ 900 110). This wall extends from a slipway, passes under the lower bridge and into the lower harbour (see Plates 4 & 5). Animals were collected monthly from the whole length of the wall and any animal which was seen was collected. There was a much larger area of habitat at Whitby than at R.H.B. allowing the collection of a substantial number of animals even in winter. Hence sampling was destructive, but the removal of animals was not thought likely to affect such an extensive population. The animals collected were either used experimentally or preserved.

There were a number of differences between the Whitby and R.H.B. sites which are summarised in Table 19. The most important of these were thought to be exposure and population size. Whitby harbour is extremely sheltered from wave and wind action, while the population size at Whitby is estimated to be about a hundred times that at R.H.B. Although there was potentially a more diverse food supply at Whitby, with Enteromorpha spp. and Fucus spp. being abundant, gut content analysis showed that animals at both sites fed almost exclusively on diatoms. Except when very young, animals would rarely be found below the top of the Enteromorpha zone, or lower in the Fucus zone. The majority of animals were seen on the apparently barren stone blocks of the harbour wall.

TABLE 19. Comparison of the Robin Hood's Bay and Whitby sampling sites.

	ROBIN HOOD'S BAY	WHITBY
WAVE EXPOSURE (Lewis, 1964)	2-3	5
WIND EXPOSURE	Exposed	Sheltered
AVAILABLE HABITAT	25 m	c. 3,500 m
POPULATION SIZE	Small (c. 3,000)	Large (c. 500,000)
SAMPLING METHOD	Replacement	Destructive
AVAILABLE FOODS	Diatoms. Small amounts of *Enteromorpha* and *Fucus* spp.	Diatoms, *Enteromorpha* and *Fucus* spp.
ASSOCIATED SPECIES	*Littorina arcana* Hannaford-Ellis, *Patella vulgata* L., *Strigamia maritima* (Leach) *Porcellio scaber* Latr.	*Petrobius maritimus* (Leach), *Porcellio scaber* Latr., *Porcellio spinicornis* Say.
POLLUTION	Little if any	Diesel oil

3. RESULTS

i. Sex ratio and maturity

The onset of maturity in the Whitby population has been studied in the same way as for the R.H.B. population. The results are shown in Fig 16. Males matured before females : about 50% of the young animals could be sexed as males at 50 mg live weight while no females could be recognised as such at this weight. The majority of animals could be sexed as either males or females when they achieved 100 mg live weight when the sex ratio was 1:1. At live weights exceeding 130 mg the sex ratio became biased towards females.

As in the R.H.B. population the proportion of immatures which were probably female was calculated up to the point at which 50% of the recruits could be sexed as males. The relationship between mean live weight and the percentage of immatures which were probably females was adequately explained by the linear equation

$$y = 1.69x + 27.66$$

($r^2 = 0.97$, $n = 5$, $P < 0.01$). This was used (Fig 17) to predict the sex of immatures of known weight in the following analyses.

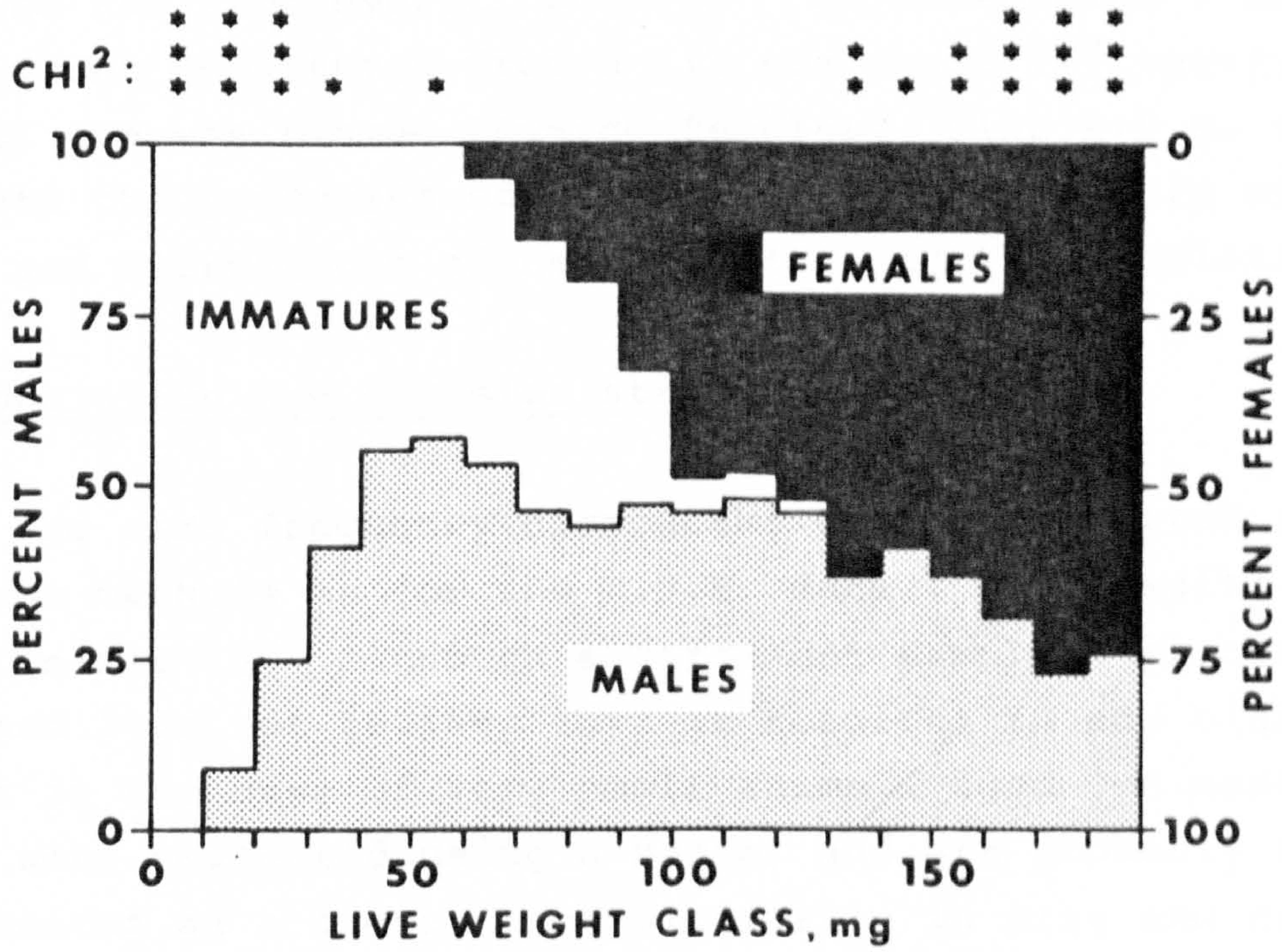
There were some slight differences between the two sites, in particular male Ligia at Whitby matured at a smaller size than their counterparts at R.H.B. (compare Figs 16 & 4, and Figs 17 & 5). The females showed no such differences, the majority showing the initial stages in the development of oostegites by about 110 mg live weight at both sites. At Whitby, as at R.H.B., there was evidence of differential survivorship in favour of the females following the onset of maturity, with significant departures from a 1:1 sex ratio when animals exceeded 130 mg live weight (χ^2 test).

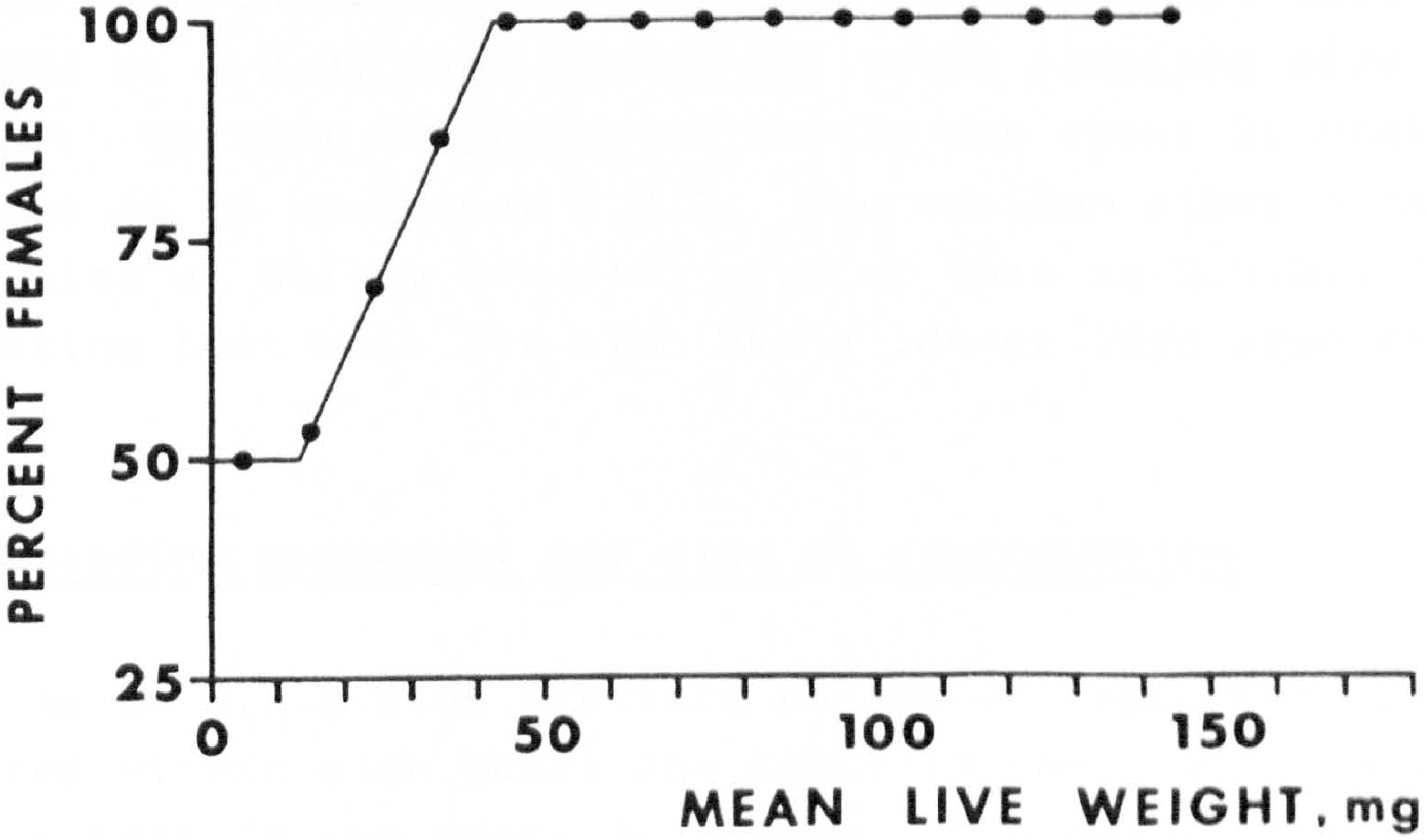
FIGURE 16

Percentage of males, females and immatures in each size class using all samples collected at Whitby. χ^2 indicates significant departures of the ratio males : females + immatures from an expected ratio of 1:1.

FIGURE 17

Percentage of immatures at Whitby which are probably female as a function of immature live weight, assuming an initial sex-ratio of 1:1.


CHI^2:
100
75
50
25
0
PERCENT MALES
IMMATURES
FEMALES
MALES
0
25
50
75
100
PERCENT FEMALES
0
50
100
150
LIVE WEIGHT CLASS, mg


100
75
50
25
PERCENT FEMALES
0
50
100
150
MEAN LIVE WEIGHT, mg

The seasonal changes in sex ratio of the adult population (taken as all animals <100 mg live weight) at Whitby were less pronounced than those at R.H.B. (Fig 6) but followed the same overall pattern. Of 19 samples 9 showed significant departures from a 1:1 sex ratio (χ^2 test), and all but one was biased towards females. Like R.H.B. this reflects the processes of differential survivorship of the sexes and recruitment of new animals into the population.

ii. Population age and size structure

The size frequency histograms were constructed using the same methods as for the R.H.B. data. The results are shown in Fig 18. Although a different sampling procedure was used I do not believe that it resulted in any bias except in the case of very small animals aged 0-6 months. These were collected using a pooter and are probably under-represented as a group. The similarity in size and age structure between Whitby and R.H.B. is striking. Again there were usually two age groups except over-winter when there were three. There is some evidence that animals at Whitby lived longer. Very large animals, especially males, were quite common at Whitby and often weighed in excess of 1000 mg. These animals, in their third year, would persist through the winter and into spring. Such animals were never observed at R.H.B. even though the total sampling size was greater. Maximum longevity at Whitby was about 36 months, compared to 30 months at R.H.B. The maximum sizes attained by females at Whitby was also greater than at R.H.B., suggesting that this sex also has a longer life span at Whitby.

iii. Breeding phenology and size at reproduction

As at R.H.B. two distinct phases of reproduction occurred within each year: one EARLY in the year in spring and one LATE in the year, in summer. The percentage of postparturient or brood carrying females of each year class in a sample is shown in Fig 19. Like R.H.B. nearly all animals at Whitby aged 18 months produced EARLY broods

FIGURE 18

Size structure of Ligia oceanica population at Whitby from February 1980 to September 1981. The percentage of each sample in each size class is shown for males (left hand side) and females (right hand side) in each histogram. Alternate year classes are indicated by alternate black and white areas. Overlapping female year classes can be distinguished by the use of reproductive criteria (see text).

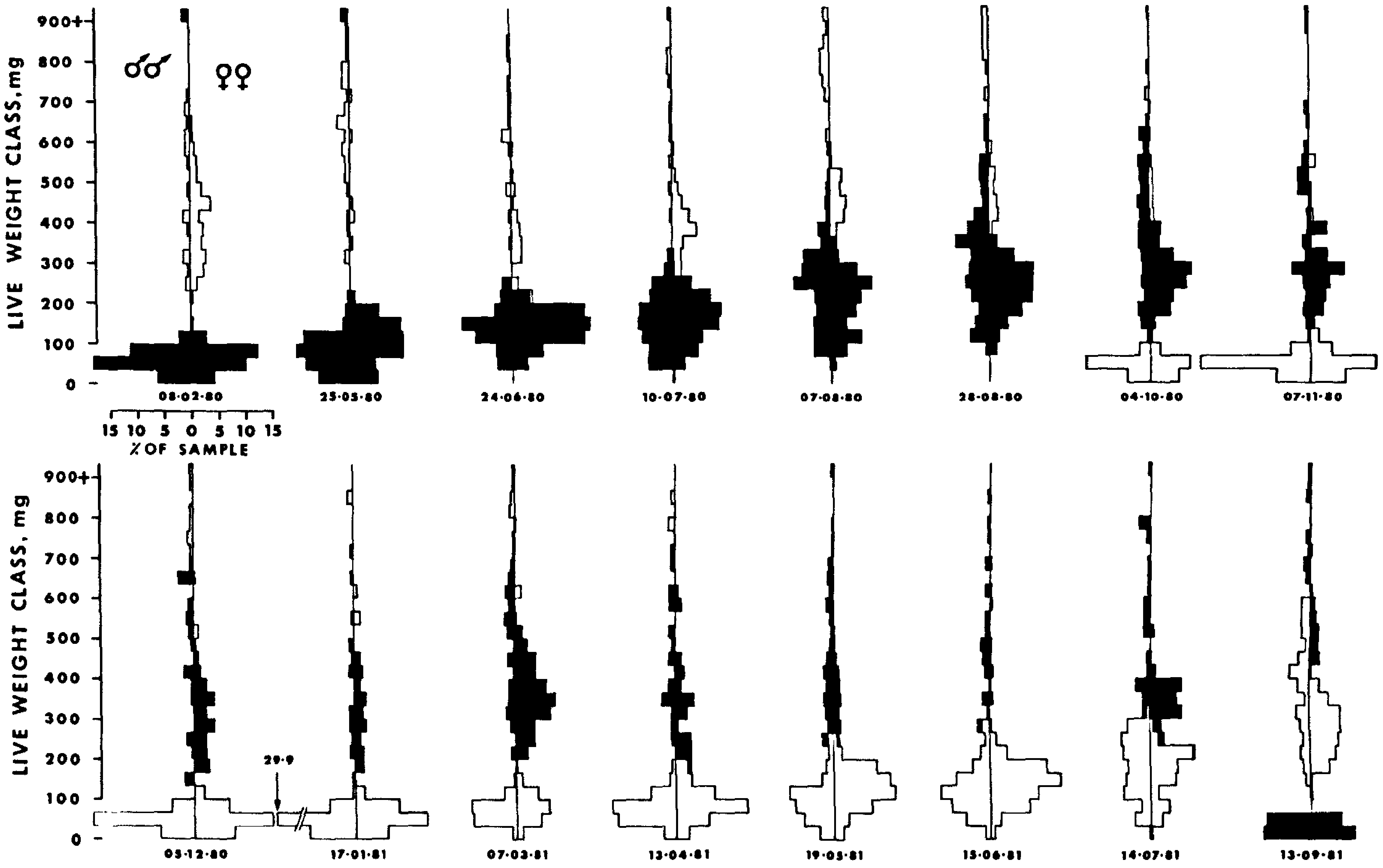

LIVE WEIGHT CLASS, mg
900+
800
700
600
500
400
300
200
100
0
♂♂
♀♀
08·02·80
25·05·80
24·06·80
10·07·80
07·08·80
28·08·80
04·10·80
07·11·80
15 10 5 0 5 10 15
% OF SAMPLE
LIVE WEIGHT CLASS, mg
900+
800
700
600
500
400
300
200
100
0
29·9
05·12·80
17·01·81
07·03·81
13·04·81
19·05·81
15·06·81
14·07·81
13·09·81

FIGURE 19

Breeding phenology of the population at Whitby. Ordinate gives the percentage of females in each age class in each sample which were gravid or post-parturient (ie having released their offspring but not undergone the following moult) for the years 1980 and 1981.

○——○ EARLY gravid
●·····● EARLY post-parturient
△——△ LATE gravid
▲·····▲ LATE post-parturient

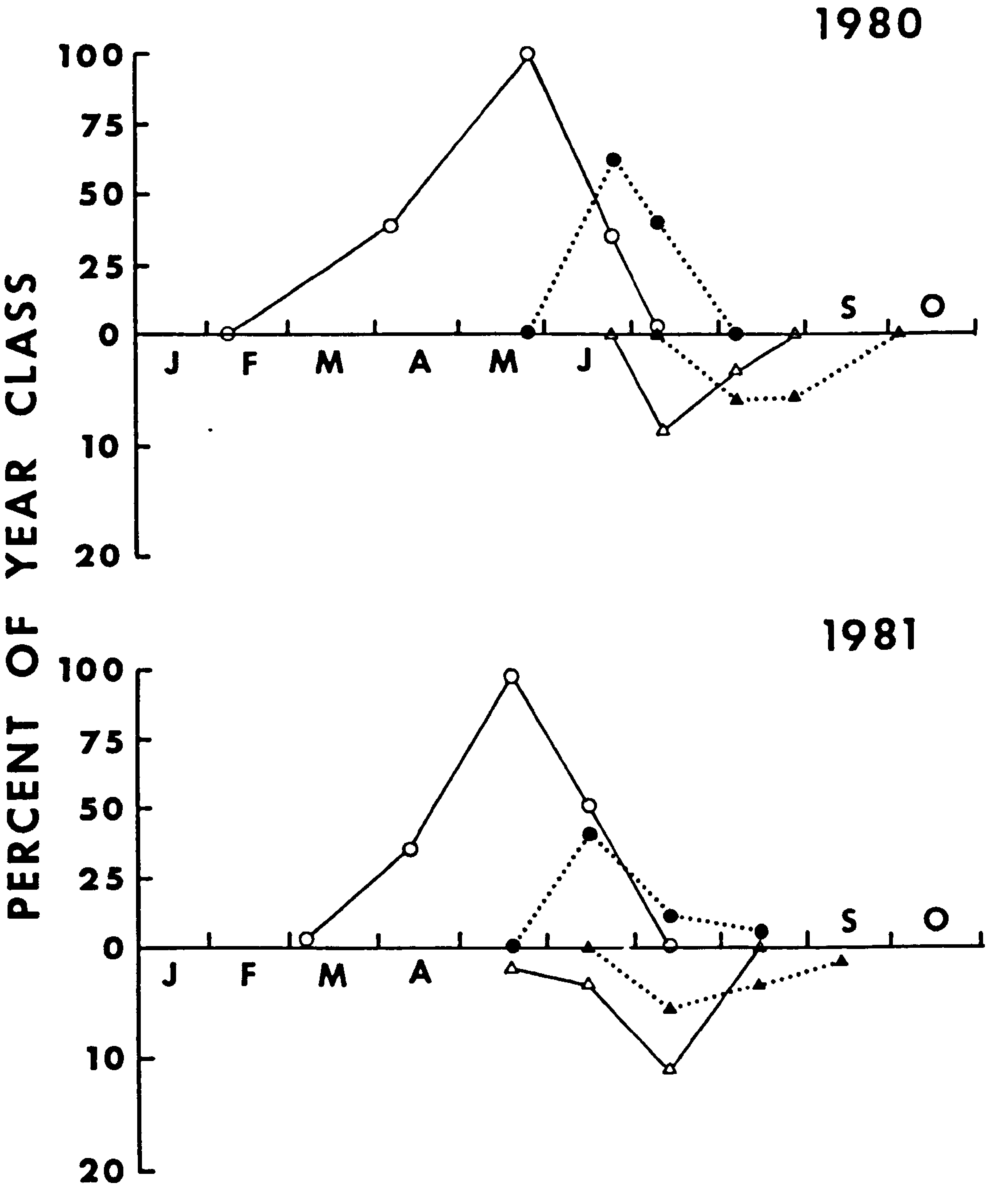

1980
100
75
50
25
0
10
20
J
F
M
A
M
J
S
O
PERCENT OF YEAR CLASS
1981
100
75
50
25
0
10
20
J
F
M
A
S
O

TABLE 20. Two way ANOVA table of the live weights of females carrying EARLY and LATE broods in the two years 1980 and 1981 at Whitby. The data was $LOG_{10}(x)$ transformed.

SOURCE OF VARIATION		D.F.	S.S.	M.S.	F
Between EARLY & LATE	:	1	1.5859	1.5859	283.68 ***
Between years	:	1	0.0086	0.0086	1.54 n.s.
Interaction	:	1	0.0003	0.0003	0.05 n.s.
Error	:	108	0.6037	0.0056	
TOTAL	:	111	2.1985		

Bartlett's test : $H = 15.55$, $P < 0.01$.

TABLE 21. Two way ANOVA table of the live weights of females carrying EARLY and LATE broods at Robin Hood's Bay and Whitby in 1980. The data was $LOG_{10}(x)$ transformed for the analysis.

SOURCE OF VARIATION		D.F.	S.S.	M.S.	F
Between EARLY & LATE	:	1	1.7583	1.7583	358.11 ***
Between sites	:	1	0.0005	0.0005	0.10 n.s.
Interaction	:	1	0.0004	0.0004	0.07 n.s.
Error	:	116	0.5696	0.0049	
TOTAL	:	119	2.3287		

Bartlett's test : H = 6.83, n.s.

TABLE 22. Two way ANOVA table of the live weights of females carrying EARLY and LATE broods at Robin Hood's Bay and Whitby in 1981. The data was $LOG_{10}(x)$ transformed for the analysis.

SOURCE OF VARIATION		D.F.	S.S.	M.S.	F
Between EARLY & LATE	:	1	1.5658	1.5658	251.13 ***
Between sites	:	1	0.0044	0.0044	0.71 n.s.
Interaction	:	1	0.0001	0.0001	0.01 n.s.
Error	:	108	0.6733	0.0062	
TOTAL	:	111	2.2436		

Bartlett's test : H = 7.67, n.s.

(97.6 ± 4.7%), while a slightly smaller proportion of those aged 12 months produced LATE broods (12.3 ± 4.8%). The differences were slight and not significant, while the overall similarities between the two sites are striking (compare Figs 10 & 19).

As at R.H.B. the sizes of females reproducing EARLY and LATE were very different, but there were no significant differences between years (Table 20). The sizes of EARLY and LATE breeding females at the two sites have been compared using a two way ANOVA for the 1980 and 1981 data separately (Tables 21 & 22). No significant differences were found between the sites in either of the two years. The mean weights of the two groups at the two sites during the study are shown in Table 27. They are clearly very constant between sites and between years.

Minimum size at first reproduction has been assessed by taking the lowest 10% of the values of live weight of pregnant females at the two sites over the three years. 10% was an arbitrary figure chosen to allow the comparison of sites with unequal sample sizes. The minimum size at first reproduction was only just significantly lower at R.H.B. than at Whitby (two-tailed Mann-Whitney U-test: $U_s = 96$; d.f. = 20,6; $P < 0.05$). The differences in minimum size were only slight (190.8 mg at Whitby, 181.5 mg at R.H.B.).

iv. Fecundity

a. Whitby

Animals with broods were collected at Whitby in 1980 and 1981 and the relationship between female live weight and egg numbers is shown in Figs 20 & 21. In 1980 no effort was made to collect only animals with undeveloped embryos. Although there was a significant linear relationship between female weight and egg numbers for EARLY breeding females in this year ($F = 41.41$; d.f. = 1,51; $P \ll 0.001$) there was no such relationship for the LATE breeding group

(F = 0.71; d.f. = 1,37; n.s.) (Fig 20). In 1981, when only animals carrying eggs not visibly developed were included, both EARLY (F = 42.90; d.f. = 1,41; $P << 0.001$) and LATE (F = 24.32; d.f. = 1,24; $P << 0.001$) breeding groups had egg numbers linearly related to body live weight (Fig 21).

In order to compare the fecundities of groups of animals whose fecundity is related to body size the data must be corrected for any differences in size between the groups. This is true whether we are comparing groups within a population within years, between years or between sites. The average fecundity of an individual will depend on the size it has reached when it reproduces and also on its weight specific fecundity. It is the latter with which I am primarily concerned here. We standardise for differences in mean weights statistically by the use of ANCOVA. However in the case of the LATE group in 1980 at Whitby, where there was no significant relationship between female live weight and fecundity, we cannot use ANCOVA. However we can test the observed number of eggs produced by the 1980 LATE group against the number predicted for a breeding group of equal average weight using a t-test. The predicted number of eggs being found from the particular fecundity regression for that group.

ANCOVA of the EARLY and LATE fecundity regressions for Whitby in 1981 (Table 23) showed that the two regressions were significantly different (F = 14.19; d.f. = 1,66; $P < 0.001$), though the slopes did not differ significantly (F = 1.18; d.f. = 1,65; n.s.) : LATE breeding females produced more eggs for their size than did EARLY breeding females in 1981. In 1980 a very similar situation was found (t = 5.02; d.f. = 89; $P << 0.001$).

The weight specific fecundities of the two breeding groups between the years 1980 and 1981 have been tested using ANCOVA (Table 24). No significant differences were revealed between the two EARLY group fecundity regressions for either slopes (F = 0.30; d.f. = 1,92; n.s.) or adjusted means (F = 1.46; d.f. = 1,93; n.s.) even though there was a

FIGURE 20

Female size fecundity regression for EARLY (□) and LATE (■) and VERY LATE (▼) breeding females at Whitby in 1980. The fecundity regression is :

EARLY : $y = 0.13x + 25.75$

where y is egg number and x is female live weight in mgs.

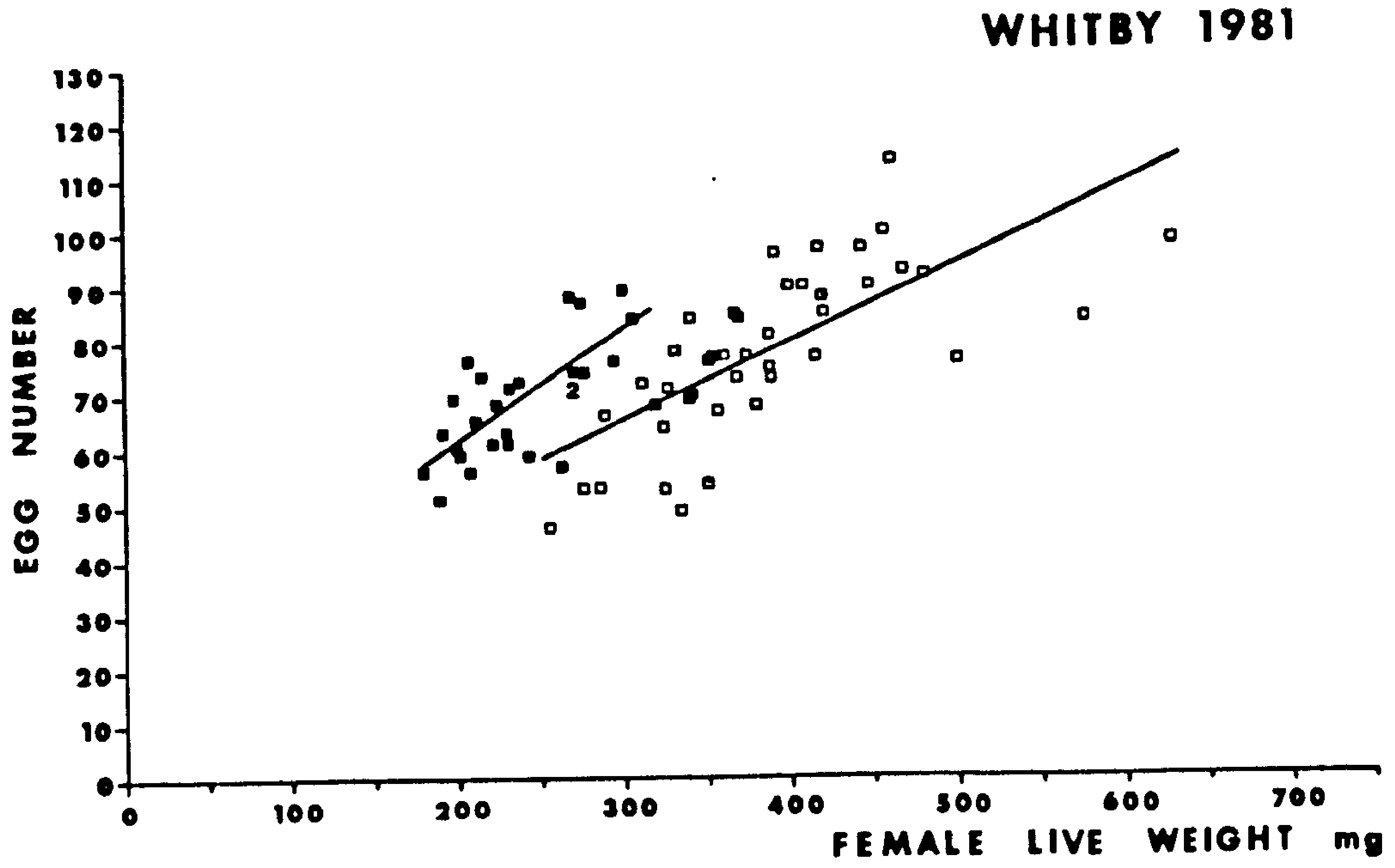
FIGURE 21

Female size fecundity regression for EARLY (□) and LATE (■) breeding females at Whitby in 1981. The fecundity regressions are :

EARLY : $y = 0.14x + 22.06$
LATE : $y = 0.20x + 20.28$

where y is egg number and x is female live weight in mgs.


WHITBY 1980
□ Early
■ Late
▼ V. Late
EGG NUMBER
0
10
20
30
40
50
60
70
80
90
100
110
120
130
0
100
200
300
400
500
600
700
FEMALE LIVE WEIGHT mg


WHITBY 1981
EGG NUMBER
0
10
20
30
40
50
60
70
80
90
100
110
120
130
2
0
100
200
300
400
500
600
700
FEMALE LIVE WEIGHT mg

slight difference in sampling technique between the two years. Nor was there a significant difference between the LATE groups in the two years ($t = 1.24$; d.f. = 62; n.s.).

To summarize, at Whitby LATE breeding animals produced more eggs for their size (ie. had a higher weight specific fecundity) than EARLY breeding animals. Even though they produced more eggs for their size than the EARLY group, LATE breeding individuals still produced fewer eggs each than their EARLY breeding counterparts in both years :

1980 : $t = 4.28$; d.f. = 90; $P \ll 0.001$
1981 : $F = 6.67$; d.f. = 1,67; $P < 0.05$

b. Comparison between Whitby and Robin Hood's Bay

The broad similarities in fecundity between the two sites can be seen clearly by comparing Figs 20 & 21 with Fig 12. Natality at both sites is due to two distinct breeding groups which differ in their weight specific fecundities. However, are there differences in weight specific fecundity between animals at the two sites? Unfortunately the interpretation of the analysis is complicated by the fact that the data were collected in different years : 1981 for Whitby and 1982 for R.H.B. However no differences could be detected between years for either breeding group at Whitby, and I assume that this is also the case at R.H.B. It seems probable that inter-year differences in natality would be brought about through differences in the size of females at reproduction, not through differences in weight specific fecundity which would remain unaltered by short term ecological conditions.

Considering the EARLY breeding groups first (Table 25) significant differences were found between total average egg production per female ($F = 12.31$; d.f. = 1,109; $P < 0.001$) and between adjusted means ($F = 11.22$; d.f. = 1,108; $P < 0.01$) : EARLY breeding females at R.H.B. produced more eggs for their weights than did equivalent animals at Whitby. For the LATE breeding group (Table 26) no significant difference was found between total average egg production per female ($F = 2.41$; d.f. = 1,68; $P \approx 0.1$; n.s.), but when adjusted for differences in the weights of females at the two sites significant differences were revealed in weight specific fecundity ($F = 4.67$; d.f. = 1,67; $P < 0.05$). Again it was the R.H.B. females which produced more eggs.

All four regression coefficients were compared by ANOVA, but no significant differences were found ($F = 2.35$; d.f. = 3,173; $P \approx 0.1$; n.s.). Hence we can consider the two breeding groups at the two sites as each having the same slope of fecundity on live weight, and calculate the differences in weight specific fecundities. LATE group females produced an extra 12.3 eggs compared to EARLY group females at R.H.B., and 15.7 more eggs at Whitby. The EARLY group females at R.H.B. each produced, on average, 6.7 more eggs than their counterparts at Whitby, and the LATE group females at R.H.B. 3.2 more eggs than those at Whitby.

c. Brood pouch mortality

Data were collected on the proportion of undeveloped eggs contained within the developing broods of EARLY and LATE breeding individuals. The data were ARCSINE $\sqrt{x}$ transformed and, as at R.H.B., there was no signiicant difference between the two groups ($t = 1.86$, d.f. = 44, n.s.). Like R.H.B. brood pouch mortality was low (4.61 ± 1.78%) but was significantly higher than that at R.H.B. (data for breeding groups combined : $t = 3.22$, d.f. = 88, $P < 0.01$).

Ligia at both sites were nearly always infected with the free-living nematode Gammarinema ligiae Gerlach. These worms occur all over the ventral surface of both sexes, particularly between the pleopods and between the eggs within the brood pouch of females. Gerlach (1965) reports that the eggs of infected individuals do not develop. Only rarely have I found animals with totally undeveloped broods and the eggs actually rotting, and these animals did not appear to be any more heavily infested than others with normal broods. Pandian (1972) reports that 95% of pregnant

TABLE 23. Analysis of covariance (ANCOVA) of the regressions of fecundity on live weight for EARLY and LATE groups of females at Whitby in 1981.

SOURCE OF VARIATION	D.F.	S.S.	M.S.	F
Due to EARLY regression	1	4901.7	4901.7	42.90 ***
Error (deviations from slope)	41	4684.7	114.3	
EARLY group TOTAL	42	9586.5		
Due to LATE regression	1	1416.2	1416.2	24.32 ***
Error (deviations from slope)	24	1397.3	58.2	
LATE group TOTAL	25	2813.5		
Between groups	1	1233.8	1233.8	6.67 *
Within groups	67	12400.0	185.1	
Common slope within groups	1	6207.1	6207.1	66.15 ***
Error (deviations from common slope)	66	6192.9	93.8	
Difference between slopes	1	110.9	110.9	1.18 n.s.
Error (deviations from slope within each group)	65	6082.1	93.5	
TOTAL (groups + within)	68	13633.8		
Common slope within study	1	6109.9	6109.9	
Error (deviations from common slope)	67	7524.0	112.3	
Among intercepts	1	1331.0	1331.0	14.19 ***
Error (deviations from common slope)	66	6192.9	93.8	

TABLE 24. Analysis of covariance (ANCOVA) of the regressions of fecundity on live weight for EARLY group females from Whitby in 1980 and 1981.

SOURCE OF VARIATION		D.F.	S.S.	M.S.	F
Due to 1980 EARLY regression	:	1	6358.6	6358.6	41.41 ***
Error (deviations from slope)	:	51	7830.5	153.5	
1980 TOTAL	:	52	14189.1		
Due to 1981 EARLY regression	:	1	4901.7	4901.7	42.90 ***
Error (deviations from slope)	:	41	4684.7	114.3	
1981 TOTAL	:	42	9586.5		
Between years	:	1	404.6	404.6	1.60 n.s.
Within years	:	94	23775.6	252.9	
Common slope within years	:	1	11219.6	11219.6	83.10 ***
Error (deviations from common slope)	:	93	12556.0	135.0	
Difference between slopes	:	1	40.7	40.7	0.30 n.s.
Error (deviations from slope within each year)	:	92	12515.3	136.0	
TOTAL (between + within years)	:	95	24180.2		
Common slope within study	:	1	11426.6	11426.6	
Error (deviations from common slope)	:	94	12753.7	135.7	
Among intercepts	:	1	197.7	197.7	1.46 n.s.
Error (deviations from common slope)	:	93	12556.0	135.0	

TABLE 25. Analysis of covariance (ANCOVA) of the regressions of fecundity on live weight for EARLY group females from Whitby in 1981 and from Robin Hood's Bay in 1982.

SOURCE OF VARIATION		D.F.	S.S.	M.S.	F
Due to R.H.B. 1982 EARLY regression	:	1	9201.2	9201.2	87.09 ***
Error (deviations from slope)	:	66	6973.4	105.7	
R.H.B. 1982 EARLY TOTAL	:	67	16174.6		
Due to Whitby 1981 EARLY regression	:	1	4901.7	4901.7	42.90 ***
Error (deviations from slope)	:	41	4684.7	114.3	
Whitby 1981 EARLY TOTAL	:	42	9586.5		
Between sites	:	1	2908.6	2908.6	12.31 ***
Within sites	:	109	25761.1	236.3	
Common slope within sites	:	1	14050.3	14050.3	129.57 ***
Error (deviations from common slope)	:	108	11710.9	108.4	
Difference between slopes	:	1	52.7	52.7	0.48 n.s.
Error (deviations from slope within each site)	:	107	11658.1	109.0	
TOTAL (between + within sites)	:	110	28669.7		
Common slope within study	:	1	15742.0	15742.0	
Error (deviations from common slope)	:	109	12927.7	118.6	
Among intercepts	:	1	1216.9	1216.9	11.22 **
Error (deviations from common slope)	:	108	11710.9	108.4	

TABLE 26. Analysis of covariance (ANCOVA) of the regressions of fecundity on live weight for LATE group females from Whitby in 1981 and from Robin Hood's Bay in 1982.

SOURCE OF VARIATION		D.F.	S.S.	M.S.	F
Due to R.H.B. 1982 LATE regression	:	1	2639.0	2639.0	160.43 ***
Error (deviations from slope)	:	42	690.9	16.5	
R.H.B. 1982 LATE TOTAL	:	43	3329.9		
Due to Whitby 1981 LATE regression	:	1	1416.2	1416.2	24.32 ***
Error (deviations from slope)	:	24	1397.3	58.2	
Whitby 1981 LATE TOTAL	:	25	2813.5		
Between sites	:	1	217.6	217.6	2.41 n.s.
Within sites	:	68	6143.4	90.3	
Common slope within sites	:	1	3982.3	3982.3	123.46 ***
Error (deviations from common slope)	:	67	2161.2	32.3	
Difference between slopes	:	1	73.0	73.0	2.31 n.s.
Error (deviations from slope within each site)	:	66	2088.2	31.6	
TOTAL (between + within sites)	:	69	6361.0		
Common slope within study	:	1	4049.1	4049.1	
Error (deviations from common slope)	:	68	2311.9	34.0	
Among intercepts	:	1	150.8	150.8	4.67 *
Error (deviations from common slope)	:	67	2161.2	32.3	

females were infected, with a similar range of brood pouch mortality as recorded here. It is possible that animals substantially reduce their infestations with each moult, while it seems unlikely that the nematodes have much affect on the eggs.

v. Field growth rates

The mean sizes (± 95% C.I.) of males and females in each year class in each sample are shown in Figs 22 & 23. There was little evidence of consistent differences in size between animals belonging to different year classes but of equivalent ages. Growth rates appeared to be remarkably constant between years. The fitted curves only represent the growth of the average individual animal if the size frequency distributions of the year classes are normal and if mortality is not size dependent.

There was little or no growth over the winter months, especially over the first winter of life. Growth was rapid between April and September, and maximal in July and August. There was no difference in size between the two sexes until females first reproduced LATE at 12 months of age, following which males were generally larger than females of equal age. A marked drop in female live weight during June is a result of these females releasing their broods at this time.

The growth curves at Whitby are very similar to those at R.H.B. (Figs 27 & 28). At Whitby, because animals survived longer, larger animals were recorded than at R.H.B., especially amongst the males (see section 2.vi below). Woodlouse growth characteristics are discussed further in Chapter 4 (section 2.ii).

FIGURE 22

Mean live weight (mgs) ± 95% C.I. of male *Ligia oceanica* separated into age classes for each sample at Whitby. Growth curve fitted by eye.

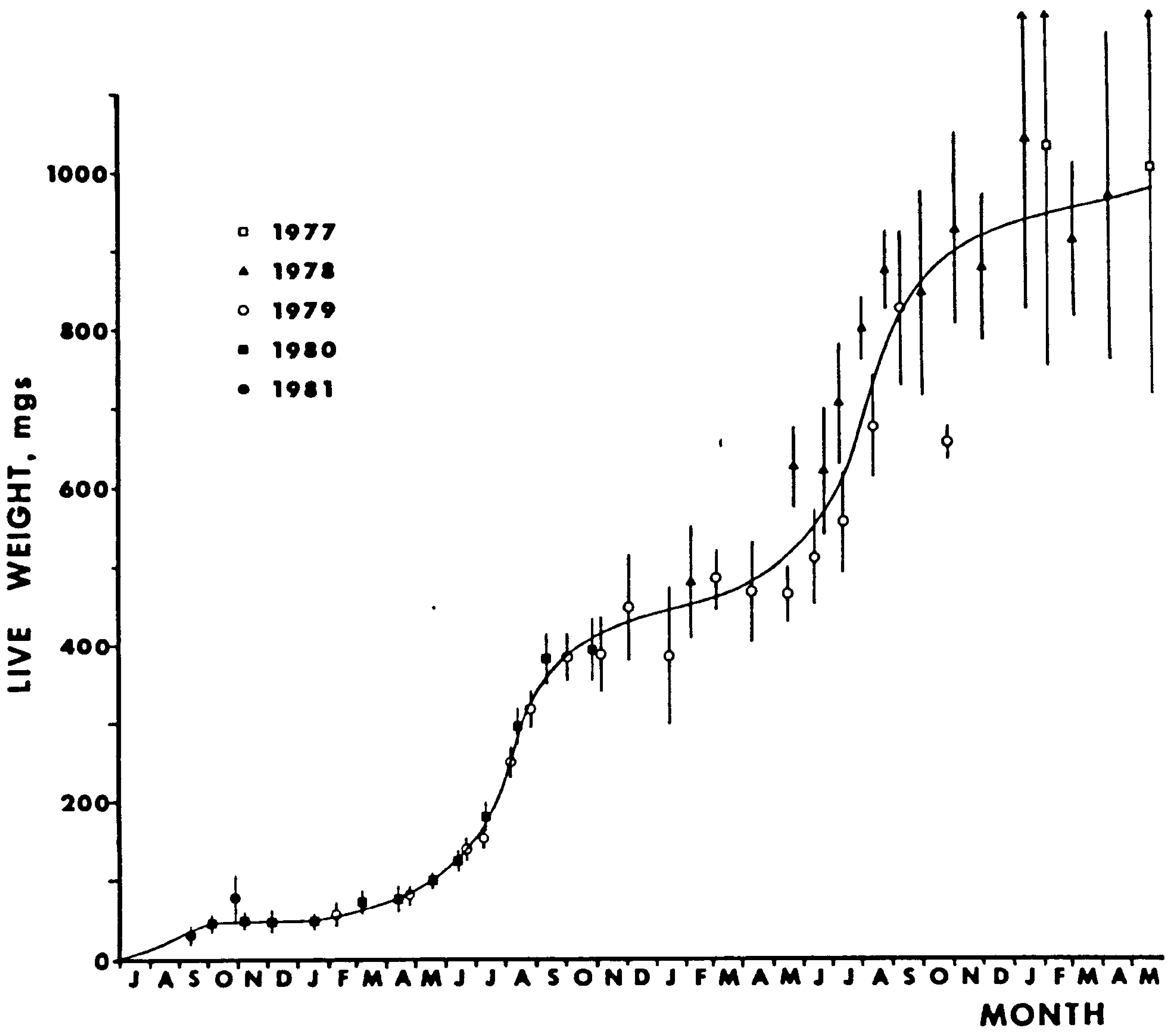
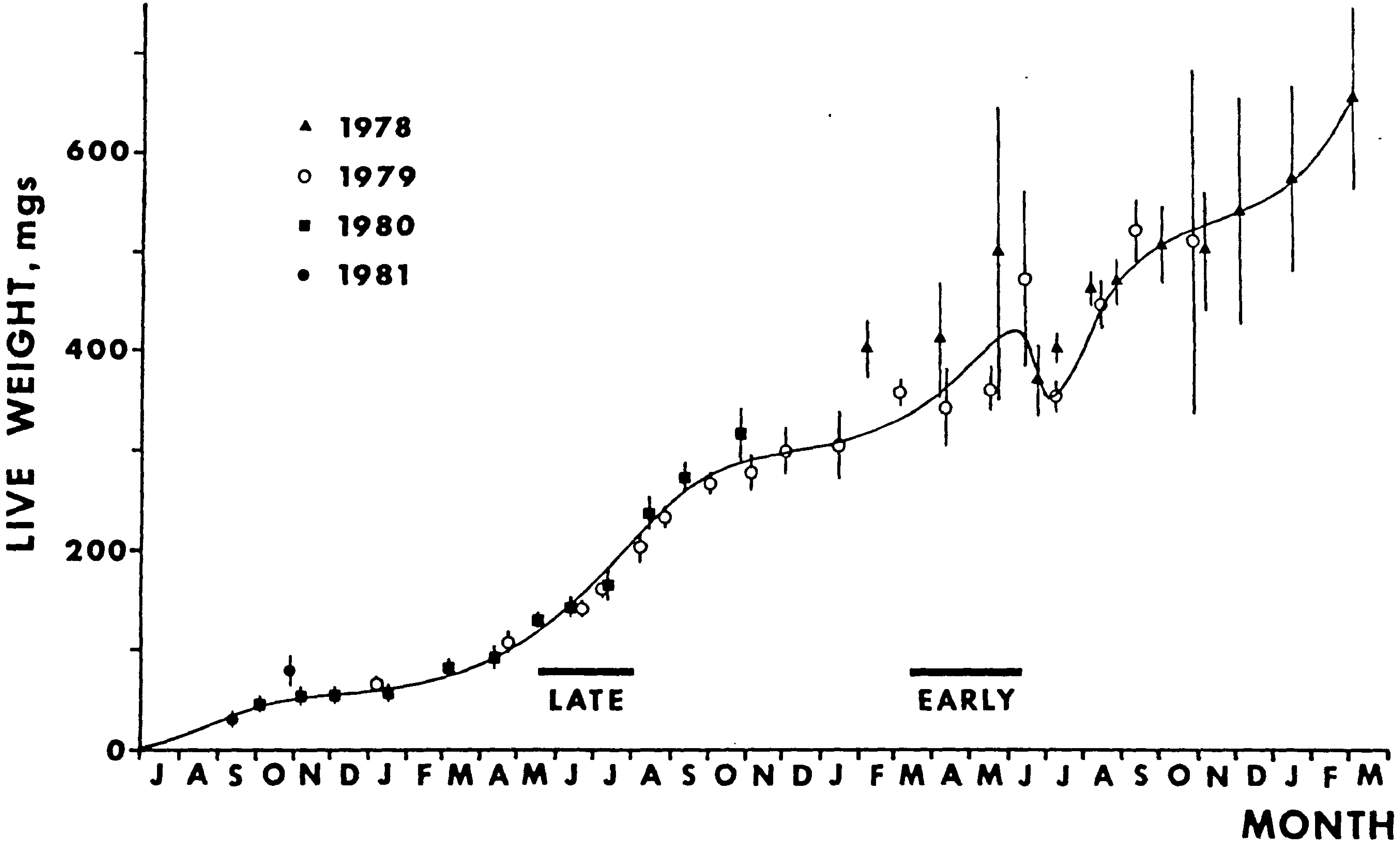

1977
1978
1979
1980
1981
LIVE WEIGHT, mgs
0
200
400
600
800
1000
J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M
MONTH

FIGURE 23

Mean live weight (mgs) ± 95% C.I. of female Ligia oceanica separated into age classes for each sample at Whitby. Growth curve fitted by eye. The periods when LATE an EARLY breeding females are carrying broods are indicated.



LIVE WEIGHT, mgs
0
200
400
600
▲ 1978
○ 1979
■ 1980
● 1981
LATE
EARLY
J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M
MONTH

vi. Survivorship

Due to the close similarities of the growth curves of the two sexes at the two sites adult survivorship can be compared directly by using an index of survival. This is the ratio of the number of animals exceeding 500 mg live weight to the total number of animals exceeding one year of age in paired samples from the two sites :

SITE	MALES	FEMALES
Whitby	0.580	0.071
R.H.B.	0.236	0.017

This indicates that both sexes exhibited better survivorship at Whitby than at R.H.B.

4. DISCUSSION

The characteristics of the two populations of Ligia at Whitby and R.H.B. are summarised in Table 27. Both populations had almost identical growth rates, breeding phenologies, sizes at reproduction and sizes at maturity. The similarities in the sizes of females reproducing EARLY and LATE at the two sites during the study were particularly remarkable : it is suggested that these similarities are brought about through intraspecific competition and not through temperature affects. Animals at Whitby lived longer, and it is probable that survivorship was better overall as a consequence of the more sheltered aspect of the population. Certainly when conditions, particularly winds, prevented animals emerging at R.H.B. numerous animals could be found at Whitby. The only other difference found between the two populations involved fecundity. Although the mean sizes of animals producing broods were so very similar at the two sites, both groups at Whitby had lower weight specific fecundities than their counterparts at R.H.B. This difference in fecundity was accentuated by a significantly greater brood pouch mortality at Whitby, the cause of which may be the fertilisation of females by senescent males (see Chapter 4, section 2.ii).

It is unfortunate that no estimates of population density and biomass were ever recorded at Whitby. If the conversion efficiencies of animals at the two sites are identical then reduced levels of density independent mortality at Whitby might be expected, through competition, to lead either to reduced average growth or to increased density dependent mortality. Reduced growth would result in smaller sizes at reproduction and hence lower individual fecundity. This is often suggested as a mechanism of density dependent regulation for populations in which fecundity is size related (eg. Eisenberg, 1966; Williamson et al., 1976; Wu, 1980). This does not appear to be the case here as the two sites have reproductive females of almost equal sizes. If there is increased density dependent mortality at Whitby it must occur before the females reproduce.

TABLE 27. Summary of the population characteristics of the Robin Hood's Bay and Whitby populations. Values are ± 95 % confidence intervals.

CHARACTERISTIC		ROBIN HOOD'S BAY	WHITBY	SIGNIFICANCE
SIZE AT SEXUAL MATURITY	: MALES	c. 60 mg	c. 45 mg	----
	: FEMALES	c. 110 mg	c. 110 mg	----
LONGEVITY		c. 30 months	c. 36 months	----
SIZE AT FIRST REPRODUCTION		181.5 ± 3.0 mg (n=20)	190.8 ± 9.0 mg (n=6)	**
FEMALE SIZE AT REPRODUCTION				
1980	: EARLY	426.6 ± 28.1 mg (n=40)	443.2 ± 22.3 mg (n=71)	n.s.
	: LATE	243.9 ± 8.4 mg (n=64)	243.8 ± 11.4 mg (n=30)	n.s.
1981	: EARLY	412.4 ± 18.0 mg (n=64)	401.4 ± 25.8 mg (n=50)	n.s.
	: LATE	237.5 ± 7.8 mg (n=78)	237.3 ± 13.4 mg (n=28)	n.s.
1982	: EARLY	415.2 ± 19.1 mg (n=91)	----- ----	----
	: LATE	232.8 ± 7.2 mg (n=99)	----- ----	----
WEIGHT SPECIFIC FECUNDITY AT SIZE 0 (1982 ONLY)	: EARLY	20.9	14.2	**
	: LATE	33.2	29.9	*
% YEAR CLASS BREEDING				
1980	: EARLY	100 %	100 %	----
	: LATE	15.7 ± 3.6 %	9.5 ± 5.4 %	----
1981	: EARLY	100 %	97.2 ± 5.6 %	----
	: LATE	15.7 ± 3.4 %	16.8 ± 4.4 %	----
1982	: EARLY	100 %	---- ---	----
	: LATE	16.6 ± 2.3 %	---- ---	----
BROOD POUCH MORTALITY				
ARITHMETIC		1.86 ± 1.32 % (n=45)	4.61 ± 1.78 % (n=45)	----
ARCSINE BACKTRANSFORMED		0.66 (0.22 - 1.34) %	2.83 (1.59 - 4.41) %	**

Can the difference in weight specific fecundity between the two sites be interpreted as adaptive? McGill (1978) has demonstrated that Ligia populations can show genetic divergence. Electrophoretic analysis of 15 gene loci from 14 populations of L. occidentalis showed substantial genetic differences, and while intrapopulation crosses produced fertile broods interpopulation crosses produced broods that were either infertile or showed reduced fertility. Interestingly his populations also showed differences in weight specific fecundity. Although we do not know that the differences between the Whitby and R.H.B. populations are genetically based the isolated nature of the populations, by reducing gene flow, would facilitate divergence. The lack of inter-year variation in weight specific fecundities of the two breeding groups at Whitby further suggests a genetic basis to the difference.

The increased weight specific fecundity of individuals in the R.H.B. population might be interpreted as an adaptive response to higher levels of density independent mortality and reduced survivorship at the more exposed site. The idea is intuitively attractive (Calow, 1973) but whereas one can argue that individuals may increase their fecundity to counter increased mortality, the converse argument, the adjustment of fecundity downwards to counter increased survivorship, implies group selection. We need to know more about how the increased fecundity at R.H.B. is achieved before we can answer the question of why it occurs. Is the elevated fecundity at R.H.B. a result of a greater reproductive investment by these animals or a differential partitioning of reproductive material between egg size and numbers? Similarly, how is the greater weight specific fecundity of LATE breeding compared to EARLY breeding animals at both sites brought about? Why should the two groups of animals have different fecundities? Are these different strategies, adopted by animals breeding at different times, to maximise their fitnesses? These questions will be considered further in Chapters 5 & 6.

The greater weight specific fecundity of *Ligia* from the exposed site is paralleled by the results of Alon & Stancyk (1982). They found that a population of shrimp (*Palaemonetes pugio*) experiencing a low and variable salinity regime had higher weight specific fecundities than a population occupying a high and constant salinity habitat. Juvenile survivorship of these shrimp is known to be reduced in low salinity conditions (Thorp & Hoss, 1975). Stearns (1983a) also found greater weight specific fecundities in mosquito fish (*Gambusia affinis*) from reservoirs with fluctuating, rather than stable, water levels. However these differences were not found to be genetically based Stearns (1983b).

In their study of the winkle *Littorina rudis* Roberts & Hughes (1980) found that snails at a more exposed site had lower growth rates and smaller maximum sizes than those from more sheltered shores. Like *Ligia*, individuals from the more exposed population had greater weight specific fecundities. However this was not achieved by elevating the relationship between female size and egg numbers but by increasing the rate at which animals produce broods in the more exposed population. In reaching this conclusion they assumed that birth rate is directly proportional to a snails' volume, which I do not find intuitively obvious. A strategy of increased weight specific brood production may not be open to *Ligia* which, unlike *L. rudis*, is essentially semelparous and has only a limited breeding season.

Hence, populations experiencing more severe conditions, as interpreted by authors on *a priori* grounds, seem to result in higher weight specific fecundities in the majority of cases. However, Menge (1974) found that the starfish *Leptasterias hexactis* from exposed sites were less fecund than those from sheltered sites. This may be an exception for, at exposed sites, the volume of the brood pouch was reduced, enabling brooding starfish to hold on to rocks more effectively under the greater wave action experienced there.

Al-Dabbagh & Block (1981) made the first intraspecific comparative study of an isopods' population dynamics and life history characteristics. They found differences in population age structure, breeding and population density of Armadillidium vulgare at two sites. At a grazed site animals bred only once, aged two years, while on an ungrazed site a small proportion bred aged two years but the majority of reproduction was due to three year old animals. Even with these differences, the overall survivorship schedules for the two populations were similar. At both sites births were synchronised into a single breeding season but, because each year class bred twice at the ungrazed site, year to year population densities were more constant than at the ungrazed site where alternate high and low density year classes bred only once, giving rise to a high or low density year class. The low densities of alternate year classes were attributed to poor juvenile survivorship in a year past. They suggest that the differences between the two populations' dynamics were due to differences in habitat structure brought about by different grazing pressures. No mechanism for this was suggested, nor any explanation of the lack of compensation by the population to alternate years of low population density. The differences in climate between the two sites were regarded as of secondary importance.

The findings of Al-Dabbagh & Block (1980) accord well with the conclusions of this study. There were no differences in habitat structure for Ligia at R.H.B. and Whitby : both populations occupied crevices of varying but similar sizes in stone sea-walls, and had identical food resources. No differences were found between the population dynamics at the two sites, but differences in life history characteristics (weight-specific fecundity and longevity) might be attributed, either directly or indirectly, to differences in physical climate, in this case exposure.

Miller & Cameron (1983) also studied populations of Armadillidium vulgare, over a single year in three coastal prairie habitats in Texas. They interpreted differences in population dynamics and life history traits between the populations in relation to the tanin content of the leaf litter at the three sites. Unfortunately their individualistic methodology precludes comparison with other data on terrestrial woodlouse populations, hinders the interpretation of their results, and leads to a number of contradictions within their paper. For example, females in the Baccharis habitat are stated to breed both earlier (first paragraph, p. 224), and later (third paragraph, p.224), than females at the other sites. Many of these problems arise from the application of methods of analysis without regard for the species' biology. For example, the use of sieves to obtain size-frequency distributions, while saving the time needed to make tedious individual measurements of size, results in a small number of size classes of unequal size without any commensurate increase in total sample size. These size classes are then used in a linear regression model to describe growth, ignoring any seasonal or size related changes in growth rate. Hubbell (1971) found that growth of A. vulgare was non-linear, and while there is disagreement over the form of the growth curve of cohorts of woodlice in the field (see Chapter 4, section 2.ii) they have not been found to be linear. Miller & Cameron (1983) state that A. vulgare at the oak site have the fastest rate of growth, yet examination of their size-frequency histograms indicates that growth is slower at this site. This is important because age is then ascribed to each size class, within a year class, on the basis of the analysis of growth at each site. Even though these derived differences in age of the size classes at each site are not statistically significant (p. 220), they are then used to derive time-specific life-tables for each site, the validity of which must be questioned. In addition significance is given to differences in the fluctuations in population density at the three sites. Regrettably only a small number of small samples were taken on each occasion, and the data was not transformed to account for contagion. Aggregation is a major problem of terrestrial isopod population studies (Sunderland et al. 1976). The degree of aggregation is frequently related to absolute population density (Taylor, 1978), and can lead to misleading impressions of density fluctuations (Southwood, 1978).

CHAPTER 4

POPULATION ENERGETICS OF LIGIA OCEANICA AT ROBIN HOOD'S BAY.

1. INTRODUCTION

Although the concept that energy is the currency of ecology is hackneyed it is still useful. Like many currencies the joule is probably overvalued. Many important attributes of an animals' population ecology may be determined by requirements other than energetic (for example nutrients, space, intraspecific interactions), or aspects of the environment (climate and interspecific interactions for example) which cannot necessarily be measured in energetic terms. These other facets of a species' biology detract from the usefulness of energy as a unit of measurement in ecology.

Nevertheless energy budget studies are useful. Firstly, they estimate the importance of the species' population in the energy flow relations of the community. Such studies on isopods include those of Saito (1965, 1969), Reichle (1967), White (1968), Standen (1973), Hassall (1976, 1977) and Hassall & Sutton (1977), Shachak, Chapman & Steinberger (1976) and Phillipson (1983) on terrestrial species, and Hayes (1974), Johnson (1976a), Strong & Daborn (1979), Shafir & Field (1980a) and Koop & Field (1981) on marine and maritime species. Swiss & Johnson (1981) have studied the effects of various algal diets on the energy dynamics of Asellus racovitzai.

The second use of information on species population energetics is that, by building up a sufficiently large data base, ecological generalisations may emerge. For example differences might be found by comparison of data on animals of different taxonomies, physiologies (eg. poikilotherms v. homeotherms), trophic modes (eg. carnivores v. herbivores v.

detritivores), habitats (eg. aquatic v. terrestrial) and life histories (eg. long v. short lived; semelparous v. iteroparous; r- v. K-selected). Following McNeill & Lawton (1970) a number of studies have taken this approach (eg. Calow & Jennings, 1974; Griffiths, 1977; Robertson, 1979; Humphreys, 1979, 1980; May, 1980; Banse & Mosher, 1980).

In this chapter I present data on various aspects of the energetics of Ligia oceanica. These data are used, together with that on the population dynamics presented in Chapter 2, to construct a population energy budget for Ligia at R.H.B. Various aspects of the energetics of this species are then discussed in the light of data on other species of terrestrial, maritime, and marine isopod. In addition the data are used in Chapter 5 to calculate an alternative estimate of reproductive effort.

2. THE DATA

i. Water, ash and caloric content

Ligia were collected from the population at Whitby on four occasions throughout the year. After being starved for 48 hours to allow the gut to be cleared they were sexed, weighed and then dryed under vacuum at 60°C until constant weight, reweighed and then ashed in a muffle furnace at 500°C for 4 hours. The relationship between live weight and dry weight is shown in Fig 24, and the relationship between dry weight and ash weight in Fig 25. In both cases there appeared to be a direct relationship between the two variables, and the variance increased with the dependent variable. Following Snedecor & Cochran (1956) I have calculated the ratio of the two variables to obtain the water and ash contents for males and females (Table 28).

Table 28. Water and ash contents (± 95% C.I.) of *Ligia*.

SEX	WATER CONTENT % of live weight	ASH CONTENT % of dry weight
Male	73.06 ± 0.48%	29.11 ± 0.56%
Female	71.02 ± 0.47%	26.54 ± 0.65%

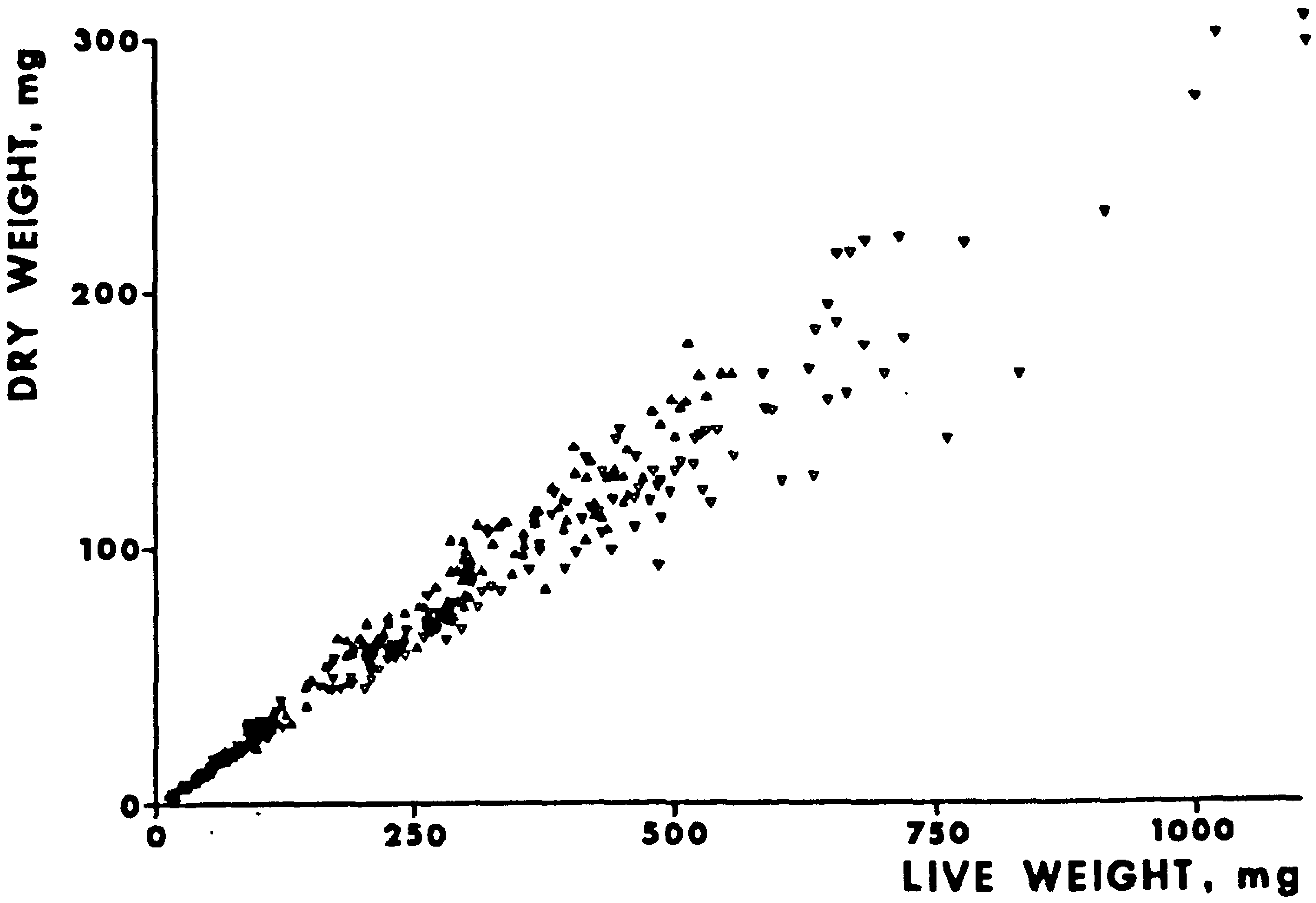
Although the difference between the two sexes is small, females had a significantly lower water content ($t = 5.96$; d.f. = 299; $P \ll 0.001$) and a significantly lower ash content ($t = 5.92$; d.f. = 213; $P \ll 0.001$) than the males. These differences are probably due to the different sizes of the gonads in the two sexes, particularly if the females are carrying developing ova in their ovarioles. The egg material has a very low ash content (see section 2.v). Females carrying broods of eggs in the brood pouch were excluded from the data.

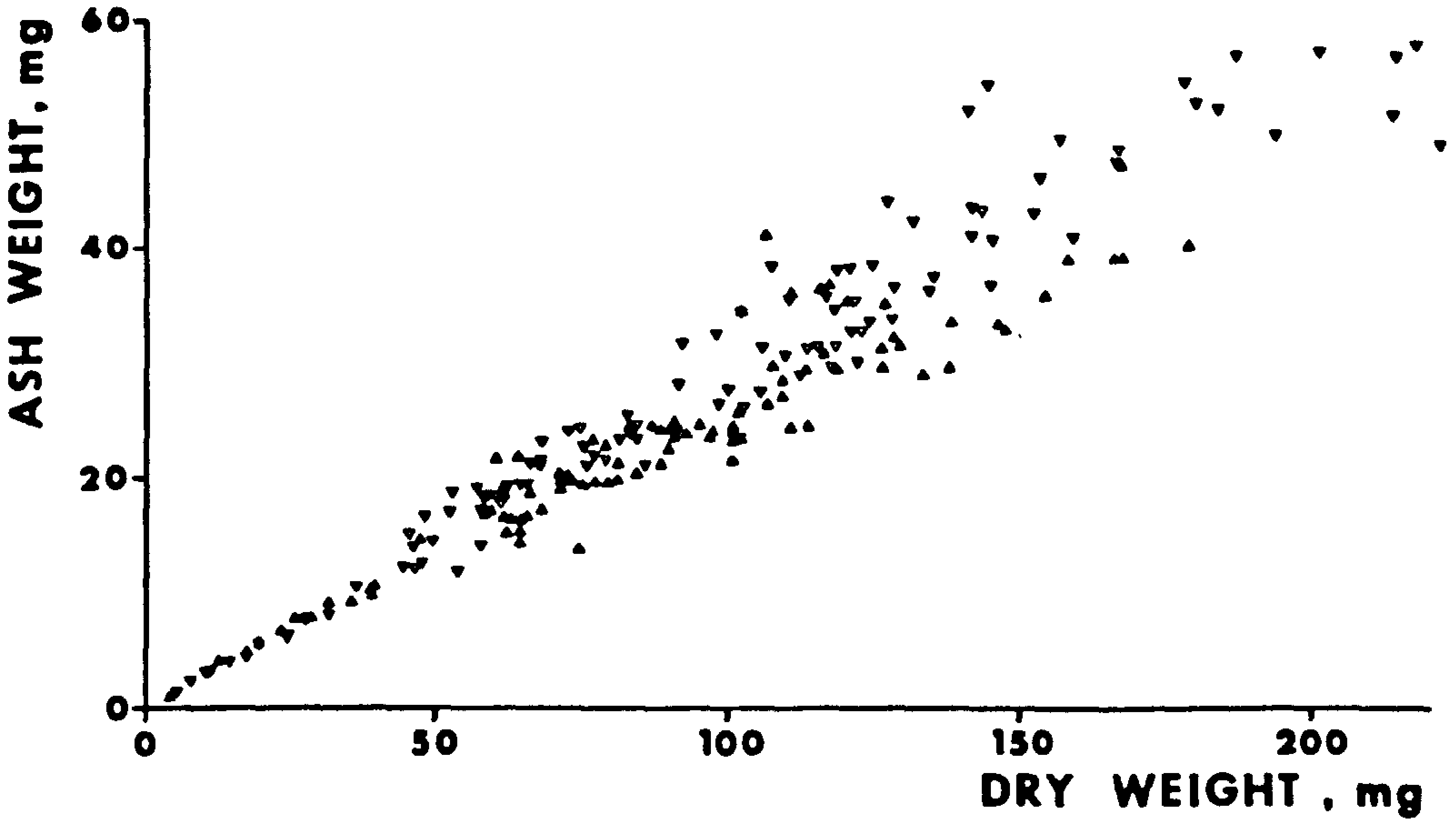
FIGURE 24

Relationship between live weight (mgs) and dry weight (mgs) of male (▽) and female (▲) Ligia oceanica collected from Whitby.

FIGURE 25

Relationship between dry weight (mgs) and ash weight (mgs) of male (▽) and female (▲) Ligia oceanica collected from Whitby.


DRY WEIGHT, mg
300
200
100
0
0
250
500
750
1000
LIVE WEIGHT, mg

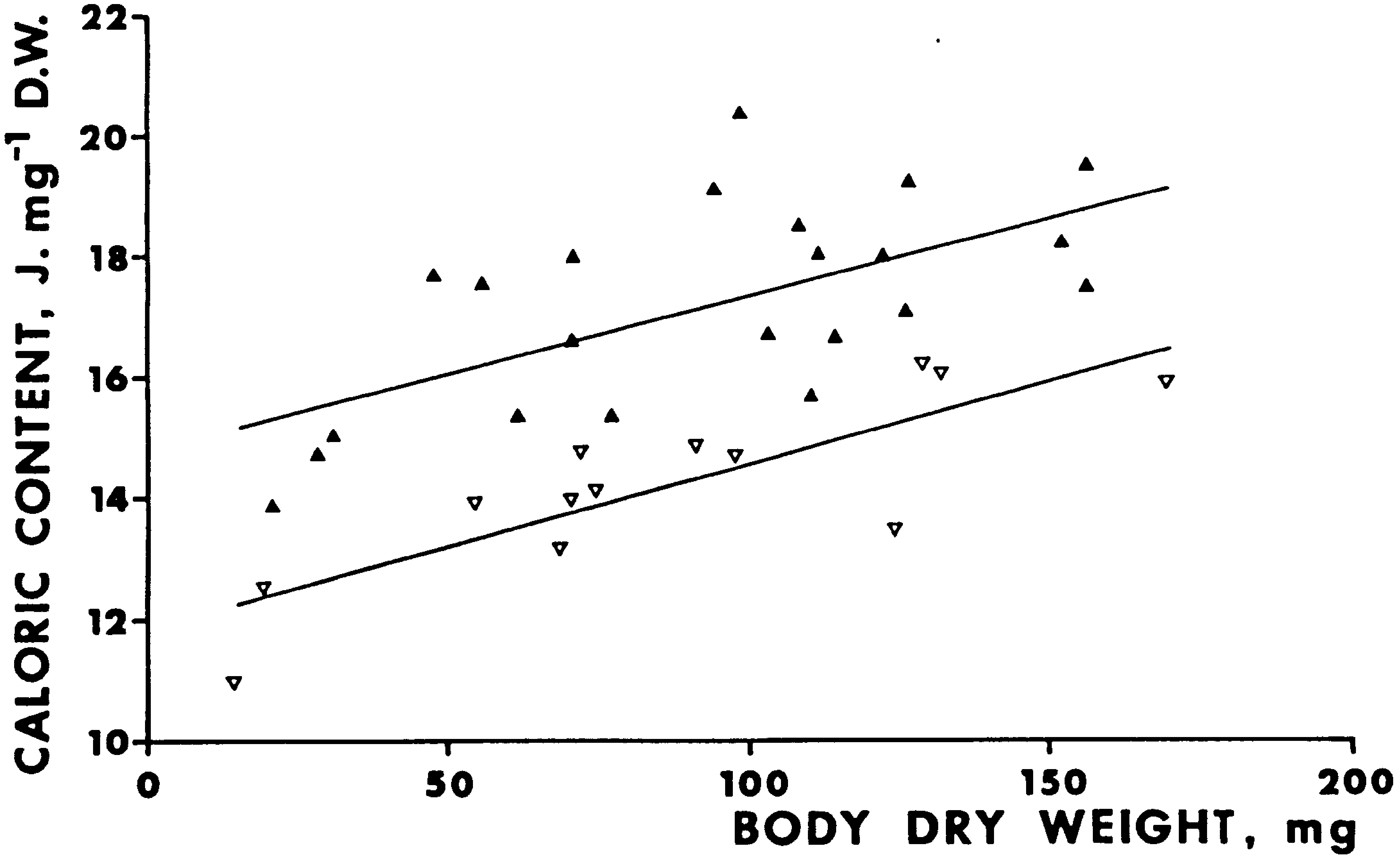

ASH WEIGHT, mg
60
40
20
0
0
50
100
150
200
DRY WEIGHT, mg

The caloric content of the two sexes was determined for individuals collected from Whitby in October and November. At this time of year females are not carrying broods but the ovarioles are moderately developed for the production of spring broods. Animals spanning the total size range of the two sexes were used. Two replicate pellets were made from each individual homogenized animal and dried at 60°C under vacuum for 12 hours. For the smaller sized animals two or three specimens of closely similar weights were used to make the two replicate pellets. The pellets were burned in a Phillipson microbomb calorimeter, calibrated using benzoic acid (Phillipson, 1964). The calibration line explained 97.7% of the variation. Due to the nature of the experimental design the data could be treated to a nested analysis of variance.

There were significant differences between the males ($F = 4.80$; d.f. = 12,13; $P < 0.01$) and between the females ($F = 5.89$; d.f. = 21,22; $P < 0.001$) in caloric value per mg dry weight of body tissue. Regression of caloric content upon body weight revealed a significant relationship between the two variables for both males ($F = 24.16$; d.f. = 1,11; $P \ll 0.001$) and females ($F = 12.32$; d.f. = 1,20; $P < 0.01$). For the females there was a small but significant amount of variation not explained by the linear regression ($F = 3.83$; d.f. = 20,22; $P < 0.01$). This may be due to females of different weights belonging to different breeding groups and having differences in the developmental state of the gonads. The relationship between individual dry weight and average caloric content is shown in Fig 26, and the full details of the analysis in Table 29. Preliminary nested ANOVA also revealed highly significant differences in caloric content between the sexes ($F = 27.88$; d.f. = 1,35; $P \ll 0.001$). Nested ANCOVA showed that this difference was not due to differences in the average size of males and females used in the study, for when adjusted for differences in average size the difference in caloric content remained highly significant ($F = 56.74$; d.f. = 1,32; $P \ll 0.001$). There remained a small but significant amount of unexplained variation ($F = 2.99$; d.f. = 32,35; $P < 0.01$), presumably due to the females.

FIGURE 26

Caloric content (J.mg^{-1} DW) of male (▽) and female (▲) Ligia oceanica collected from Whitby. Each point is the mean of two determinations for an individual animal.



CALORIC CONTENT, J. mg^{-1} D.W.
22
20
18
16
14
12
10
0
50
100
150
200
BODY DRY WEIGHT, mg

TABLE 29. Nested analysis of covariance (ANCOVA) of the regressions of energy content ($J.mg^{-1}DW$) on dry weight of male and female *Ligia oceanica* from Whitby.

SOURCE OF VARIATION		D.F.	S.S.	M.S.	F
Between MALE weights	:	12	51.71	4.309	4.80 **
Due to regression	:	1	35.53	35.528	24.16 ***
Error (deviations from slope)	:	11	16.18	1.471	1.64 n.s.
Within MALE weights	:	13	11.66	0.897	
MALE TOTAL	:	25	63.37		
Between FEMALE weights	:	21	118.26	5.632	5.89 ***
Due to regression	:	1	45.08	45.081	12.32 **
Error (deviations from slope)	:	20	73.18	3.659	3.83 **
Within FEMALE weights	:	22	21.03	0.956	
FEMALE TOTAL	:	43	139.29		
Between sexes	:	1	143.62	143.62	27.88 ***
Within sexes	:	33	169.97	5.15	5.12 ***
Common slope within sexes	:	1	80.51	80.51	28.75 ***
Error (deviations from common slope)	:	32	89.46	2.80	
Difference between slopes	:	1	0.10	0.10	0.03 n.s.
Error (deviations from slope within each group)	:	31	89.36	2.88	
Within individuals	:	35	32.69	0.93	
TOTAL (between + within sexes + within individuals)	:	69	346.27		
Common slope within study	:	1	65.52	65.52	
Error (deviations from common slope)	:	33	248.06	7.52	
Among intercepts	:	1	158.60	158.60	56.74 ***
Error (deviations from common slope within sexes)	:	32	89.46	2.80	2.99 **

Hence females have a higher energetic content per unit body mass than do males, and in both sexes the energetic content per unit body mass increases with size. The difference between the sexes is only slightly reduced by correcting for their different ash contents (Table 31). That females should have a higher caloric content per mg dry weight of tissue than males is perhaps not surprising. Females contain a large amount of yolk material within the ovarioles which is rich in lipid (Saudray, 1954; Pandian 1972), and this will tend to increase the caloric content of the females. What is perhaps more surprising is the very nearly parallel increase in caloric content with size in both sexes. Large animals are more energy rich than smaller animals. Indeed large females can have up to 30% more energy per unit mass, and males, which grow to a larger size than females, can have up to 50% more energy per unit mass than small males. Such differences could well be important in determining the optimal foraging strategy of a predator on such a prey species.

While seasonal variation in the caloric content per unit mass of Crustacea has frequently been found (Eg. Wissing & Hassler, 1971; Strong & Daborn, 1978 on Idotea baltica), often associated with the reproductive cycle of the species, generally no attempt is made to examine the effects of size on the caloric content of an organisms' tissue. Griffiths (1977) has noted that such seasonal variation is, in some species, correlated with variation in body size, while Snow (1972), on the cladoceran Daphnia pulicaria, has specifically looked for and found such a relationship. It is possible that larger animals are able to accumulate more food reserves per unit mass than smaller animals.

ii. Field growth

Growth by males and females at R.H.B. is shown in Figs 27 & 28. These figures show the mean sizes (± 95% C.I.) of animals belonging to each year class, as distinguished by the size frequency analysis in Figs 7 & 8. The growth curves appeared to be very constant between years. Little growth occurred over the winter months, followed by an exponential phase of increase in live weight during the spring. Growth rate was highest in July, August and early September when the increase in live weight was approximately linear. The growth curves were very similar to those at Whitby and, like Whitby, the marked drop in live weight in June of the second year of life was due to release of broods by all animals breeding EARLY at this time.

The pattern of growth shown by Ligia oceanica was found to be too complex to be described easily by an equation or limited number of equations relating body weight to time. The lines fitted in Figs 27 & 28 have therefore been fitted by eye.

Hubbell (1971), in his very thorough study of the growth of Armadillidium vulgare, distinguished two phases of growth. An initial exponential phase as a juvenile was followed by a linear phase as an adult. He found no evidence of a decrease in growth rate as an upper, asymptotic size, is approached. Growth by Ligia oceanica in the field at R.H.B. is also apparently indeterminate. Hassall (1976) found no evidence of decreased growth rates at large sizes in Philoscia muscorum. Strong & Daborn (1979) described the growth of Idotea baltica by a combination of Gompertz and linear equations. However the Gompertz equation was used to describe the initial stages of growth and its cessation over the winter period. This was followed by a linear phase during the subsequent summer, with no evidence of a further reduction in growth rate. McQueen & Carnio (1974) on Porcellio spinicornis, and McQueen (1976c) on Tracheoniscus rathkei, studied growth in the laboratory at constant temperatures and present evidence which suggests

FIGURE 27

Mean live weight (mgs) ± 95% C.I. of male *Ligia oceanica* separated into age classes for each sample at Robin Hood's Bay. Growth curve fitted by eye.

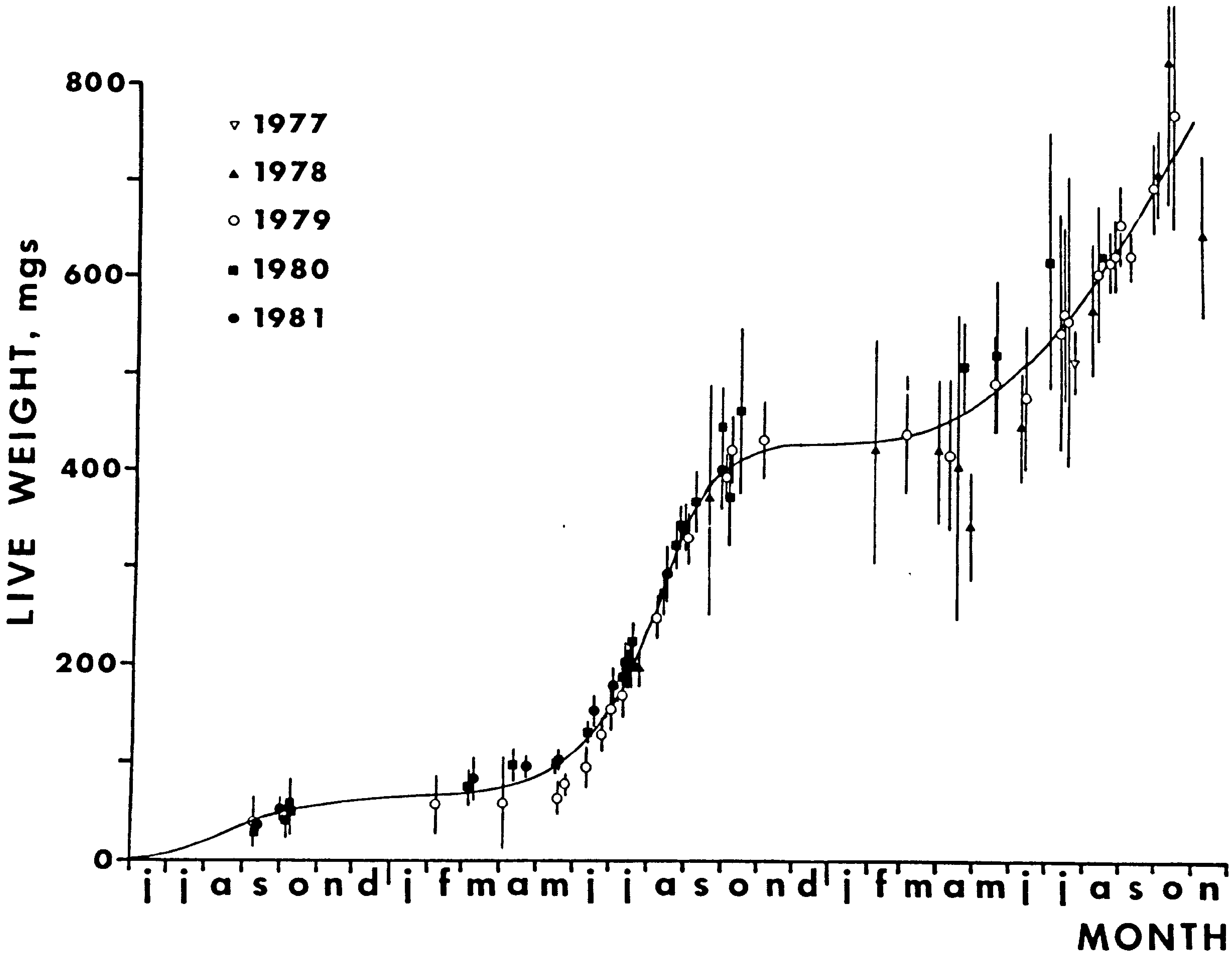
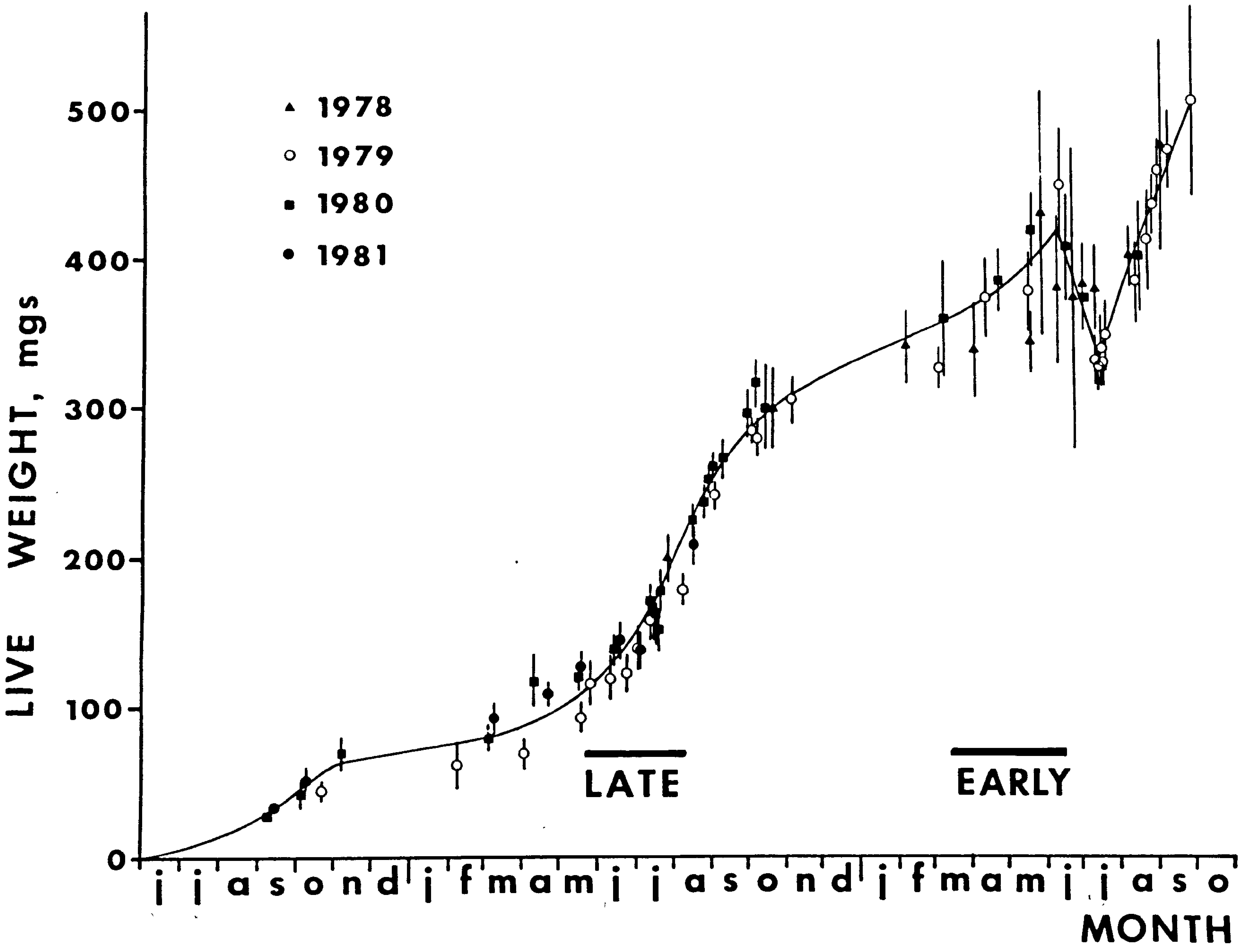

800
600
400
200
0
LIVE WEIGHT, mgs
▽ 1977
▲ 1978
○ 1979
■ 1980
● 1981
j j a s o n d j f m a m j j a s o n d j f m a m j j a s o n
MONTH

FIGURE 28

Mean live weight (mgs) ± 95% C.I. of female *Ligia oceanica* separated into age classes for each sample at Robin Hood's Bay. Growth curve fitted by eye. The periods when LATE an EARLY breeding females are carrying broods are indicated.


1978
1979
1980
1981
LIVE WEIGHT, mgs
500
400
300
200
100
0
LATE
EARLY
j j a s o n d j f m a m j j a s o n d j f m a m j j a s o
MONTH

that an upper asymptotic size might have been approached. These authors found that the von Bertalanffy equation gave the best fit to their data, but had to assume that the maximum size observed in the field represented the upper asymptotic body size. Clearly not enough is known about the growth of isopods at large sizes. If growth rate does decrease at large sizes then this would appear to be above the maximum sizes observed in many field populations. However the relationship between growth and senescence in Ligia oceanica has been studied by Inagaki (1971, 1974), Inagaki & Berreur-Bonnenfant (1970), and Berreur-Bonnenfant & Inagaki (1970). These authors showed that although large male Ligia continue to grow they do so at a reduced rate (Inagaki, 1974). This is associated with the senescence of these individuals, as indicated by the ending of spermatogenesis by the testes (Berreur-Bonnenfant & Inagaki, 1970) and an increase in the variability in weight and calcium content of the exuvia (Inagaki, 1971). This transition to senescence occurs at a head-width of about 5.5mm (Inagaki, 1971, 1974). I have found the relationship between head-width (x, in micrometer units) and live weight (y, in g) for L. oceanica to be $y = 0.0003x^{3.445}$ ($r^2 = 0.992$, $n = 288$), where 1m.u. = 0.562mm. Hence senescence occurs at a male live weight of about 776 mg. Whereas very few males reach this size at R.H.B. (see Fig 27) it is commonly achieved at Whitby (see Fig 23). At R.H.B. it seems that the majority of adult males die before the onset of senescence, while at Whitby senescence is a common feature of this populations' ecology. Interestingly, although these animals are senescent they are still capable of fertilisation through the storage of spermatozoids in the seminal vesicles (Inagaki & Berreur-Bonnenfant, 1970). Amplexus in woodlice is a rare event, and only four males have been found in precopula in the field, two each at R.H.B. and Whitby. Both those at R.H.B. were less (541 mg and 688 mg respectively) than the size at which senescence occurs, while both those at Whitby were greater than this size (813 mg and 849 mg respectively). The greater instance of brood pouch mortality observed at Whitby (see Chapter 3, section 3.iv.c) may be due to fertilisation by senescent males using "old" sperm.

iii. Assimilation efficiency

Assimilation efficiency has been estimated in the laboratory for animals collected at Whitby. These animals were kept in the laboratory to acclimatise for about a month under the experimental conditions of food and temperature before commencing the experiment. The food used was *Enteromorpha*, thoroughly washed in sea water to remove sand grains and other contaminants, and then dried at 60°C under vacuum to constant weight. Weighed amounts were rewetted with distilled water and presented to groups of 15 animals. There were four experimental groups consisting of small and large males and females respectively. Starvation for 24 hours prior to the start of the experiment allowed time for most of the material in the gut to be voided before the animals were provided with the experimental food. The experimental temperature was 11.90 ± 0.36 °C (S.D.). Faeces were collected every 12 hours and immediately dried at 60°C under vacuum. The experiment continued for 96 hours when the remaining food was removed, redried and weighed. The animals were maintained for a further 24 hours, and the faeces produced collected, before being sacrificed to determine dry weights. In an initial experiment it was found that the food gained in weight during the experiment. This was believed to be due to photosynthetic activity of microalgae. Hence the experiments were conducted in continuous darkness. Replicated control quantities of food, treated as the experimental quantities but in the absence of animals, then showed no change in weight over the 96 hours of the experiment.

The caloric and ash content of *Enteromorpha* and faeces were determined in the standard manner and the results shown in Table 31. Ingestion (I) and egestion (E) are shown in Table 30 in gravimetric (mg AFDW) and energetic (J) terms. Assimilation efficiency has been calculated as

$$((I - E)/I).100$$

TABLE 30. Summary of assimilation experiment with *Ligia oceanica* feeding on dried *Enteromorpha*.

GROUP	No.	MEAN	MEAN	INGESTION		EGESTION		ASSIMILATION EFFICIENCY %		INGESTION INDEX %	ASSIMILATION
		LW	DW	mg AFDW	Joules	mg AFDW	Joules	mg	Joules		$J.g^{-1}DW.day^{-1}$
Small Males	15	240.6 ±19.5	60.97 ±5.11	72.79	7200	41.04	3089	43.62	57.10	2.58	1124
Small Females	15	291.0 ±8.2	82.14 ±4.57	79.76	7889	45.91	3455	42.44	56.20	2.35	900
Large Males	15	547.4 ±53.6	128.16 ±11.88	133.11	13165	68.29	5140	48.70	60.96	2.35	1044
Large Females	15	361.5 ±21.7	105.47 ±6.13	78.60	7774	43.86	3301	44.19	57.54	1.74	707
GRAND MEANS								44.74 ±4.36	57.95 ±3.31	2.26 ±0.57	944 ±291

This quantity is frequently termed the absorption or digestive efficiency (see Petrusewicz, 1967). The faeces contained a slightly higher ash content than the food. The crude, gravimetric estimate of assimilation efficiency was 44.7 ± 4.4% , and the energetic estimate was higher 58.0 ± 3.3% (95% C.I.). Also calculated was an ingestion index (Grahame, 1973), as

(Daily ingestion in mg DW / Body dry weight in mg).100

This is an index of appetite, corrected for body size. Three of the groups had very similar ingestion indices, but that for large females was considerably lower. Although precautions were taken to avoid including moulting animals, two females of this group moulted during the experiment. Moulting animals do not feed, and this might be expected to reduce the ingestion index. The value of the index, after excluding the two moulting individuals, becomes 2.01. The close agreement of these four estimates suggests that ingestion is directly related to body weight.

iv. Moulting

Woodlice have to moult in order to grow and reproduce (Steel, 1980), and in moulting the animals will incur costs. The moulted exoskeleton contains mineral elements and energy previously assimilated by the animals. While the nutrient drain may be inconsequential for a marine organism (Wieser, 1968) the energetic loss might be significant and is evaluated here. Additional costs might well include a metabolic element, the physiological organisation required to moult, inability to feed for a short period, and increased susceptibility to death.

My observations on moulting support those of previous workers on Ligia, and are generally typical of woodlice (Sutton, 1972; Steel, 1980). Prior to the actual moult a white deposit of material containing calcium carbonate (Nicholls, 1931a) is seen on the anterior ventral surface. In many cases this deposit is extensive and conspicuous but, especially in small specimens, may be confined to the base of the legs. This pre-moult stage precedes the ecdysis of the posterior part of the cuticle. The period between this and the anterior moult lasts two to three days according to Nicholls (1931a). Carlisle (1956) states that the intermoult period can be as short as one, or as long as six days.

To examine the time sequence of moulting in *Ligia oceanica* a large number of post-parturient females were collected from Whitby. These animals were selected because, being of similar physiological state, they could all be expected to moult in the succeeding few days. They were held in the laboratory at 12.0°C under natural daylength. The time taken by woodlice to moult is highly temperature dependent (Steel, 1980). 12°C was chosen as being close to the yearly average temperature. The results are shown in Fig 29. The duration of the premoult stage was 4.19 days, and the intermoult lasted 1.69 days.

The weights of all animals collected in field samples which were in the premoult stage were recorded. The frequency of such animals in each sample was generally low. In Fig 30 the percentage frequency of premoult animals is shown for each 50 mg size class of the totalled samples. A clear trend is seen relating moulting frequency to live weight. The best fit to the data was found to be a logarithmic curve

$$y = 29.90 - 4.11 \, \mathrm{Ln}(x)$$

where y is the % frequency of moults and x the mean live weight in mgs ($r^2 = 0.92$, $n = 13$, $P \ll 0.001$). Sutton (1972) noted that moulting frequency decreases with size, and Strong & Daborn (1979) showed that the intermoult period increased with size in *Idotea baltica*. The equation gives the proportion of animals in the premoult stage at any size. To find the proportion actually moulting we divide by the duration of the premoult stage (4.19 days). Fig 30 includes some seasonal, temperature dependent variation in moulting frequency because it is derived from field samples. However

FIGURE 29

Sequence of events asssociated with moulting in a sample (n=50) of post-parturient female Ligia oceanica maintained in the laboratory at 12°C.

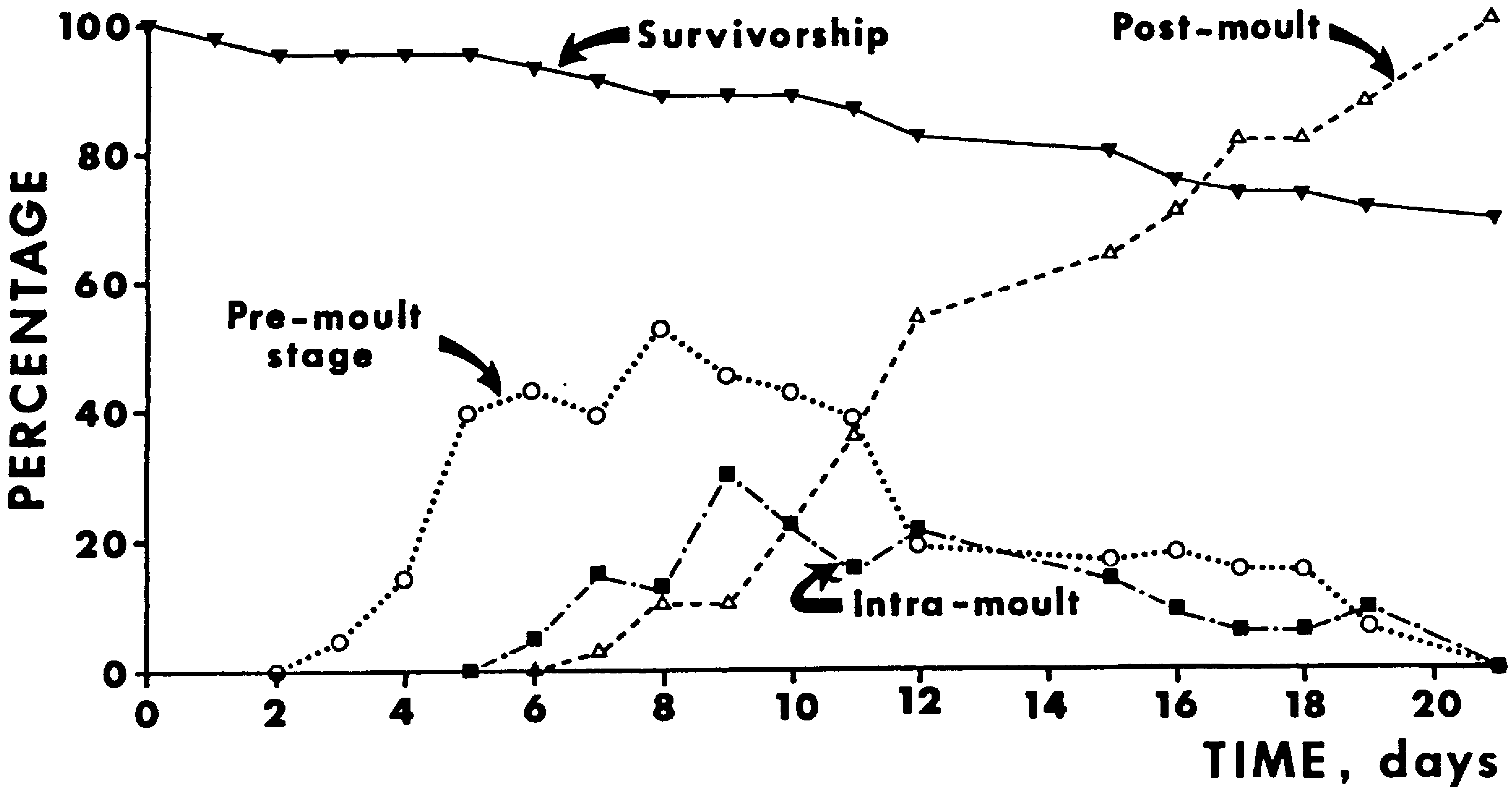

Survivorship
Post-moult
Pre-moult stage
Intra-moult
PERCENTAGE
100
80
60
40
20
0
0
2
4
6
8
10
12
14
16
18
20
TIME, days

FIGURE 31

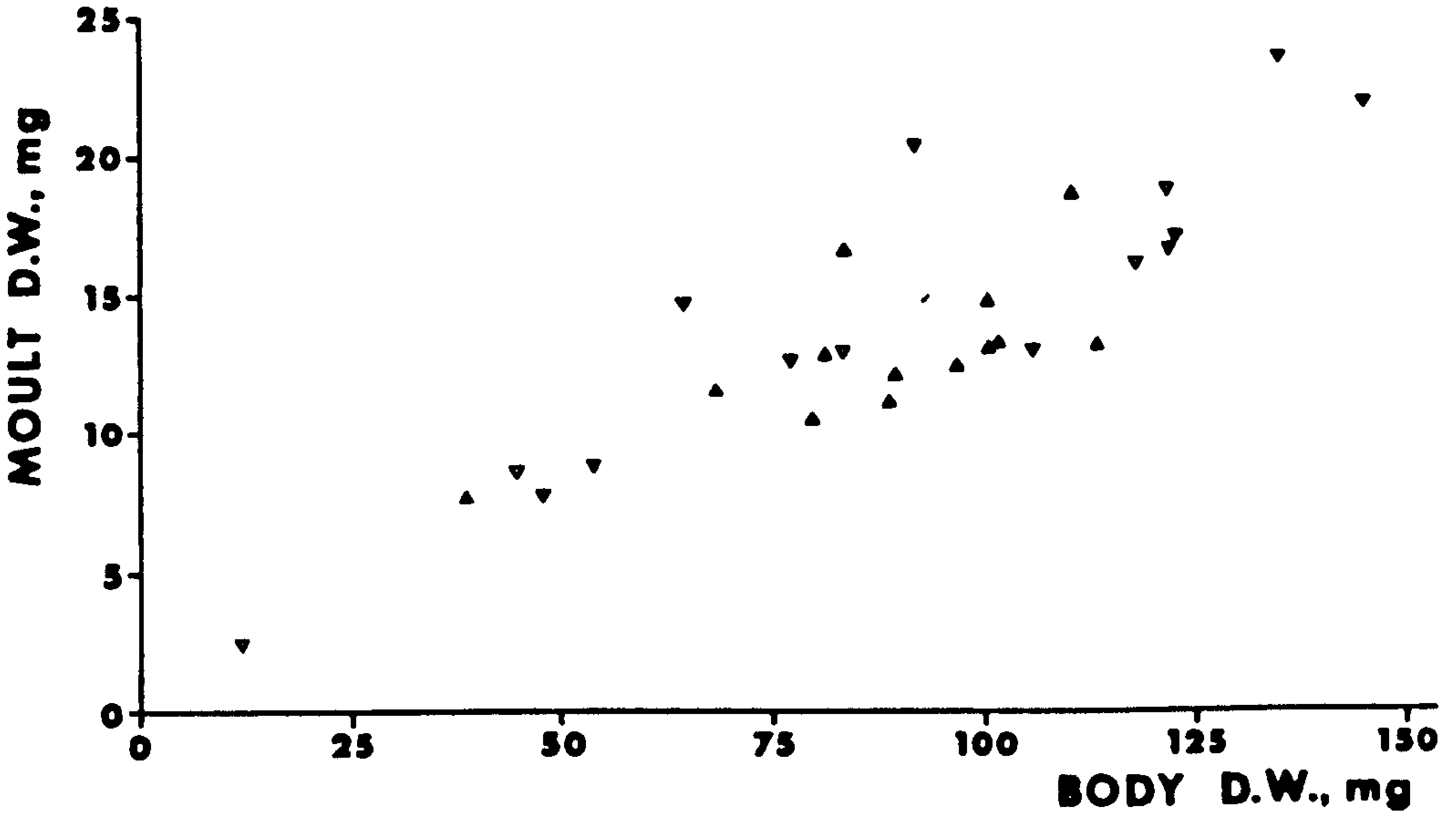
Dry weight (mgs) of the moult (anterior + posterior portions) against the post-moult dry weight (mgs) of the animal.

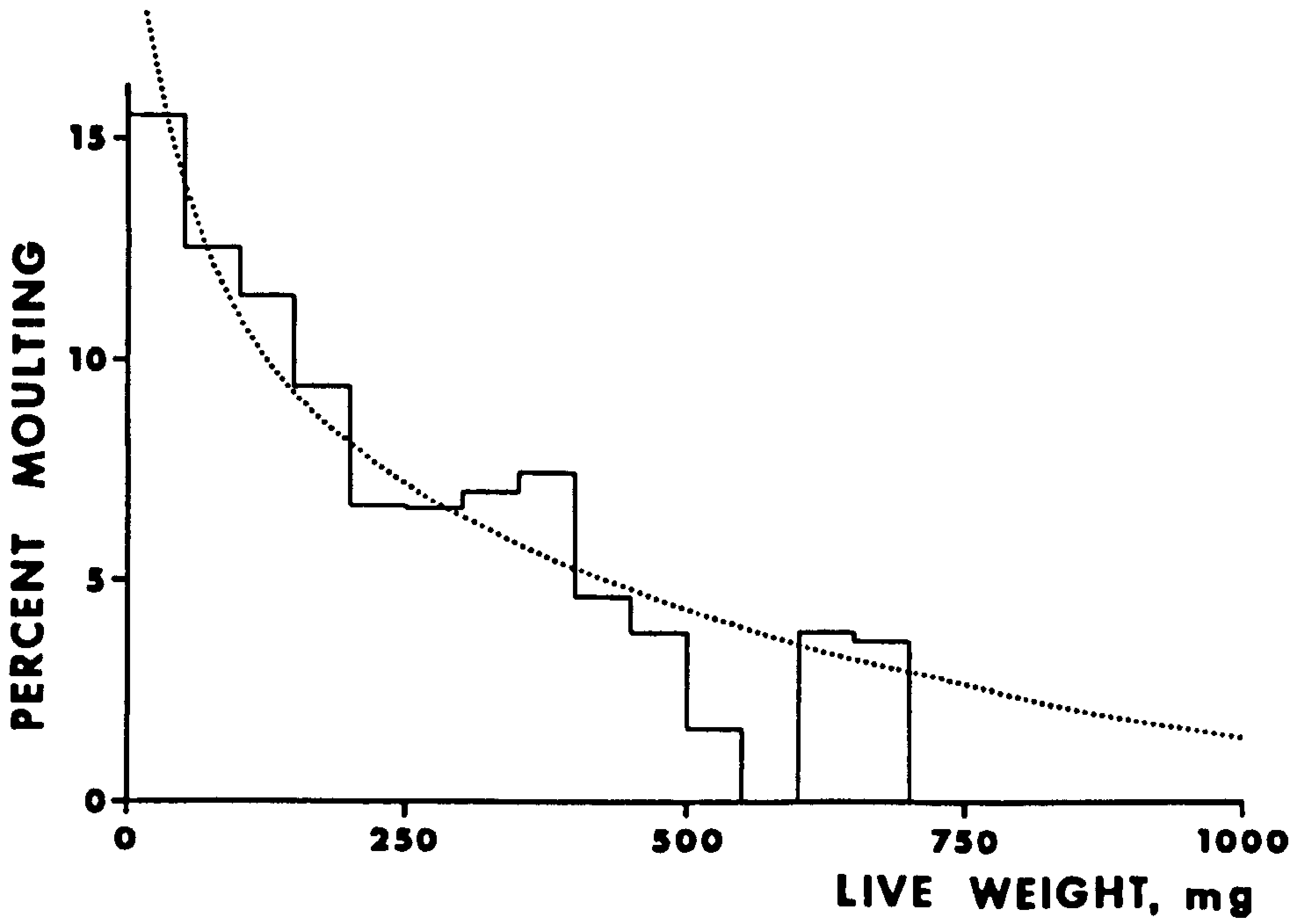
FIGURE 30

Percentage of all animals (male + female) in the premoult stage in each size class for all samples collected at Robin Hood's Bay. The fitted line is a logarithmic curve with the parameters :

$$y = 29.90 - 4.11 \ln(x)$$

where x is live weight in mgs and y is the percentage frequency of moults.


MOULT D.W., mg
0
5
10
15
20
25
0
25
50
75
100
125
150
BODY D.W., mg


PERCENT MOULTING
0
5
10
15
0
250
500
750
1000
LIVE WEIGHT, mg

more samples were taken in summer than in winter possibly resulting in an upwards bias in the estimates of weight specific moulting frequency.

The energy lost in ecdysis was determined by keeping individual animals in the laboratory. These were examined daily until both halves of the moult had been collected, when the animals were sacrificed to determine post-moult weights. Dry weight of the moult was directly related to the post-moult weight of the animal (Fig 31) and, expressed as a percentage of an animals initial (ie. premoult) weight, is a substantial fraction of body weight (13.58 ± 0.86%, 95% C.I.). The initial weight is taken as being the dry weight of body tissue following the moult plus the dry weight of the moult. The ash and caloric content of the moults are shown in Table 31. Because of the very high ash content we can expect a significant underestimate of caloric content due to endothermy. Paines' (1966) correction factor of 0.574 $J.mg^{-1}$ of ash was therefore applied. This assumes that the ash is entirely $CaCO_3$; Strong & Daborn (1979) found that about 95% of the ash content of the exuvia of <u>Idotea baltica</u> was $CaCO_3$, so this is not unreasonable. Applying this correction factor increased the caloric content of moults by about 5% to 7.38 ± 0.43 $J.mg^{-1}$ DW or 22.12 ± 1.29 $J.mg^{-1}$ AFDW (± 95% C.I.).

From these data we can calculate the fraction of the energy budget lost through moulting. This fraction would not be lost if the animals consumed their own moults. However the individuals maintained in the laboratory never ate their moults, while in large laboratory cultures moults could frequently be observed to remain uneaten for a period of days. Similarly exuvia were frequently observed in the field.

TABLE 31. Summary of ash and caloric content determinations. All values ± 95% C.I. Numbers in brackets are the number of determinations.

MATERIAL	ASH CONTENT % of D.W.	CALORIC CONTENT J.mg^{-1} D.W.		CALORIC CONTENT J.mg^{-1} A.F.D.W.
Ligia males	29.11 ± 0.56 (115)	14.57 ± 1.57 *	(26)	20.56 ± 2.18 *
Ligia females	26.54 ± 0.65 (100)	17.34 ± 1.46 #	(44)	23.60 ± 1.99 #
Ligia moults	66.65 ± 1.07 (4)	7.38 ± 0.43	(4)	22.12 ± 1.29
Ligia eggs	5.55 ± 0.53 (32)	26.19 ± 0.94	(9)	27.72 ± 0.99
EARLY breeding females	29.63 ± 0.57 (44)	16.31 ± 1.46	(6)	23.18 ± 2.07
LATE breeding females		14.40 ± 0.70	(5)	20.46 ± 1.00
Enteromorpha	41.89 ± 2.20 (3)	13.73 ± 0.74	(5)	23.62 ± 1.29
Faeces	43.05 ± 1.03 (3)	10.24 ± 0.53	(5)	17.98 ± 0.94

* Calculated for an individual male weighing 100mg dry weight from the regression $y = 0.027x + 11.85$

\# Calculated for an individual female weighing 100mg dry weight from the regression $y = 0.025x + 14.81$

v. Reproduction

The relationship between female somatic weight and the dry weight of the brood is discussed in Chapter 5 (section 3.ii.a,b), and the seasonality of brood production in Chapter 2 (section 3.ii.e) and Willows (1984).

Saudray (1954) showed that the dry weight of the eggs increased as development proceeded, and claimed that this was due to maternal secretions. However Pandian (1972) has shown that the ash content of Ligia eggs increases substantially as embryonic development proceeds, while their caloric content decreases. There is no evidence of maternal nutrition of the eggs once deposited within the brood pouch, but the considerable increase in the ash content during the later stages of development suggests that mineral nutrients are absorbed by the embryos while in the brood pouch. In determining the caloric content of eggs I have only used those in the earliest stages of development (stage I of Pandian, 1972). The caloric and ash contents of egg material is shown in Table 31. Because of the small size of individual broods I combined a number of broods to obtain two groups, one from EARLY and one from LATE breeding individuals. There were no significant differences between the egg material of the two groups for either caloric content (t = 0.53, d.f. = 7, n.s.) or ash content (t = 0.27, d.f. = 30, n.s.). The caloric content of the eggs was found to be 26.19 ± 0.94 $J.mg^{-1}$ DW (± 95% C.I.), slightly greater than Pandian's (1972) estimate of 24.94 $J.mg^{-1}$ DW.

The caloric and ash content of the somatic tissue of EARLY and LATE breeding females was also determined (Table 31). As would be expected from Fig 25 there was no difference in ash content (t = 1.94, d.f. = 43, n.s.). There was a significant difference in caloric content (t = 2.87, d.f. = 9, $P < 0.02$) but this was to be expected from Fig 26. LATE breeding females are considerably smaller than those breeding EARLY, and so are less energetic. The difference in caloric content per mg of body tissue does not necessarily mean that the LATE breeders have made a greater reproductive investment. Saudray (1954) showed that the lipid content of female tissue is markedly reduced on the production of a brood, but by the completion of embryonic development this had returned to its initial level through feeding.

vi. Respiration

Metabolic rate, usually measured as O_2 consumption per unit time, is allometrically related to body size following the familiar equation

$$M = a \cdot W^b$$

where M = rate of O_2 consumption and W = body size. In order to determine the weight specific O_2 consumption rate it is necessary to obtain estimates of the parameters a and b. The value of b is generally found to be about 0.75 when body size is measured as weight (Alexander, 1971). Ellenby (1951) measured O_2 consumption of eighty male Ligia oceanica at 25°C and found a value of 0.726. In a particularly thorough study of the factors affecting O_2 consumption in this species Newell, Roy & Armitage (1976) also determined an average value of b = 0.72. Metabolic rate is very sensitive to temperature, and so the latter must be taken into account when constructing an energy budget. Newell et al. (1976) found that the most important factors affecting metabolic rate were temperature and body size, followed by starvation period, feeding period, acclimation temperature and % lipids. From their data (their Fig 2) I have calculated the values of a and b at six temperatures (Table 32). From Ellenby (1951) (his Fig 3) I have calculated a value of a at 25°C as 1.23. Clearly the two studies are in general agreement about the magnitude of O_2 consumption of Ligia oceanica in the laboratory. Using the parameters given in Table 32, and the oxycaloric constant for poikilothermic herbivores given by Elliot & Davison (1975) of 14.14 $J.mg^{-1}$ O_2 consumed (which is equivalent to 20.20 $J.ml^{-1}$ O_2 consumed), the energy lost through respiration can be estimated.

TABLE 32. Values of the parameters a and b for the regressions of log oxygen consumption (ml $O_2.hr^{-1}$) on log dry weight (mg) at five temperatures (from Newell, Roy & Armitage, 1976).

TEMPERATURE °C	INTERCEPT a	SLOPE b
5	0.68	0.73
10	2.01	0.56
15	0.93	0.79
20	2.00	0.72
25	2.58	0.72
30	1.10	0.99

3. THE MODEL

Using the notation of Petrusewicz & MacFadyen (1970), the energy budget of isopods may be expressed by the equation

$$C = P_g + P_r + R + E_x + U + F$$

where C = energy consumed;
P_g = energy accumulated in growth;
P_r = energy devoted to gametes;
R = respiratory energy loss;
E_x = energy lost through ecdysis;
U = energy lost as soluble excretory products;
F = energy eliminated as faeces.

Ideally each parameter in the equation would be estimated independently for the population throughout the complete life cycle (Strong & Daborn, 1979). Such perfection is rarely achieved, and this study is no exception.

i. The methodology

In constructing an energy budget for Ligia oceanica at R.H.B. values of P_g, P_r, R, and E_x have been estimated for 30-day periods throughout life for males and females separately, starting from July 1st when all births are assumed to occur. These values are multiplied by the average number of survivors per m^2 using the survivorship schedules (values of L_x) for the two sexes (Tables 16 & 17) and assuming an initial starting number of 144.6 m^{-2} of each sex (from Table 14). These 30-day periods are approximated to months from July and summed to obtain the monthly population energy budget over a whole year. These monthly values are then summed to obtain the yearly energy flow. Details of the calculation of the individual estimates in the energy budget are given below.

a. Growth, P_g

The energy devoted to growth was determined by estimating the increment in energy between the start of each 30-day period. This was determined from the values of live weight read from the lines fitted in Figs 27 & 28 for males and females. These were converted to dry weights and then to initial and final total caloric contents using the equations determined in section 2.i and Table 31. The difference is the energetic increment due to growth over the 30-day period.

When females are producing broods the monthly value of P_r (calculated in section 3.i.d) is subtracted to give the value of P_g. A slight difficulty arises because the loss of weight shown by the EARLY breeding females upon brood release would result in apparent degrowth. Hence growth was assessed up to the peak live weight immediately preceding brood release. For the next 30-day period the live weight immediately following brood release was taken as the initial live weight. In the laboratory the weight loss on release of a brood was found to be 22.2 ± 1.7% (95% C.I.). The mean live weight of all females found gravid at this time was 416.6 mg, so the immediate post-parturient live weight was taken to be 324.1 mg, and is in good agreement with the data shown in Fig 28. This procedure was not necessary when the LATE and VERY LATE groups were producing broods because only a proportion are breeding and the 'average animal' at these times does not lose weight.

b. Respiration, R

For each 30-day period the average live weight of males and females is calculated. This is converted to average dry weight (Table 28). For each month the average maximum (daily) and minimum (nightly) temperatures are taken from the continuous temperature records of the former Wellcome Marine Laboratory. The appropriate parameters are selected from those in Table 32, and the oxygen consumption calculated for animals of that size at that temperature.

These figures are multiplied by the average hours of daylight and darkness for that 30-day period, and summed to obtain the total monthly oxygen consumption in ml O_2. This is then converted to joules using the oxycaloric constant of 20.20 $J.ml^{-1}$ O_2.

c. Moulting, E_x

The average live weight is taken as the starting point in assessing E_x. The proportion of animals in the premoult stage was found using the equation determined in section 2.iv (see Fig 30). Moulting is likely to be temperature dependent but unfortunately it did not prove possible to estimate the duration of the premoult period at different temperatures. To allow for the effect of temperature on moulting I have assumed that the duration of the premoult period, found to be 4.19 days at 12°C, is inversely related to temperature with a $Q_{10} = 2.5$. Again the monthly average maximum and minimum temperatures were used, together with the average hours of daylight and darkness, to calculate the duration of the premoult period for each month, and hence the number of moults per individual of each sex over the 30-day period. The dry weight of the moults is then calculated from the average dry weight of the animals (section 2.iv, Fig 31), and converted to joules (Table 31).

For females, which do not moult while carrying their broods, the proportion moulting is reduced by the proportion gravid at that time (see section 3.i.d). Following release of the brood all these females, the total proportion that became gravid, are assumed to moult once in the succeeding 30-day period in addition to the proportion calculated from the average weight of the females at that time.

d. Reproduction, P_r

The average live weight of LATE, EARLY and VERY LATE breeding females at R.H.B. was found to be 237.3, 416.6 and 437.7 mg respectively (from Table 14). These figures were used to obtain estimates of the dry weight of egg material produced from the data in Chapter 5 (section 3.ii.b). The proportion of each age group which produced broods over each 30-day period was determined from Fig 5 in Willows (1984), which represents all the data on breeding phenology from the two sites shown here in Figs 10 & 19. The amount of egg material produced per individual multiplied by the proportion producing broods gives a gravimetric estimate of P_r. This is then converted to joules using the data in Table 31.

Although it proved possible to dissect sperm from the oviducts of recently mated females as a discrete globular mass, insufficient material could be collected to estimate P_r for males, which is therefore assumed to be negligible.

e. Excretion, U

U can be estimated from knowledge of monthly O_2 consumption and the protein content of the food (Elliot & Davison, 1975). However as I have estimates only of the former, and because U tends to be very small, I have assumed that it is zero. Hassall (1976) estimated U to be only 0.6% of the total digested energy of Philoscia muscorum, while Strong & Daborn (1979) give a figure of 2.1% for Idotea baltica.

f. Consumption, C and Egestion, F

By summation we obtain the total assimilated energy, A, as

$$A = P_g + P_r + R + E_x$$

Since I assume U = 0, this is equal to the total energy digested, D. From the assimilation experiment (section 2.iii) the total amount of energy consumed (C) and egested (F) can be calculated from the assimilation (= digestion) efficiency of 58.0%.

ii. The results

Fig 32 shows the distribution of total assimilated energy (A) over the period of a year. This peaks in July and August, when growth and respiration rates are highest. Total energy assimilated in July and August is over twice that achieved in other months with the exception of September. Clearly production in the upper intertidal zone is highly seasonal. Also shown in Fig 32 is the monthly biomass predicted from the schedules of male and female growth and survivorship. This also reflects the rapid growth which occurs in July and August. The decline in biomass over the winter is due to the cessation of growth and the action of mortality, particularly on the older age groups.

Fig 33 shows the seasonal distribution of P_g, P_r, R and E_x throughout the year expressed as a percentage of the total assimilated energy for that month. The relative magnitudes of P_g, R and E_x vary little over the year even though the magnitude of A varies by a factor of x8. Respiration and moulting account for slightly more of the monthly energy budget in the winter than in the summer months, when growth and reproduction account for slightly more.

FIGURE 32

Seasonal variation in biomass ($g.m^{-2}$) and assimilated energy ($kJ.m^{-2}$) calculated for the population of *Ligia oceanica* at Robin Hood's Bay.

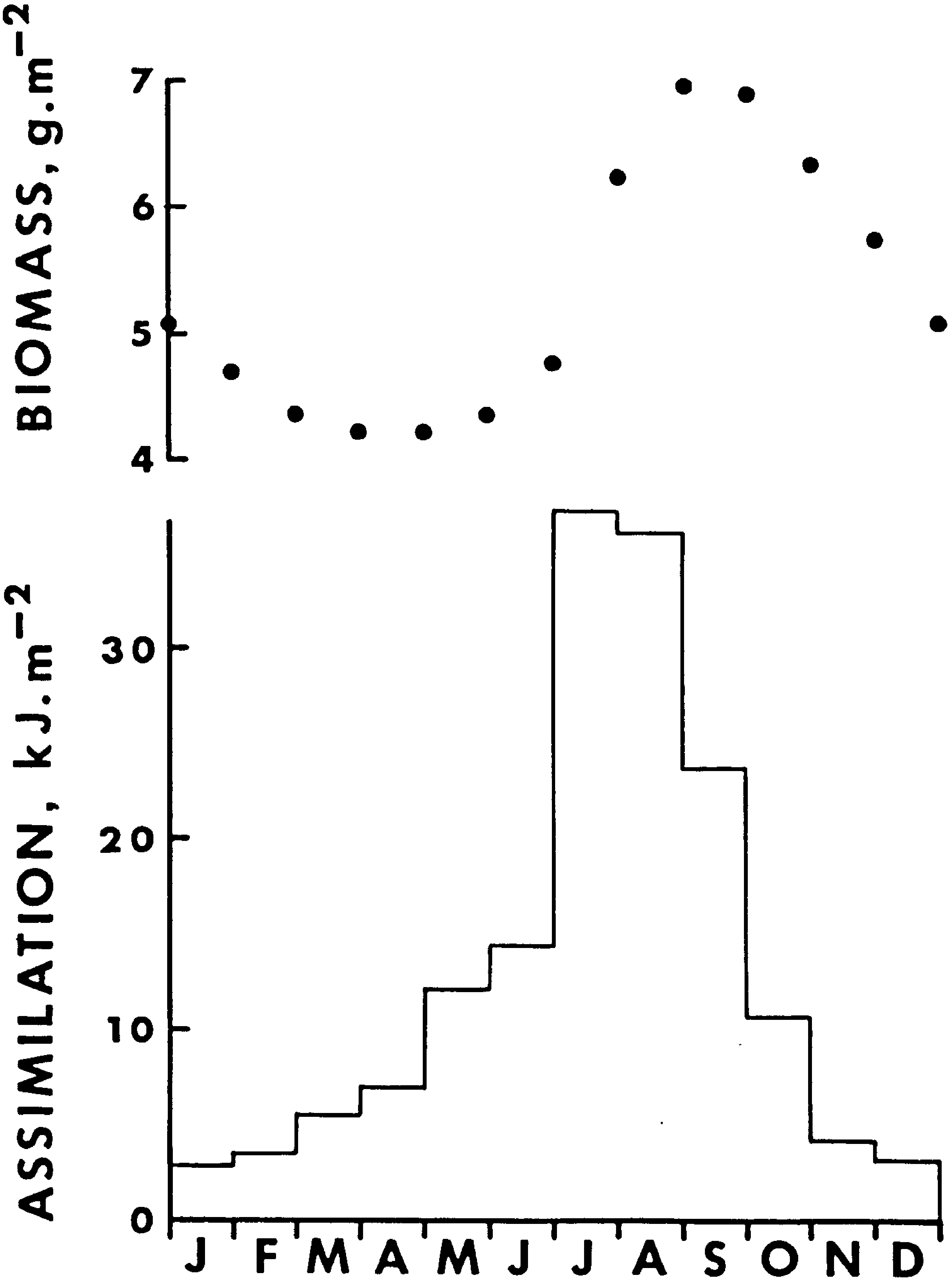

BIOMASS, g.m^{-2}
7
6
5
4
ASSIMILATION, kJ.m^{-2}
30
20
10
0
J
F
M
A
M
J
J
A
S
O
N
D

FIGURE 33

Seasonal distribution of production due to growth (P_g), production due to reproduction (P_r), respired energy (R), and energy lost through ecdysis (E_x), as a percentage of monthly total assimilated energy (A), caculated for the population of Ligia oceanica at Robin Hood's Bay.

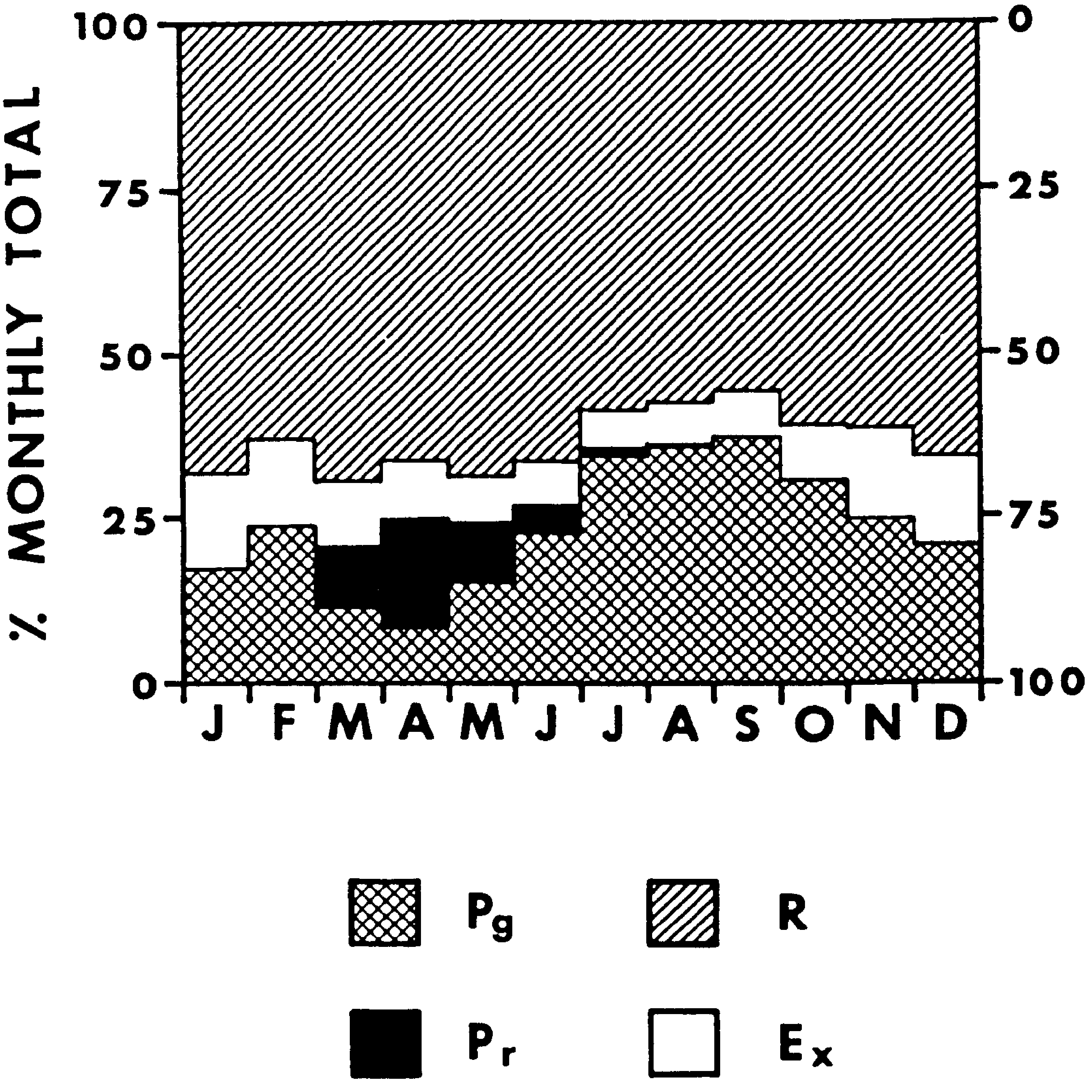

% MONTHLY TOTAL
100
75
50
25
0
0
25
50
75
100
J F M A M J J A S O N D
P$_g$
R
P$_r$
E$_x$

TABLE 33. Energy budget for average male and female *Ligia oceanica* at Robin Hood's Bay.

COMPONENT	MALES		FEMALES	
	J	%	J	%
P_g	157.4	31.5	163.4	26.9
P_r	-----	----	26.5	4.4
R	299.7	60.0	369.5	60.7
E_x	42.7	8.5	24.5	8.1
A = D	499.7	100.0	608.3	100.0

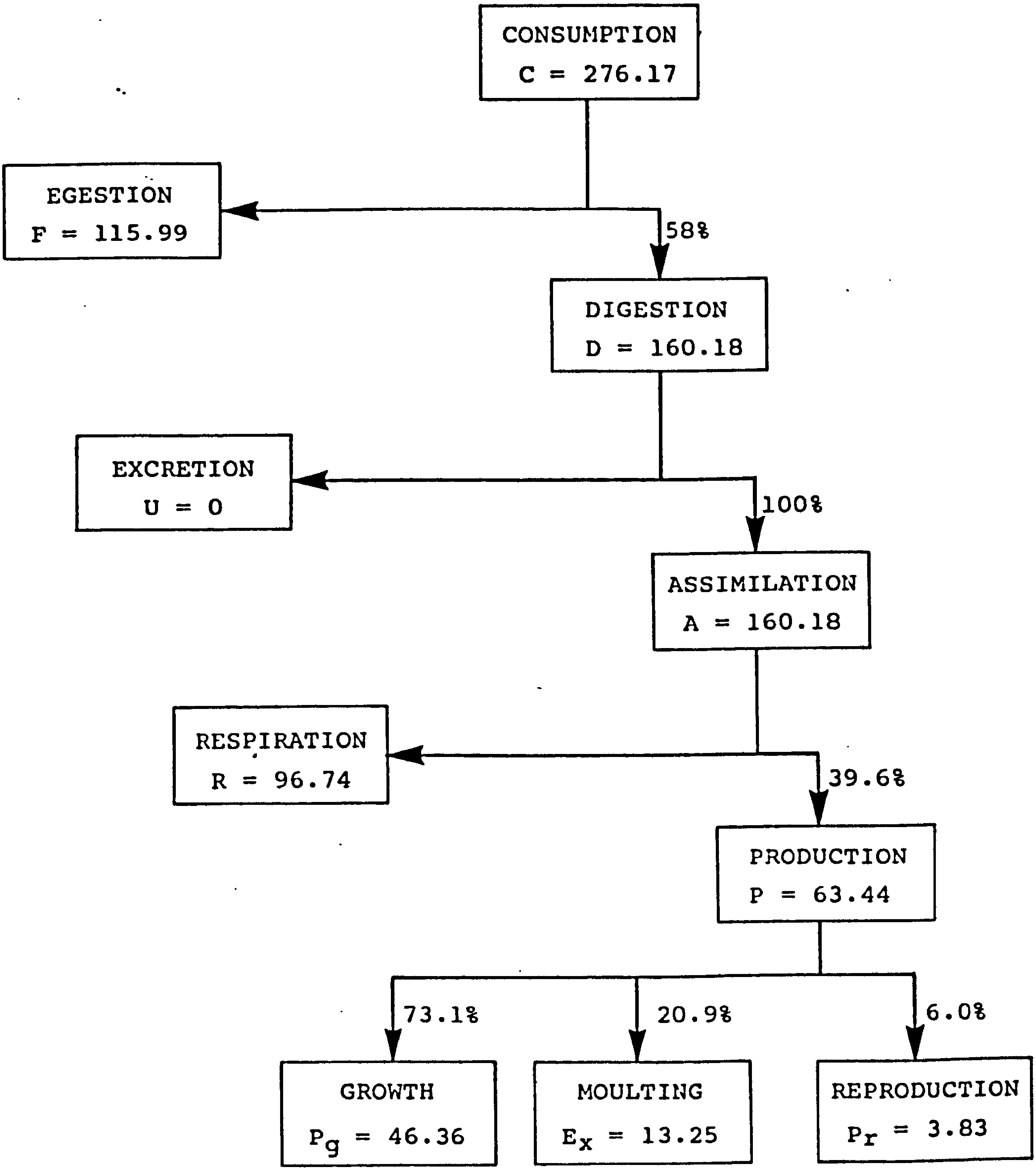


Figure 34. Population energy budget for Ligia oceanica at Robin Hood's Bay. Values are $kJ.m^{-2}.yr^{-1}$.

The yearly budgets for the average male and female at R.H.B. are shown in Table 33. Females account for slightly more (55%) of the total energy budget than males. Although males grow faster and can live longer, the generally better survivorship of females results in the marginally greater total energy budget of this sex. Respiration by the two sexes is a very similar proportion of their respective budgets (about 60%), as is moulting (about 8%). Growth forms a slightly lower fraction of the females total energy budget, presumably due to their reproductive output of 4.4%.

Fig 34 details the population energy budget (in $kJ.m^{-2}.yr^{-1}$), and follows the layout used by Hassall (1976) and Hassall & Sutton (1977), except that the magnitude of E_x is evaluated, and U is not. Following Petrusewicz (1967) moulting is considered as a component of production in Fig 34, which gives a population estimate of P_r as 6.0% of production P. If moulting is considered as an unavoidable cost of growth, then the magnitude of P_r becomes 8.3% that of P_g.

Average population biomass (B) has also been calculated in energetic terms as 23.21 $kJ.m^{-2}$, giving a value for P/B of 2.73. The ratio of P/R is 0.656.

iii. Evaluation of the model

The greatest sources of error and bias incorporated in models of this sort do not derive from the estimation of the various components and conversion factors but in their extrapolation to the field population throughout the year. Here I wish to discuss some of the less sound of these assumptions.

Assimilation efficiences are usually derived from laboratory experiments, and only rarely are animals given the choice of foods likely to be experienced in the field at all seasons. Examination of the gut contents of *Ligia oceanica* from the R.H.B. and Whitby populations showed that, at these sites at least, *Ligia* is essentially herbivorous, feeding on encrusting diatoms and green algae, probably Enteromorpha spp. This alga is present on the sampling site at R.H.B. in small quantities. The young of L. oceanica shelter within growths of Enteromorpha and Carefoot (1979) has suggested that the young of L. pallasii may feed on the new growth of this algae. Although the relative quantities of Enteromorpha, diatoms and other unicellular algae in the diet of L. oceanica have not been evaluated, my impression is that Enteromorpha was not a major food resource at this site. However animals fed well on both fresh and remoistened Enteromorpha in the laboratory, exhibiting growth and survivorship as good as in the field, and the females reproduced. However the consumption figures generated using an assimilation efficiency calculated from laboratory experiments using what is probably a minor food resource must be open to question.

Due to the nature of the food resource, consumption could not be measured directly in the field. Indirect estimates would have been possible by measuring faeces production of animals taken from the field throughout the year. Although one would still have had to assume the assimilation efficiency determined in the laboratory, the indirect estimate of C would have been useful in providing an alternative estimate of assimilation, from which respiration could have been derived as $R = A - P$. Respiration is probably the most inaccurate of all population energy budget estimates (MacFadyen, 1967; Humphreys, 1978). The close agreement of the two studies by Ellenby (1951) and Newell et al. (1967) suggests that the laboratory estimates are reasonably accurate. In extrapolating these to the field I have used measurements of average monthly maximum (day time) and minimum (night time) rock temperatures on the shore, which are probably not those experienced by the woodlice. The maximum values especially are likely to be overestimates of the temperature of animals protected within crevices and capable of thermoregulation by evaporative water loss (Edney, 1951, 1953, 1954, 1968). In addition these temperatures have been approximated to the nearest $5^{o}C$ to obtain size specific rates of O_2 consumption, adding a further source of error.

Further error arises because the rate of O_2 consumption is related to weight by a power function, and hence small animals have a disproportionately higher rate of O_2 consumption. By using the mean dry weight of an animal within each age class for every 30-day period in the calculations there will be a consistent tendency to underestimate respiration. This would be reduced if each age class was itself divided into size classes, allowing a 'best estimate' of population respiration (Phillipson, 1963). However the error involved here will be less than that which would result from the use of monthly estimates of population biomass without any account being taken of the populations' age and size structure (Phillipson, 1963).

On the positive side account has been taken of both diurnal and seasonal temperatures throughout the life of Ligia, while Newell et al. (1976) show that exposure temperature and body size were the two most important factors, of those they tested, to affect O_2 consumption. Hassall (1983) has shown that O_2 consumption by Philoscia muscorum is also affected by temperature fluctuations, sex and breeding condition. Phillipson & Watson (1965) also showed that the maturation of the ovaries raises O_2 consumption in Oniscus asellus.

In using the data of Newell et al. (1976) I have taken the temperature specific equations relating body size to the rate of O_2 consumption for animals taken immediately from the field. These rates were generally lower than those determined for animals acclimated to laboratory conditions by a factor of about x2. Hassall (1983) considered that the errors involved in extrapolating laboratory data on respiratory rate to field populations under natural conditions are far less than those associated with estimating field population densities. However he did not consider the effect of activity on respiratory rate and yet a major criticism of the application of laboratory derived respiratory data to field populations is that no account is taken of activity (Humphreys, 1978). For example Newell, Wieser & Pye (1974) showed that O_2 consumption by active Porcellio scaber is from x1.3 to x2.4 higher than the standard (resting) rate in the laboratory. Reichle (1967) demonstrated that active Cylisticus convexus and Armadillidium vulgare had active rates x1.5 that of the basal rate. Newell et al. (1976) noted that their Ligia remained inactive while in the respirometers. Following Mann (1965) a factor of x2 is frequently included in energy budgets to correct for field activity, and Humphreys (1978) suggests a factor of x3. For Ligia oceanica both daylight and low night time temperatures reduce activity, and both these factors should be included in any model incorporating activity related respiratory costs. Accepting Humphreys (1978) factor of x3 would increase the value of A to 354 $kJ.m^{-2}.yr^{-1}$, and reduce the production efficiency (P/(P+R)) to 17.9%

Probably the most accurate estimates are those used in assessing production, P. Ideally the model would not take increments and averages over 30-day intervals, but use the integrals of equations relating growth and survivorship of the two sexes to time, and moulting to size. However the difficulty of fitting suitable functions to the data precluded such sophistication, which itself is probably unwarranted by the data. Clearly assuming a Q_{10} = 2.5 for moulting rate is arbitrary, but is more realistic than assuming that moulting rate is unrelated to temperature. The effect of assuming a Q_{10} = 2.0 or Q_{10} = 3.0 gives values for A of 158.9 and 161.6 $kJ.m^{-2}.yr^{-1}$, and values of E_x as a percentage of P of 19.2 and 22.6% respectively. Hence the effect on the overall energy budget of assuming quite different values of Q_{10} are slight. The calculation of moulting rate from the measured field temperatures again assumes that these are the temperatures experienced by the animals in the field.

In the model reproduction (P_r) is estimated as egg material produced over each 30-day period. For species such as Ligia this is somewhat unrealistic for the ripening of the ovaries occurs over an extended period. For example EARLY breeding females, which grow little over the winter months, already have well developed ovaries when dissected in November. As the weight of brood material is directly related to female body weight (Chapter 5, section 3.ii.a), it might be more reasonable to consider energy allocated to reproduction to be a constant fraction of P, but I have followed convention and estimated P_r when the eggs are released, in this case into the brood pouch. While not affecting the magnitude of annual P_r, it suggests that the partitioning of P_r from P is more seasonal than it really is.

4. DISCUSSION

Given the nature of the assumptions frequently necessitated when constructing an energy budget, assumptions which probably result in bias and loss of accuracy, it would not be surprising if no patterns emerged when such budgets are compared for different species with different ecologies. However Humphreys (1979), in an analysis of 235 energy budgets, found that contrary to his earlier expectations (Humphreys, 1978), such patterns did appear, but that the resolution was not good.

Robertson (1979), in a review of the literature on the energy budgets of marine benthic invertebrates (including many intertidal species), found a negative relationship between the annual ratio of P/B and lifespan. Using a value of 30 months for the maximum lifespan of L. oceanica gives, from his equation, a value for P/B of 2.35, which is in accord with the value of 2.73 determined in this study. This would seem to support the evidence for such a relationship. For woodlice, ratios of P/B generally fall between 2.0 and 3.0, regardless of habitat (see Table 35). The value of 5.56 for Cirolana imposita is regarded as exceptionally high (Koop & Field, 1981). The ratio of P/B reflects the efficiency with which the population uses its biomass to produce more biomass. The value of 2.73 for L. oceanica is about intermediate for isopods. While individuals living in equilibrium populations should devote more resources to maintenance and survival than those in non equilibrium populations (Pianka, 1970), the ratio of P/B includes the effects of mortality on the population, and so the evolutionary significance of the relationship between lifespan and P/B, found by Robertson (1979), is not clear.

Both McNeill & Lawton (1970) and Humphreys (1979) give, using published data, equations relating population respiration to production. Using the value for production of 63.4 $kJ.m^{-2}.yr^{-1}$ calculated here for L. oceanica, gives estimates for R of 137.7 and 347.8 $kJ.m^{-2}.yr^{-1}$ respectively. The equation from Humphreys (1979) is based on a larger data set, that for non-insect invertebrates. The fact that this estimate is so much greater than that calculated from the data suggests that respiration may have been underestimated. He also found that the average production efficiency (100.P/A) for herbivorous non-insect invertebrates was 20.8%, almost half the value of 39.6% calculated for L. oceanica, which again suggests that respiration may have been underestimated.

Humphreys (1981) derived equations relating the level of assimilation (in $kcal.m^{-2}.yr^{-1}$, not $cal.m^{-2}.yr^{-1}$ as stated in his paper) to an index he termed the "metabolic index". This is the ratio of average annual biomass (in $cal.m^{-2}$) to maximum live weight (in mg) to the 0.75 power. Taking a value of maximum live weight of 700mg for L. oceanica at R.H.B., his predictive equation for long-lived terrestrial invertebrates gives a predicted value for A of 37.5 $kJ.m^{-2}.yr^{-1}$, which is not at all close to that calculated from the data (160.2 $kJ.m^{-2}.yr^{-1}$). This figure may suggest that P+R has been overestimated, however such estimates depend substantially on the value of maximum body size used. This is not easily determined for species with indeterminate growth. For this species there is a large difference in maximum size between the sexes, making the choice of a value difficult. In addition, the largest animals are, by their nature, very rare, and so the maximum size observed will depend on the sample size.

Comparing the data on the energetics of L. oceanica with that on other isopods a number of generalisations and points of interest emerge. However such comparisons are not facilitated by the the large differences in quality of the data on the different species, nor by (often unavoidable) differences in the units in which the budget is expressed.

Grahame (1983), in a review of crustacean feeding mechanisms, has noted that there is a trend toward higher assimilation of animal versus plant food. Such certainly appears to be the case amongst the isopods. I have collected data on the assimilation efficiences of 16 species of terrestrial, maritime, marine and freshwater isopods (Table 34). These were ranked according to trophic mode (carnivore $<$ herbivore $<$ herbivore/detritivore $<$ detritivore) using the authors trophic classification where possible. I have not included the data on Cylisticus convexus and Armadillidium vulgare feeding on lettuce (Reichle, 1967) in the analysis because lettuce is not a likely field food resource for these species. There is a significant correlation between trophic mode and assimilation efficiency (Kendall's rank correlation, $\tau = -0.711$, $n = 18$, $P < 0.01$). Clearly the carnivorous species have much higher assimilation efficiencies than the detritus feeders. Herbivorous species, such as L. oceanica, have intermediate values, ranging from 50-80%. These differences in the digestibility of food are probably related to differences in the quality of the organic component of the food (Grahame, 1983).

Unlike many studies of crustacea, this one has evaluated the magnitude of energy loss through ecdysis. This loss has proved to be quite substantial. E_x for an isopod has only been determined previously for Idotea baltica (Strong & Daborn, 1979), who also found that E_x was a significant component of the energy budget (5.2-7.9%) for this species. Other authors have assumed either that E_x is negligible (though it is probably greater than U), or that isopods consume and digest totally their exuvia. This may be true for terrestrial species, but for marine species this option is probably not available as the exuvia would wash away. Ligia oceanica does not eat its exuvia, and the energy and minerals contained therein are lost. For terrestrial isopod species the loss of mineral nutrients contained within the exoskeleton may be a significant drain, and perhaps for this reason they consume their moults. Wieser (1968) has suggested that coprophagy and the low assimilation efficiencies of terrestrial species may also be adaptations to the reduced availability of certain mineral nutrients in terrestrial habitats.

TABLE 34. Assimilation efficiences of marine and terrestrial isopod species.

SPECIES	TROPHIC STATUS	FOOD GIVEN	ASSIMILATION EFFICIENCY %	METHOD	REFERENCE
Glyptonotus antarcticus	Marine carnivore	*Chorismus (shrimp)*	95	Gravimetric	Clarke (1979)
Cirolana imposita	Marine carnivore	*Syllis* (polychaete)	97	Gravimetric	Shafir & Field (1980a)
Cirolana harfordi	Marine carnivore	Fish flesh	88	Caloric	Johnson (1976a)
Idotea baltica	Marine algivore	*Ascophyllum*	56	Caloric	Strong & Daborn (1979)
Idotea baltica	Marine algivore	*Enteromorpha*	63	Caloric	Tsikhon-Lukanina *et al*. (1968)
Tylos punctatus	Maritime detritivore	*Macrocystis*	64	Gravimetric	Hayes (1974)
Ligia pallasii	Maritime algivore	*Ulva*	78	Caloric	Carefoot (1973a)
		Nereocystis	74	Caloric	
Ligia oceanica	Maritime algivore	*Enteromorpha*	58	Caloric	This study
Ligia dilatata	Maritime detritivore	Kelp (mostly *Ecklonia*)	25	Caloric	Koop & Field (1981)

TABLE 34 (cont). Assimilation efficiences of marine and terrestrial isopod species.

SPECIES	TROPHIC STATUS	FOOD GIVEN	ASSIMILATION EFFICIENCY %	METHOD	SOURCE
Cylisticus convexus	Terrestrial detritivore	Lettuce	70	Caloric	Reichle (1967)
Armadillidium vulgare	Terrestrial herb./detrit.	Lettuce	73	Caloric	Reichle (1967)
Armadillidium vulgare	Terrestrial herb./detrit.	*Silybum* (thistle leaves)	50-75	Gravimetric	Hubbell *et al*. (1965)
Hemilepistus reamuri	Desert herb./detrit.	*Artemisia* & *Hammada* leaves	51-82	Caloric	Shachak *et al*. (1976)
		Leaves + soil	25-35	Caloric	
Tracheoniscus rathkei	Terrestrial detritivore	Dried *Asimina* leaves	33	Caloric	White (1968)
Porcellio scaber	Terrestrial detritivore	Assorted leaf litter	29	Gravimetric	Watson (1966)
Oniscus asellus	Terrestrial detritivore	Assorted leaf litter	27	Gravimetric	Watson (1966)
Oniscus asellus	Terrestrial detritivore	*Acer* litter	16	Gravimetric	Hartenstein (1964)
Philoscia muscorum	Terrestrial detritivore	Assorted leaf litter	21	Gravimetric	Hassall (1976,1977)
Asellus aquaticus	Aquatic detritivore	Decayed *Alnus* leaves	30	Gravimetric	Prus (1971)

Energy budgets are often used to assess the relative importance of a species in the energy relations of the community (eg. Shafir & Field, 1980; Koop & Field, 1981). Unfortunately little is known of the population energetics of species inhabiting the supralittoral fringe. Certainly at R.H.B. and Whitby *L. oceanica* appears to be the only herbivore of any significance at this particular tidal level. The magnitude of energy flow through this population is much less than that for *L. dilatata* in South Africa (Koop & Field, 1981). This species is a detritivore feeding on the large amounts of kelp debris cast up onto the shore. They concluded that the major role of this species was in recycling organic material, in the form of their faeces, to the coastal community.

On an absolute basis it is clear that populations of the marine and maritime species are much more energetic, by at least an order of magnitude, than the terrestrial species (see Table 35). The marine species include a carnivorous isopod, *Cirolana imposita*. Hassall (1976) noted that *Philoscia muscorum*, a terrestrial detritivore, had consumption rates greater than many terrestrial herbivores, and substantially greater than the other terrestrial isopods. Although this terrestrial species consumes more energy than *L. oceanica*, the low assimilation and production efficiencies of *P. muscorum* result in a much lower level of population production. Generally, the marine and maritime species have higher production efficiencies than the terrestrial species, and the difference is marginally significant (Mann-Whitney U-test, $U_s = 30.5$, $P = 0.1-0.05$). The value of 42% for *Trichoniscus pusillus* (Phillipson, 1983) seems exceptionally high for a terrestrial species, possibly as a result of estimating population production indirectly from respiration using McNeill & Lawton's (1970) empirically derived equation. The other values in Table 35 have been derived independently. This reduction in production efficiency between terrestrial and marine species, if indeed it is real, might reflect the cost to woodlice of the less equable environment, especially temperature regimes, experienced by terrestrial species.

TABLE 35. Summary of data on the population energetics of isopod species. Values have been converted to kJ.m^{-2}.yr^{-1} where necessary.

SPECIES	C	A	R	P	P/B	PRODUCTION EFFICIENCY	SOURCE
Cirolana imposita	9899	4051	1822	2229	5.56	55	Shafir & Field (1980a)
Cirolana harfordi	----	----	----	----	2.39	40	Johnson (1976a)
Idotea baltica	----	----	----	----	----	42	Strong & Daborn (1979)
Ligia dilatata	8217	452	346	106	3.75	23	Koop & Field (1981)
Ligia oceanica	276.2	160.2	96.7	63.4	2.73	40	This study
Tylos punctatus	----	----	----	----	----	39	Hayes (1974)
Philoscia muscorum	700.4	135.0	113.2	21.8	----	16	Hassall (1976)
Trichoniscus pusillus	----	0.270	0.203	0.070	2.32	25	Standen (1973)
Trichoniscus pusillus	----	0.779	0.454	0.327	3.5	42	Phillipson (1983)
Tracheoniscus rathkei	0.669	0.222	-----	-----	----	--	White (1968)
Porcellio scaber	3.70	1.84	1.58	0.31	1.93	15	Saito (1969)
Armadillidium vulgare	16.80	8.39	6.79	1.60	2.03	19	Saito (1969)
Ligidium japonicum	3.30	1.65	1.43	0.22	2.12	13	Saito (1969)

Slobodkin & Richman (1961) argued that because natural selection will usually have acted to maximise the number of offspring produced it will only rarely have acted to maximise the energetic content of the body tissue. Hence they predicted that the distribution of caloric content of species' tissue should be skewed to the right. High energetic content should only occur in species which have to sustain a period of stress. In essence they argued that a trade-off should exist between caloric content and fecundity.

The energetic content of L. oceanica increases with size, suggesting that larger animals may be better able to withstand periods of food shortage. In Table 36 I have summarised the available data on caloric content of isopod tissue (converted to $J.mg^{-1}$AFDW where necessary : 1 cal = 4.1855 J). Due to the high and variable ash content of isopod tissue the only meaningful comparisons are on an ash-free dry weight (AFDW) basis. Generally the values have not been corrected for either endothermy (Paine, 1966) or acid production (Paine, 1971). For Ligia I have used the values calculated for females of LATE and EARLY breeding size. These values are close to the average for other isopods of 21.62 $J.mg^{-1}$ AFDW (Table 36), which itself is less than the mean value for all species studied of 24.36 $J.mg^{-1}$ AFDW (Cummins & Wuychek, 1971). The distribution of these values for isopods is not significantly skewed ($g_1 = 0.774$, one-tailed t-test, $t = 1.30$, $n = 14$, n.s.), though the sample size is small.

Following Richman & Slobodkin (1961), Calow & Jennings (1974) noted a relationship between mode of life and caloric content for species of platyhelminth. Amongst this group high energetic content, as a result of the use of lipid rather than glycogen as an energy storage compound, was associated with the lower fecundity of the free-living life mode. Free-living species, unlike those with various forms of commensal and parasitic relationships, are more likely to experience periods of food shortage.

In Fig 35 I show the available data for isopod species. I have used weight specific fecundity (average fecundity/mean breeding female AFDW), so as to express fecundity as the number of eggs per unit of body tissue. Fecundity is related to body size interspecifically amongst woodlouse species (Sutton et. al, 1984). Although the data base is small there are indications of a relationship between weight specific fecundity and caloric content. Ideally more data are needed, especially on highly fecund species like Idotea baltica. Most of the species in Table 36 and Fig 35 have large body size. On a per unit weight basis the smaller species, such as Trichoniscus pusillus, tend to be more fecund, but suitable (AFDW) data are lacking.

The interpretation of the relationship in Fig 35, if indeed it is real, is difficult. To support Richman & Slobodkins' (1961) hypothesis one would ideally need data on isopod somatic tissue, excluding the reproductive tissue. The species concerned are all essentially semelparous, and a premium is likely to be placed on reproduction, rather than on post-reproductive survival (Williams, 1966a; Gadgil & Bossert, 1970; Calow, 1979). The post-reproductive survival of these species is usually slight. In isopods the partitioning of material between reproduction and growth is a process which takes place over an extended period preceding the production of the brood. For example female Ligia oceanica, taken in November, at the beginning of the period of no-growth during the winter, have well-developed ovaries for reproduction in the spring. Therefore to examine properly the relationship between tissue energy content and fecundity one would need data either on the energy levels of isopods which have just produced broods, or on the somatic tissue only, excluding gonad tissue. The values in Fig 35 include both somatic and non-somatic, and male and female tissue, but appear to support Richman & Slobodkins' (1961) hypothesis.

FIGURE 35

Caloric content of body tissue (J.mg^{-1} AFDW) against weight specific fecundity of an average breeding female for eight species of isopod.

1. *Ligia dilatata*
2. *Ligia oceanica* EARLY
3. *Ligia oceanica* LATE
4. *Cirolana harfordi*
5. *Cirolana imposita*
6. *Oniscus asellus*
7. *Porcellio scaber*
8. *Philoscia muscorum*
9. *Idotea baltica*

For sources see Table 36.

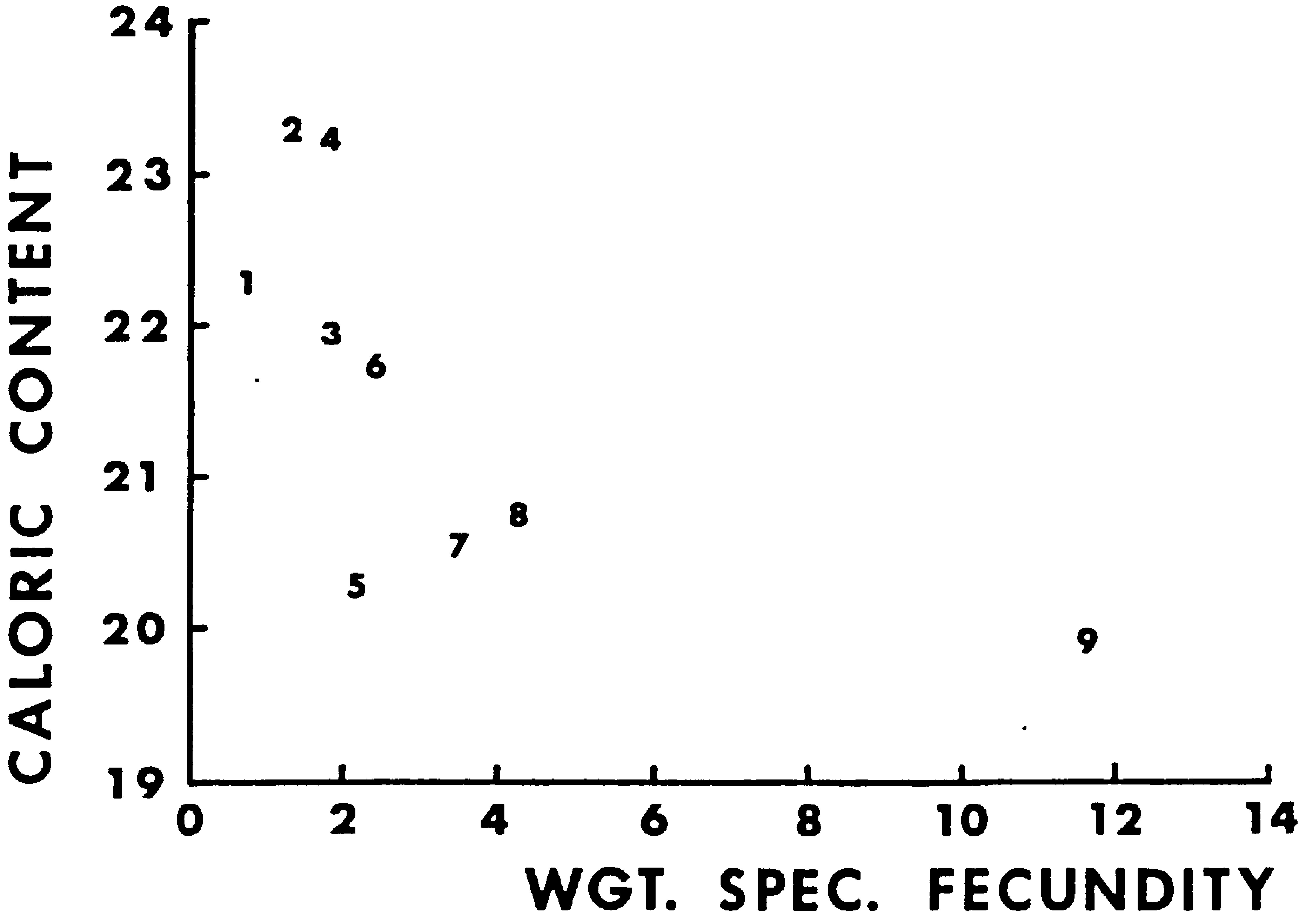

CALORIC CONTENT
24
23
22
21
20
19
0
2
4
6
8
10
12
14
WGT. SPEC. FECUNDITY
1
2
3
4
5
6
7
8
9

TABLE 36. Average breeding body size, ash content, fecundity, and caloric content of isopod species.

SPECIES		WEIGHT mg AFDW	ASH % DW	AVERAGE FECUNDITY	WGT SPEC FECUNDITY	ENERGY CONTENT $J.mg^{-1}$AFDW	SOURCE
Oniscus asellus		19.03	31.2	46.1	2.42	21.70	Watson (1966)
Porcellio scaber		11.79	29.2	41.0	3.48	20.54	Watson (1966)
Philoscia muscorum		4.32	25.6	18.5	4.28	20.73	Hassall (1976)
Idotea baltica		15.50	39.5	180.7	11.66	19.94	Strong & Daborn (1978,1979)
Cirolana harfordi		20.62	35	37.4	1.81	23.22	Johnson (1976a,b)
Cirolana imposita		10.81	27.6	23.5	2.17	20.27	Shafir & Field (1980a,b)
Ligia dilatata		33.71	17.4	28.6	0.85	22.29	Koop & Field (1980,1981)
Ligia oceanica	EARLY	67.34	26.5	88.0	1.31	23.28	This study
	LATE	38.22	26.5	72.1	1.88	21.94	
Tylos punctatus		-----	57.6	----	----	19.87	Hayes (1974)
Ligidium japonicum		-----	19.8	27.3	----	25.05	Saito (1969)
Armadillidium vulgare		-----	37.5	26.5	----	20.95	Saito (1969)
Porcellio scaber		-----	36.9	16.0	----	26.08	Saito (1969)
Asellus aquaticus		-----	20.1	----	----	18.74	Prus (1977)

An additional criticism is that animals may not necessarily be selected for high fecundity, but for large egg size. Fecundity *per se* is not a reliable index of reproductive effort (Hirshfield & Tinkle, 1975). A large reproductive effort, involving a concommitant low somatic energy content, may involve a small number of large eggs. Unfortunately data on the reproductive effort of isopods are few.

The low weight specific fecundity, coupled with a high caloric content per mg of tissue, of *Ligia oceanica* relative to the other species shown in Fig 35, given the limitations of the data, suggests that this species devotes resources to survival rather than to reproduction. This is in accord with the conclusions of Chapters 2 and 3, based on the population dynamics of this species.

CHAPTER 5

COMPARISON OF FECUNDITY, REPRODUCTIVE ALLOCATION AND EGG SIZE BETWEEN BREEDING GROUPS AND POPULATIONS.

1. INTRODUCTION

In this chapter I will consider in detail the inter- and intra-population variation in fecundity found between the two sites (see Chapter 3, section 3.iv.b.), between individuals, and between individuals comprising the EARLY and LATE breeding groups, at both Whitby (see Chapter 3, section 3.iv.a) and R.H.B. (Chapter 2, section 5.ii.a). In particular I will examine whether the increased weight specific fecundities of LATE, compared to EARLY, breeding group females at both sites, and of the R.H.B. over the Whitby population as a whole, are due to an increased allocation of resources to reproduction. Reproductive allocation, the weight of the brood mass, is here used as an estimate of an individuals reproductive effort (Williams, 1966a,b; Hirshfield & Tinkle, 1975). In section 3.ii.b. I use a modified form of the energy budget model described in the previous chapter to evaluate reproductive effort in terms of the energy budgets of individuals comprising the two groups. Variation between broods in mean ovum size is also examined.

2. METHODS AND STATISTICAL TREATMENT

The relationships between female weight and fecundity, brood weight and the average egg size of the brood of EARLY and LATE breeding females have been analysed by regression, analysis of covariance, partial correlation and path analysis (Sokal & Rohlf, 1981; Nie *et al.*, 1975). Data are presented for Whitby for 1981 and R.H.B. for 1982. In addition a small amount of data was obtained for Whitby in 1980. Female weight is taken to be the dry weight of the body after dissection of the contents of the brood pouch. Brood weight is taken as the dry weight of the whole brood. Average egg size is the dry weight of the brood divided by the number of eggs. All dry weights were determined by drying at 60°C under vacuum until constant weight, and weighed on a Mettler HL52 or Cahn 4400 balance to 0.01 mg. Only females carrying broods in the earliest stages of development (stage I of Pandian, 1972) were used.

3. RESULTS

i. Fecundity

a. Differences between breeding groups

The relationships between fecundity and female dry weight are analysed in Tables 39 & 40. The differences in weight specific fecundity found when female live body weight (which includes the weight of the brood) was used as the independent variable (see Chapter 2, section 5.ii.b., and Chapter 3, section 3.iv.a.) remained significant. In each case the LATE breeding animals had greater weight specific fecundities than their EARLY counterparts, and the conclusions of the previous analyses remain unaltered.

b. Differences between populations

Using dry body weight as the independent variable, the differences in weight specific fecundities of the EARLY and LATE breeding groups at Whitby (1981) and R.H.B. (1982) have been compared by ANCOVA. The results are shown in Tables 41 & 42. Using live weight as the independent variable both breeding groups showed elevated weight specific fecundity at R.H.B. (Chapter 3, section 3.iv.b.). Using dry weight only the EARLY group showed significantly greater weight specific fecundity ($F = 10.56$; d.f. = 1,105; $P < 0.01$) at R.H.B., the elevated fecundity of the LATE group at this site becoming non-significant ($F = 1.48$; d.f. = 1,63; n.s.).

ii. Reproductive allocation

a. Differences between breeding groups

The relationship between female dry weight and the dry weight of the brood are shown for Whitby for 1980 and 1981 in Figs 36 & 37, and for R.H.B. for 1982 in Fig 38. ANCOVA (Tables 43, 44 & 45) indicated no significant differences between the EARLY and LATE breeding groups for either the slopes or the elevations (adjusted means) of the paired regressions. Examination of Figs 36, 37 & 38 suggests that

FIGURE 36

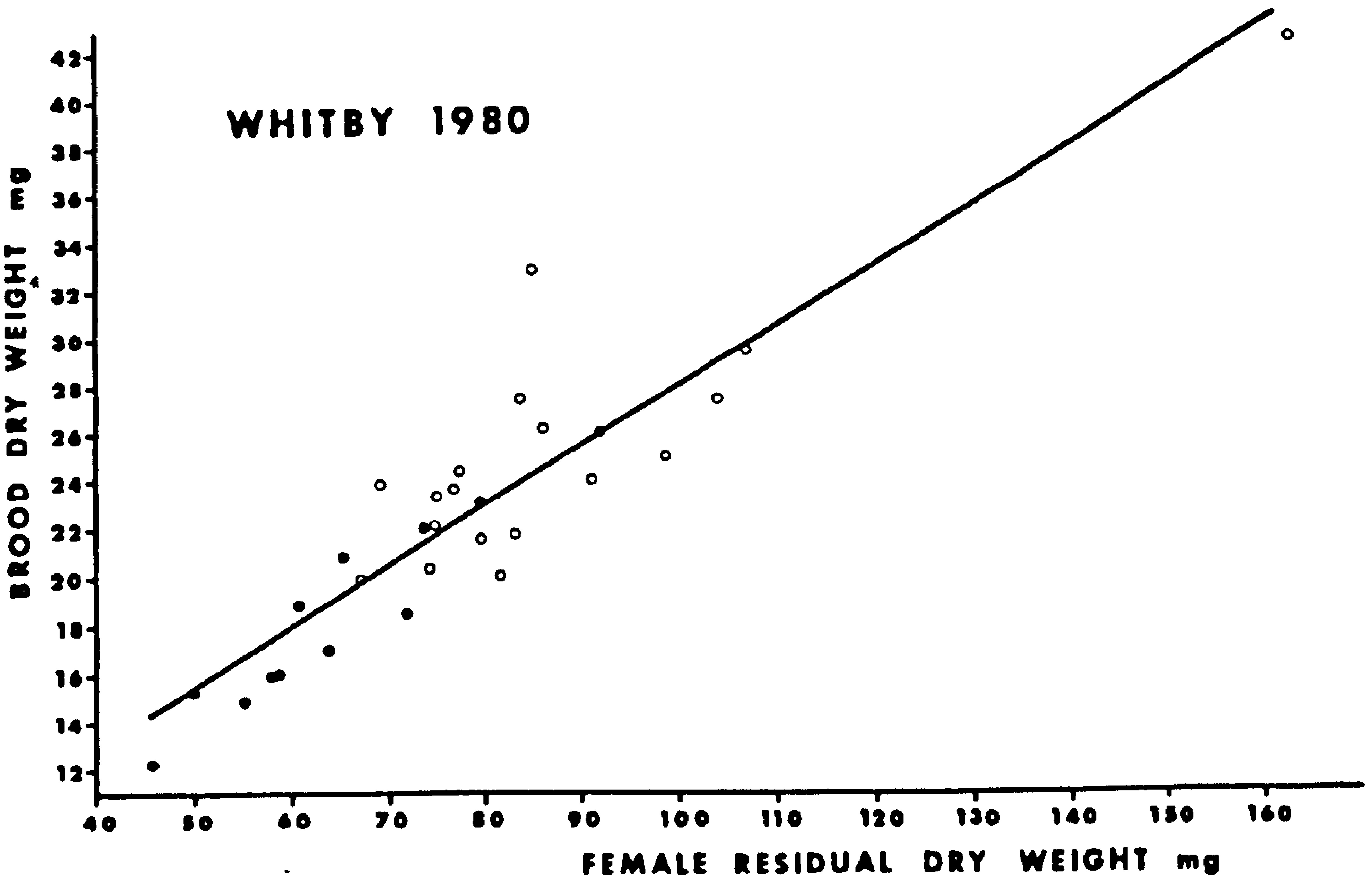
Regression of brood dry weight (y in mgs) against dry body weight after removal of the brood (x in mgs) for EARLY (○) and LATE (●) breeding female Ligia oceanica collected from Whitby in 1980.

EARLY & LATE combined : $y = 0.25x + 2.88$

FIGURE 37

Regression of brood dry weight (y in mgs) against dry body weight after removal of the brood (x in mgs) for EARLY (○) and LATE (●) breeding female Ligia oceanica collected from Whitby in 1981.

EARLY & LATE combined : $y = 0.26x + 2.14$


WHITBY 1980
BROOD DRY WEIGHT mg
FEMALE RESIDUAL DRY WEIGHT mg
12
14
16
18
20
22
24
26
28
30
32
34
36
38
40
42
40
50
60
70
80
90
100
110
120
130
140
150
160

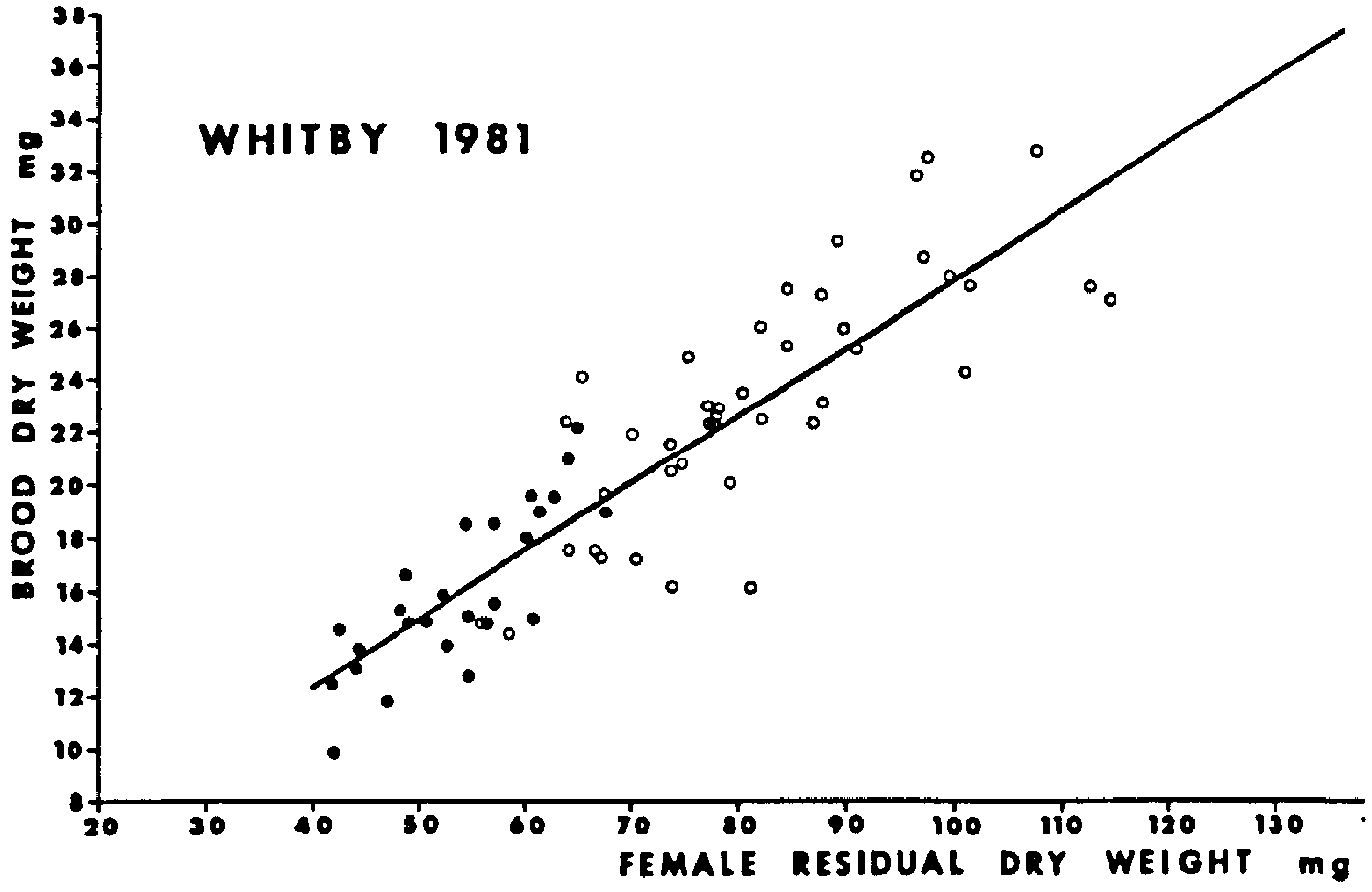
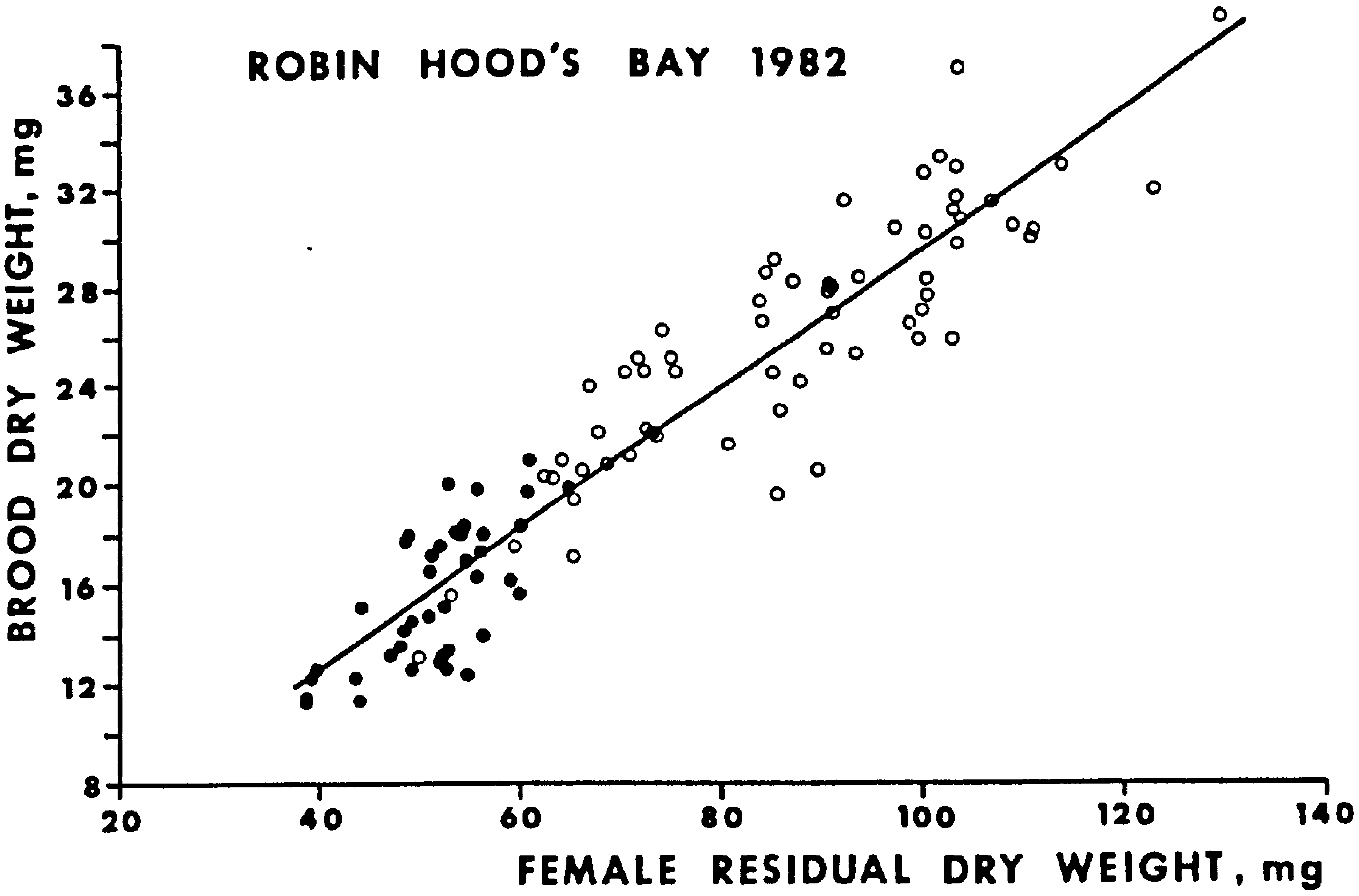

WHITBY 1981
BROOD DRY WEIGHT mg
FEMALE RESIDUAL DRY WEIGHT mg
8
10
12
14
16
18
20
22
24
26
28
30
32
34
36
38
20
30
40
50
60
70
80
90
100
110
120
130

FIGURE 38

Regression of brood dry weight (y in mgs) against dry body weight after removal of the brood (x in mgs) for EARLY (○) and LATE (●) breeding female Ligia oceanica collected from Robin Hood's Bay in 1982.

EARLY & LATE combined : $y = 0.28x + 1.39$


ROBIN HOOD'S BAY 1982
BROOD DRY WEIGHT, mg
8
12
16
20
24
28
32
36
20
40
60
80
100
120
140
FEMALE RESIDUAL DRY WEIGHT, mg

reproductive allocation is directly related to female body size. Data for EARLY and LATE groups were combined and the regression intercepts then tested for significant departures from the origin :

	t	d.f.	P
Whitby 1980	1.60	28	n.s.
Whitby 1981	1.87	67	n.s.
R.H.B. 1982	1.78	103	n.s.

Hence there were no significant differences in reproductive allocation, as a proportion of body weight, between the two breeding groups, and the reproductive allocation is directly proportional to female body weight.

Tinkle & Hadley (1975) and Hirshfield & Tinkle (1975) have argued that the only meaningful estimate of reproductive effort is that proportion of the total energy budget of an individual allocated to a single reproductive episode. While the above results suggest that there is no difference between individuals in the two breeding groups in reproductive effort, I have used a modified form of the energy budget model described in Chapter 4 (section 3) to calculate alternative estimates of reproductive effort for typical EARLY and LATE breeding group females. In order to do this I have had to make a number of assumptions concerning the two breeding groups :

a) those animals breeding LATE were all born to EARLY breeding animals the previous year;
b) the LATE breeding group makes up the upper 16% of the 0-1 year old animals in the size-frequency distributions of samples taken up to the time at which the LATE group reproduces;
c) the typical LATE breeding female dies following reproduction;
d) the EARLY breeding group is made up of all those offspring born LATE in the year, plus the slower growing of the EARLY born progeny;
e) that there is no differential mortality of EARLY and LATE born progeny;

f) that there is no correlation between growth rate and mortality within an age class.

These assumptions are justified to varying degrees below, and the basic assumed breeding pattern shown in Fig 15a. The assumptions concerning mortality will be considered later (Chapter 6, section 3.ii). That the LATE breeding group, breeding early in life, were themselves all born EARLY the previous year is likely because :

a) offspring born EARLY in the year experience more degree days of growth than those born LATE, and are likely to be larger at the end of the summer of their birth.
b) EARLY born progeny result from larger eggs (see section 3.iii.a), and are likely to be larger at birth. Cooney & Gehrs (1980) have shown that larger eggs of the copepod Diaptomus clavipes give rise to larger naupliar larvae. Boddeke (1982) has shown the same effect in the shrimp Crangon crangon. That larger embryos result in larger offspring within populations of anamniotes is generally acknowledged (Kaplan, 1980a). In addition, because initial growth rate is usually size dependent (eg. Hubbell, 1971; Kaplan, 1980a; Kaufmann, 1981), larger eggs will result in larger, faster growing offspring. Lawlor (1976a) found that this was the case for Armadillidium vulgare.
c) EARLY born offspring make up about 56% of the year's recruits (Chapter 2, section 6.i.), but only 16% of those surviving to one year of age produce LATE broods. Although there is some slight overlap in the range of egg sizes produced by EARLY and LATE breeding groups (see Figs 40 & 41), the LATE breeding group would only account for 28% of the EARLY born progeny. Hence, because of the magnitude of the variation in EARLY egg size, for the reasons given in (a) & (b) above, it is unlikely that any LATE breeding female can have a LATE breeding female as its immediate ancestor.

In order to describe the growth of the two groups I have taken the largest 16% of the 0-1 year old animals taken in samples (shown as size-frequency histograms in Figs 7 & 8 and as a growth curve in Fig 28) and found the mean sizes of the largest 16% and the smallest 84%. All LATE breeding females carrying broods were included as the largest 16% until peak brood production had been reached (as determined from Fig 10). Brood production retards growth in woodlice (Hubbell, 1971; Lawlor, 1976b; Chapter 6, section 2.iii.a), and because of this some of the EARLY breeding group will have exceeded the sizes obtained by LATE group females with broods, but have presumably done so too late in the season to produce broods themselves (see Chapter 6). The growth curves of average EARLY and LATE breeding animals are shown in Fig 39, and these have been used in the energy budget model in place of that shown in Fig 28. It may be significant that the post-parturient weight of the average LATE breeding group female is very similar to that achieved by the average EARLY group female at this time. Not only does the LATE breeding group lose weight (relative to the non-reproducing EARLY group) due to the release of their offspring, but also due to the reduced growth while incubating the brood (Chapter 6, section 2.iii.a). From the moment that the LATE group have released their offspring, the growth by the EARLY group is taken to be the growth of all surviving females.

The model is essentially that described previously, with the modified growth for each breeding group described above and the removal of all mortality. Clearly any differences in reproductive allocations given by the model will reflect the different temperature regimes experienced by the two breeding groups throughout their lives, and the slower growth of the LATE breeding group, resulting in differing respiratory costs.

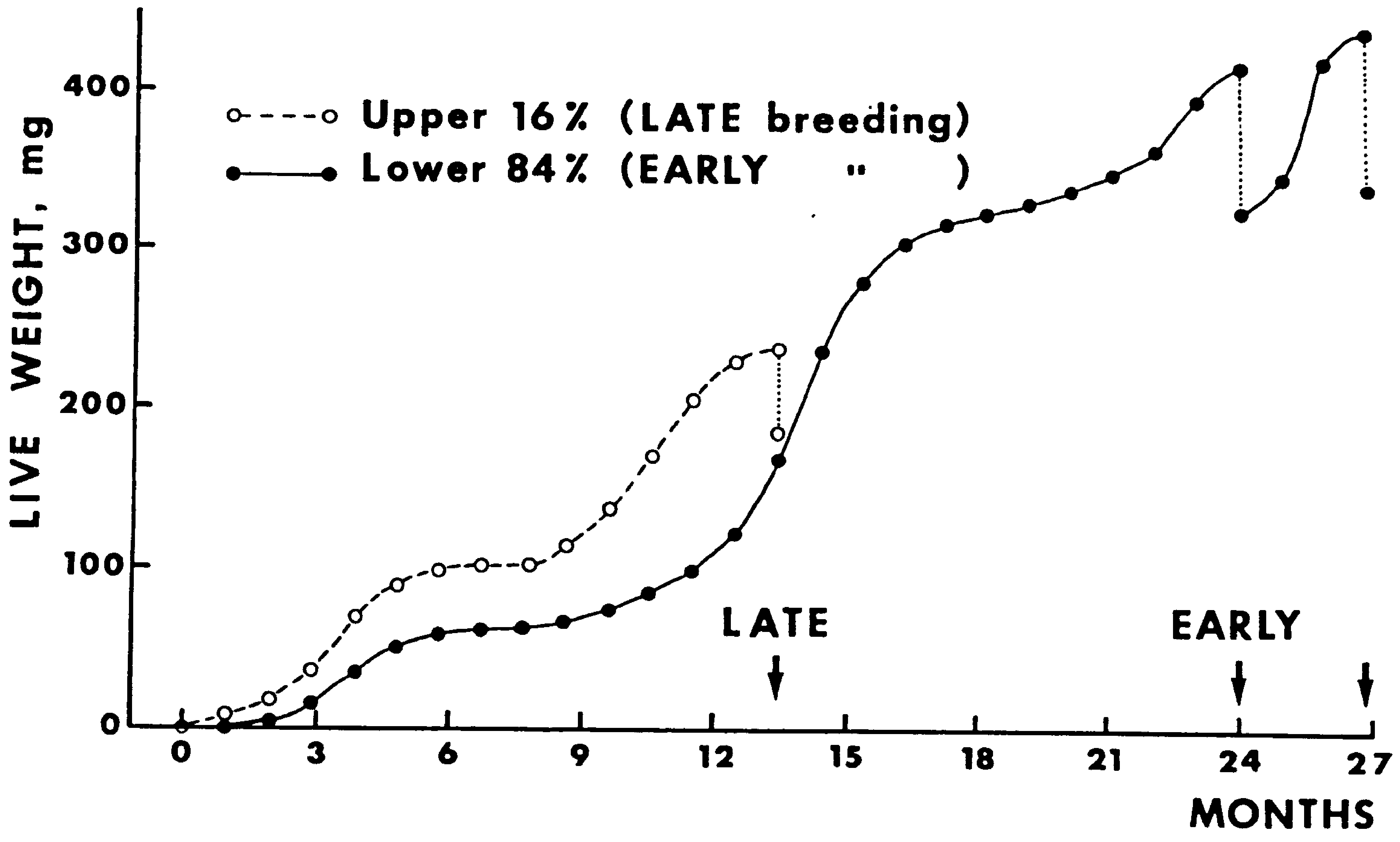
The results are shown in Table 37. Although reproduction is essentially semelparous, results are also shown for a female which survives to reproduce a second time, either EARLY (for a LATE breeder breeding again) or VERY

Table 37. Energy budget components for individual females in each breeding group. Values are also presented for possible, rare animals producing second broods.

	FAST GROWING LATE BREEDING				SLOW GROWING EARLY BREEDING			
	SEMELPAROUS		ITEROPAROUS		SEMELPAROUS		ITEROPAROUS	
	kJ.♀$^{-1}$	%	kJ.♀$^{-1}$	%	kJ.♀$^{-1}$	%	kJ.♀$^{-1}$	%
R	2.39	56.4	5.87	58.2	4.95	59.2	7.04	58.0
P_g	1.14	26.7	2.42	24.0	2.15	25.7	2.82	23.2
P_r	0.43	10.1	1.13	11.2	0.70	8.4	1.43	11.8
E_x	0.29	6.8	0.66	6.5	0.56	6.7	0.84	7.0
A	4.25	100.0	10.08	100.0	8.36	100.0	12.13	100.0

FIGURE 39

Growth curves for EARLY and LATE breeding females. The curves are derived from the upper 16% and lower 84% of females 0-1 years of age in size frequency samples from Robin Hood's Bay (see also Figs 7,8 and 28). The curves are fitted by eye.


Upper 16% (LATE breeding)
Lower 84% (EARLY ")
LIVE WEIGHT, mg
400
300
200
100
0
0
3
6
9
12
15
18
21
24
27
MONTHS
LATE
EARLY

LATE (for an EARLY breeder breeding again). The total energy budget increases with lifespan. As a fraction of the total energy budget, P_r remains remarkably constant at about 10% of the total budget, irrespective of the timing of breeding or whether individuals have one or two broods. I take these results, together with the direct relationship between female size and brood weight, to indicate that there are no differences in energy allocated to reproduction between individuals in the two breeding groups.

b. Differences between populations

The differences between the two sites have been tested by ANOVA of the brood dry weight : body dry weight ratios (Table 38). This showed significant differences between the reproductive allocations ($F = 3.59$; d.f. = 2,201; $P < 0.05$). An a posteriori S.N.K. test indicated that a significant difference existed between Whitby 1981 and R.H.B. 1982, while there was no significant difference between the two Whitby samples, the reproductive allocations being very similar for both years.

The data are not entirely adequate for such analysis. Ideally replicate data for each site over a number of years would be needed to reveal whether the differences in reproductive allocation between the sites are real and consistent, but the small size of the R.H.B. population precluded this. However the results do indicate a slightly greater weight specific fecundity at the more exposed site.

iii. Egg weight

a. Differences between breeding groups

Because females belonging to the two breeding groups differ in weight specific fecundity, but not in weight specific reproductive allocation, the difference in fecundity must be brought about by the production of eggs of different sizes. This is shown in Figs 40 & 41. Perhaps surprisingly, within both breeding groups at both sites, egg size depended not only on breeding group but also on female

Table 38. Analysis of variance of *Ligia* reproductive allocation (brood dry weight / body dry weight).

SOURCE OF VARIATION	d.f.	S.S.	M.S.	F	P
Between sites and years	2	0.00786	0.00393	3.59	*
Within sites and years	201	0.21987	0.00109		
TOTAL	203	0.22774			

S.N.K. Test. Those values asterisked differ at $P < 0.05$

SAMPLE	WHITBY 1981	WHITBY 1980	R.H.B. 1982
WHITBY 1980	0.0019		
R.H.B. 1982	0.0130 *	0.0111	

SAMPLE	REPRODUCTIVE ALLOCATION (± 95% C.I.)
WHITBY 1980	28.93 ± 1.14%
WHITBY 1981	28.74 ± 0.83%
R.H.B. 1982	30.04 ± 0.64%

FIGURE 40

Relationship between female size (dry weight of body after removal of the brood, x in mgs) and individual egg dry weight (y in mgs) for EARLY (○) and LATE (●) breeding females from Whitby in 1981. The regression equations are :

EARLY : $y = 0.00067x + 0.2457$
LATE : $y = 0.00180x + 0.0233$

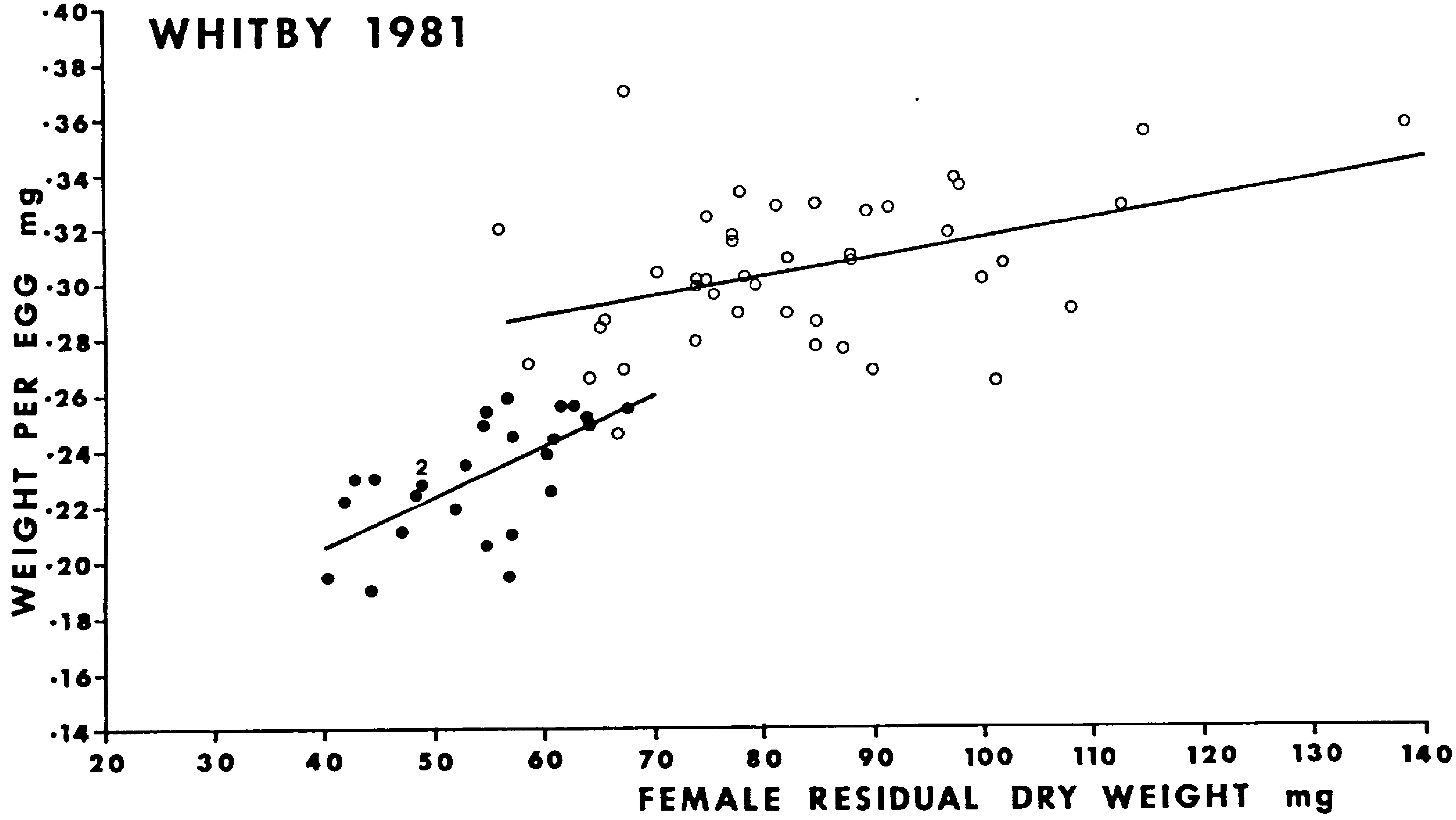
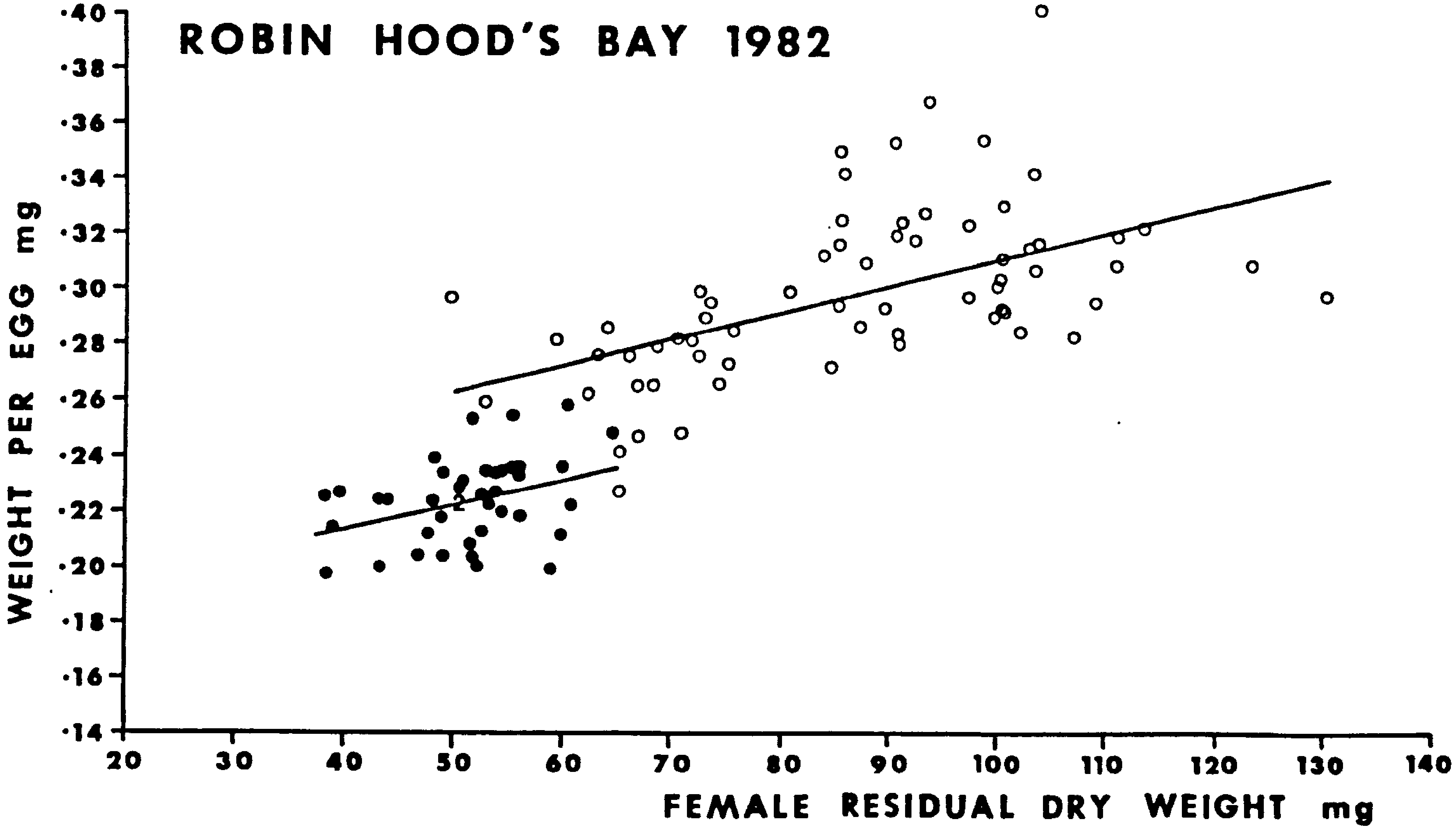

WHITBY 1981
·40
·38
·36
·34
·32
·30
·28
·26
·24
·22
·20
·18
·16
·14
WEIGHT PER EGG mg
2
20
30
40
50
60
70
80
90
100
110
120
130
140
FEMALE RESIDUAL DRY WEIGHT mg

FIGURE 41

Relationship between female size (dry weight of body after removal of the brood, x in mgs) and individual egg dry weight (y in mgs) for EARLY (○) and LATE (●) breeding females from Robin Hood's Bay in 1982. The regression equations are :

EARLY : $y = 0.00097x + 0.2146$
LATE : $y = 0.00090x + 0.1340$


ROBIN HOOD'S BAY 1982
WEIGHT PER EGG mg
·40
·38
·36
·34
·32
·30
·28
·26
·24
·22
·20
·18
·16
·14
20
30
40
50
60
70
80
90
100
110
120
130
140
FEMALE RESIDUAL DRY WEIGHT mg
2

size. Females produced significantly smaller eggs if they reproduced LATE in comparison to those produced by EARLY breeders :

R.H.B. : $F = 206.49$; d.f. = 1,103; $P \ll 0.001$
Whitby : $F = 142.06$; d.f. = 1, 67; $P \ll 0.001$

but in addition small females, within any breeding group, produced smaller eggs than larger females (ie egg weight is related to female size within a breeding group) :

R.H.B. EARLY : $F = 27.40$; d.f. = 1, 63; $P \ll 0.001$
LATE : $F = 6.01$; d.f. = 1, 40; $P < 0.025$
Whitby EARLY : $F = 8.11$; d.f. = 1, 41; $P < 0.01$
LATE : $F = 19.20$; d.f. = 1, 24; $P \ll 0.001$

When corrected for differences in female size between the two breeding groups, EARLY breeding females still produce larger eggs than do LATE breeding females :

R.H.B. : $F = 32.37$; d.f. = 1,102; $P \ll 0.001$
Whitby : $F = 37.94$; d.f. = 1, 66; $P \ll 0.001$

The full details of the analyses are given in Tables 46 & 47

b. Differences between populations

I have already shown that females at R.H.B. have higher weight specific fecundities than their counterparts at Whitby (Chapter 3, section 3.iv.b; this chapter, section 3.i.b.), and also tend to have higher reproductive allocations (section 3.ii.b.). The possibility also exists that egg size might vary between the two sites. The analyses are shown in Tables 48 & 49. In neither case was there a significant difference in weight specific egg weight when the two breeding groups were compared between sites, though the data for the EARLY group tended towards significance :

EARLY : $F = 2.89$; d.f. = 1,105; $0.1 > P > 0.05$
LATE : $F = 0.78$; d.f. = 1, 63; n.s.

TABLE 39. Analysis of covariance (ANCOVA) of the regressions of fecundity on female dry weight for EARLY and LATE group females from Whitby in 1981.

SOURCE OF VARIATION	D.F.	S.S.	M.S.	F
Due to EARLY regression	1	4411.3	4411.25	34.95 ***
Error (deviations from slope)	41	5175.2	126.22	
EARLY TOTAL	42	9586.5		
Due to LATE regression	1	1025.9	1025.88	13.77 **
Error (deviations from slope)	24	1787.7	74.49	
LATE TOTAL	25	2813.5		
Between groups	1	1233.8	1233.82	6.67 *
Within groups	67	12400.0	185.07	
Common slope within groups	1	5380.9	5380.92	50.60 ***
Error (deviations from common slope)	66	7019.1	106.35	
Difference between slopes	1	56.2	56.21	0.52 n.s.
Error (deviations from slope within each group)	65	6962.9	107.12	
TOTAL (between + within groups)	68	13633.8		
Common slope within study	1	5769.6	5769.58	
Error (deviations from common slope)	67	7864.3	117.38	
Among intercepts	1	845.2	845.16	7.95 **
Error (deviations from common slope)	66	7019.1	106.35	

TABLE 40. Analysis of covariance (ANCOVA) of the regressions of fecundity on female dry weight for EARLY and LATE group females from R.H.B. in 1982.

SOURCE OF VARIATION	D.F.	S.S.	M.S.	F
Due to EARLY regression	1	6805.5	6805.54	46.92 ***
Error (deviations from slope)	63	9138.7	145.06	
EARLY TOTAL	64	15944.2		
Due to LATE regression	1	1890.8	1890.78	32.49 ***
Error (deviations from slope)	38	2211.1	58.19	
LATE TOTAL	39	4101.9		
Between groups	1	8407.9	8407.94	43.20 ***
Within groups	103	20046.1	194.62	
Common slope within groups	1	8324.3	8324.31	72.44 ***
Error (deviations from common slope)	102	11721.8	114.92	
Difference between slopes	1	372.0	372.02	3.31 n.s.
Error (deviations from slope within each group)	101	11349.8	112.37	
TOTAL (between + within groups)	104	28454.1		
Common slope within study	1	16554.4	16554.43	
Error (deviations from common slope)	103	11899.6	115.53	
Among intercepts	1	177.8	177.83	1.55 n.s.
Error (deviations from common slope)	102	11721.8	114.92	

TABLE 41. Analysis of covariance (ANCOVA) of the regressions of fecundity on female dry weight for EARLY group females from Whitby in 1981 and R.H.B. in 1982.

SOURCE OF VARIATION		D.F.	S.S.	M.S.	F
Due to R.H.B. 1982 EARLY regression	:	1	6805.5	6805.54	46.92 ***
Error (deviations from slope)	:	63	9138.7	145.06	
R.H.B. 1982 EARLY TOTAL	:	64	15944.2		
Due to WHITBY 1981 EARLY regression	:	1	4411.3	4411.25	34.95 ***
Error (deviations from slope)	:	41	5175.2	126.22	
WHITBY 1981 EARLY TOTAL	:	42	9586.5		
Between sites	:	1	2618.2	2618.24	10.87 **
Within sites	:	106	25530.7	240.86	
Common slope within sites	:	1	11209.0	11208.99	82.18 ***
Error (deviations from common slope)	:	105	14321.7	136.40	
Difference between slopes	:	1	7.8	7.80	0.06 n.s.
Error (deviations from slope within each site)	:	104	14313.9	137.63	
TOTAL (groups + within)	:	107	28148.9		
Common slope within study	:	1	12387.2	12387.15	
Error (deviations from common slope)	:	106	15761.8	148.70	
Among intercepts	:	1	1440.1	1440.07	10.56 **
Error (deviations from common slope)	:	105	14321.7	136.40	

TABLE 42. Analysis of covariance (ANCOVA) of the regressions of fecundity on female dry weight for LATE group females from Whitby in 1981 and R.H.B. in 1982.

SOURCE OF VARIATION		D.F.	S.S.	M.S.	F
Due to R.H.B. 1982 LATE regression	:	1	1890.8	1890.78	32.49 ***
Error (deviations from slope)	:	38	2211.1	58.19	
R.H.B. 1982 LATE TOTAL	:	39	4101.9		
Due to WHITBY 1981 LATE regression	:	1	1025.9	1025.88	13.77 **
Error (deviations from slope)	:	24	1787.7	74.49	
WHITBY 1981 LATE TOTAL	:	25	2813.5		
Between sites	:	1	2.0	2.02	0.02 n.s.
Within sites	:	64	6915.4	108.05	
Common slope within sites	:	1	2862.7	2862.67	44.50 ***
Error (deviations from common slope)	:	63	4052.8	64.33	
Difference between slopes	:	1	54.0	54.00	0.84 n.s.
Error (deviations from slope within each site)	:	62	3998.8	64.50	
TOTAL (groups + within)	:	65	6917.5		
Common slope within study	:	1	2769.4	2769.38	
Error (deviations from common slope)	:	64	4148.1	64.81	
Among intercepts	:	1	95.3	95.30	1.48 n.s.
Error (deviations from common slope)	:	63	4052.8	64.33	

TABLE 43. Analysis of covariance (ANCOVA) of the regressions of reproductive allocation on female dry weight for EARLY and LATE group females from Whitby in 1980.

SOURCE OF VARIATION	D.F.	S.S.	M.S.	F
Due to EARLY regression	1	374.85	374.85	48.02 ***
Error (deviations from slope)	17	132.70	7.81	
EARLY TOTAL	18	507.55		
Due to LATE regression	1	91.35	91.35	47.31 ***
Error (deviations from slope)	9	17.38	1.93	
LATE TOTAL	10	108.73		
Between groups	1	409.73	409.73	18.62 ***
Within groups	28	616.28	22.01	
Common slope within groups	1	461.06	461.06	80.20 ***
Error (deviations from common slope)	27	155.22	5.75	
Difference between slopes	1	5.14	5.14	0.89 n.s.
Error (deviations from slope within each group)	26	150.08	5.77	
TOTAL (between + within groups)	29	1026.01		
Common slope within study	1	856.71	856.71	141.60 ***
Error (deviations from common slope)	28	169.31	6.05	
Among intercepts	1	14.08	14.08	2.45 n.s.
Error (deviations from common slope)	27	155.22	5.75	

TABLE 44. Analysis of covariance (ANCOVA) of the regressions of reproductive allocation on female dry weight for EARLY and LATE group females from Whitby in 1981.

SOURCE OF VARIATION	D.F.	S.S.	M.S.	F
Due to EARLY regression	1	690.30	690.30	84.51 ***
Error (deviations from slope)	41	334.90	8.17	
EARLY TOTAL	42	1025.20		
Due to LATE regression	1	145.83	145.83	43.34 ***
Error (deviations from slope)	24	80.75	3.36	
LATE TOTAL	25	226.58		
Between groups	1	948.66	948.66	50.78 ***
Within groups	67	1251.78	18.68	
Common slope within groups	1	830.34	830.34	130.04 ***
Error (deviations from common slope)	66	421.45	6.39	
Difference between slopes	1	5.79	5.79	0.91 n.s.
Error (deviations from slope within each group)	65	415.65	6.39	
TOTAL (between + within groups)	68	2200.44		
Common slope within study	1	1778.91	1778.91	282.75 ***
Error (deviations from common slope)	67	421.52	6.29	
Among intercepts	1	0.08	0.08	0.01 n.s.
Error (deviations from common slope)	66	421.45	6.39	

TABLE 45. Analysis of covariance (ANCOVA) of the regressions of reproductive allocation on female dry weight for EARLY and LATE group females from Robin Hood's Bay in 1982.

SOURCE OF VARIATION	D.F.	S.S.	M.S.	F
Due to EARLY regression	1	1264.76	1264.76	200.54 ***
Error (deviations from slope)	63	397.33	6.31	
EARLY TOTAL	64	1662.08		
Due to LATE regression	1	149.54	149.54	36.94 ***
Error (deviations from slope)	38	153.85	4.05	
LATE TOTAL	39	303.39		
Between groups	1	2797.50	2797.50	146.60 ***
Within groups	103	1965.47	19.08	
Common slope within groups	1	1410.11	1410.11	258.99 ***
Error (deviations from common slope)	102	555.36	5.44	
Difference between slopes	1	4.19	4.19	0.77 n.s.
Error (deviations from slope within each group)	101	551.17	5.46	
TOTAL (between + within groups)	104	4762.97		
Common slope within study	1	4191.34	4191.34	755.20 ***
Error (deviations from common slope)	103	571.64	5.55	
Among intercepts	1	16.28	16.28	2.99 n.s.
Error (deviations from common slope)	102	555.36	5.44	

TABLE 46. Analysis of covariance (ANCOVA) of the regressions of brood average egg weight on female dry weight for EARLY and LATE group females from Whitby in 1981.

SOURCE OF VARIATION	D.F.	S.S.	M.S.	F
Due to EARLY regression	1	0.0051	0.00507	8.11 **
Error (deviations from slope)	41	0.0256	0.00062	
EARLY TOTAL	42	0.0307		
Due to LATE regression	1	0.0048	0.00482	19.20 ***
Error (deviations from slope)	24	0.0060	0.00025	
LATE TOTAL	25	0.0109		
Between groups	1	0.0881	0.08805	142.06 ***
Within groups	67	0.0415	0.00062	
Common slope within groups	1	0.0082	0.00821	16.25 ***
Error (deviations from common slope)	66	0.0333	0.00050	
Difference between slopes	1	0.0017	0.00169	3.46 (<0.1)
Error (deviations from slope within each group)	65	0.0316	0.00049	
TOTAL (between + within groups)	68	0.1296		
Common slope within study	1	0.0771	0.07710	
Error (deviations from common slope)	67	0.0525	0.00078	
Among intercepts	1	0.0192	0.01915	37.94 ***
Error (deviations from common slope)	66	0.0333	0.00050	

TABLE 47. Analysis of covariance (ANCOVA) of the regressions of brood average egg weight on female dry weight for EARLY and LATE group females from Robin Hood's Bay in 1982.

SOURCE OF VARIATION	D.F.	S.S.	M.S.	F
Due to EARLY regression	1	0.0183	0.01832	27.40 ***
Error (deviations from slope)	63	0.0421	0.00067	
EARLY TOTAL	64	0.0604		
Due to LATE regression	1	0.0013	0.00127	6.01 **
Error (deviations from slope)	38	0.0080	0.00021	
LATE TOTAL	39	0.0093		
Between groups	1	0.1398	0.13981	206.49 ***
Within groups	103	0.0697	0.00068	
Common slope within groups	1	0.0196	0.01958	39.82 ***
Error (deviations from common slope)	102	0.0502	0.00049	
Difference between slopes	1	0.0000	0.00001	0.01 n.s.
Error (deviations from slope within each group)	101	0.0501	0.05015	
TOTAL (between + within groups)	104	0.2095		
Common slope within study	1	0.1435	0.14348	
Error (deviations from common slope)	103	0.0661	0.00064	
Among intercepts	1	0.0159	0.01592	32.37 ***
Error (deviations from common slope)	102	0.0502	0.00049	

TABLE 48. Analysis of covariance (ANCOVA) of the regressions of brood average egg weight on female dry weight for EARLY group females from R.H.B. in 1982 and Whitby in 1981.

SOURCE OF VARIATION	D.F.	S.S.	M.S.	F
Due to R.H.B. 1982 EARLY regression	1	0.0183	0.01832	27.40 ***
Error (deviations from slope)	63	0.0421	0.00067	
R.H.B. 1982 EARLY TOTAL	64	0.0604		
Due to WHITBY 1981 EARLY regression	1	0.0051	0.00507	8.11 **
Error (deviations from slope)	41	0.0256	0.00062	
WHITBY 1981 EARLY TOTAL	42	0.0307		
Between sites	1	0.0006	0.00064	0.74 n.s.
Within sites	106	0.0911	0.00086	
Common slope within sites	1	0.0227	0.02274	34.92 ***
Error (deviations from common slope)	105	0.0684	0.00065	
Difference between slopes	1	0.0006	0.00064	1.00 n.s.
Error (deviations from slope within each site)	104	0.0677	0.00065	
TOTAL (between + within sites)	107	0.0917		
Common slope within study	1	0.0215	0.02150	
Error (deviations from common slope)	106	0.0703	0.00066	
Among intercepts	1	0.0019	0.00188	2.89 (<0.1)
Error (deviations from common slope)	105	0.0684	0.00065	

TABLE 49. Analysis of covariance (ANCOVA) of the regressions of brood average egg weight on female dry weight for LATE group females from R.H.B. in 1982 and Whitby in 1981.

SOURCE OF VARIATION		D.F.	S.S.	M.S.	F
Due to R.H.B. 1982 LATE regression	:	1	0.0013	0.00127	6.01 *
Error (deviations from slope)	:	38	0.0080	0.00021	
R.H.B. 1982 LATE TOTAL	:	39	0.0093		
Due to WHITBY 1981 LATE regression	:	1	0.0048	0.00482	19.20 ***
Error (deviations from slope)	:	24	0.0060	0.00025	
WHITBY 1981 LATE TOTAL	:	25	0.0109		
Between sites	:	1	0.0006	0.00064	2.04 n.s.
Within sites	:	64	0.0202	0.00315	
Common slope within sites	:	1	0.0055	0.00547	23.48 ***
Error (deviations from common slope)	:	63	0.0147	0.00023	
Difference between slopes	:	1	0.0006	0.00062	2.74 n.s.
Error (deviations from slope within each site)	:	62	0.0141	0.00023	
TOTAL (between + within sites)	:	65	0.0208		
Common slope within study	:	1	0.0059	0.00593	
Error (deviations from common slope)	:	64	0.0149	0.00023	
Among intercepts	:	1	0.0002	0.00018	0.78 n.s.
Error (deviations from common slope)	:	63	0.0147	0.00023	

iv. Variation in reproductive allocation, fecundity and egg size

It is apparent from the relationships shown in Figs 12,20,21,36,37,38,40 & 41 that while a large amount of the variation in fecundity, reproductive allocation and egg size can be explained by the size of the female parent and the breeding group or season in which it breeds, a substantial amount of the variation remains unexplained (about 45% of the variation in fecundity, and 25% of that in egg size). This is important because an individual with high reproductive success, equated here with numbers of offspring, will, all other things being equal, leave more breeding progeny and thus will have greater fitness. However all other things are clearly not equal, for example female size affects both fecundity and egg size. It is clear that larger woodlice will be more successful than smaller individuals, at least within a breeding group. However the substantial remaining variation in individual weight specific fecundity and egg size, with important implications in terms of individual fitness, requires explanation.

One approach to the examination of the residual variation about regression lines is by means of partial correlation. This allows us to examine the covariation between two variables when the affect of a third is removed statistically. Body size is frequently used as the independent variable in species' fecundity regressions, implying causality of the observed fecundities. The question of causality will be taken up later. Using partial correlation the effect of body size on the relationships between fecundity, egg weight and reproductive allocation for each breeding group has been removed, and the results for the two populations detailed in Table 50. In all four groups of data there are highly significant ($P \ll 0.001$) positive correlations between fecundity and reproductive allocation. This implies that individuals with greater reproductive allocations <u>for their size</u> produced significantly more eggs, while those with smaller reproductive allocations for their size produced fewer eggs. In three of the four cases

Table 50. First order partial correlations between fecundity, egg size and reproductive allocation (R.A.) when the effect of female dry body weight is removed. Data for EARLY and LATE breeding group females from R.H.B. in 1982 and Whitby in 1981.

SITE	GROUP	VARIABLES	r	t	P
R.H.B	EARLY	Fecundity & R.A.	+0.812	10.95	<<0.001
		Fecundity & Egg size	-0.704	7.80	<<0.001
		Egg size & R.A.	-0.165	1.31	n.s.
	LATE	Fecundity & R.A.	+0.858	10.17	<<0.001
		Fecundity & Egg size	0.000	0.00	n.s.
		Egg size & R.A.	+0.510	3.61	<0.001
WHITBY	EARLY	Fecundity & R.A.	+0.834	9.58	<<0.001
		Fecundity & Egg size	-0.545	4.11	<0.001
		Egg size & R.A.	-0.009	0.06	n.s.
	LATE	Fecundity & R.A.	+0.834	7.24	<<0.001
		Fecundity & Egg size	-0.407	2.14	<0.05
		Egg size & R.A.	+0.152	0.74	n.s.

increased fecundity was also associated with smaller egg sizes, ie. a trade-off exists between fecundity and egg size. Lawlor (1976a) found a similar result in Armadillidium vulgare. For one group (R.H.B. 1982 LATE) no trade-off between fecundity and egg size was found. Instead there is a positive correlation between greater reproductive allocation and greater egg size. This anomalous result is unexplained, but may be the result of the more complex interrelationship between the variables detailed below.

Although brood average egg weight has been derived from the measures of reproductive allocation and fecundity by division, rather than by direct measurement, and is therefore not independent of them, I do not believe that this matters for the analysis. Animals themselves are constrained by the fact that the product of egg size and fecundity equals the reproductive allocation, yet there is no reason why they should not vary egg numbers from the extremely numerous and small to a single, large egg equal to the total reproductive allocation. Likewise the total allocation is under the individuals control (in an evolutionary sense). More importantly, there is no reason why these variables should covary between individuals in a consistent way. Fecundity is likely to have been measured without error, while the residual variation in weight specific reproductive allocation is large relative to the accuracy to which it was measured. What I have shown is that, although there is large variability in absolute egg numbers and egg weights, this variation can be related in a systematic way to the other features of the reproductive biology.

Clearly many of the variables I have been considering (season, dry weight, reproductive allocation, etc.) are all interrelated and not independent. An appropriate method of analysis of such data is by means of path diagrams (Nie et al. 1975; Sokal & Rohlf, 1981). This technique utilizes multiple regression to examine the amount of variation in variables explained by other variables in a causal hierarchy, and allows the effect of any causal variable on criterion variables to be evaluated. In this case fecundity and egg size are the criteria variables, determined by season, female dry weight and reproductive allocation, the causal or predictor variables. These variables can be placed in a causal hierarchy based on time precedence: season affects dry weight (through growth), and reproductive allocation must depend on how much growth has taken place. Any variable can affect other variables further down the causal hierarchy.

The multiple regressions were carried out in a stepwise manner, and where a variable explained a non-significant part of the residual variation it was excluded from the path diagram (ie there is no effect of season on reproductive allocation, nor reproductive allocation on egg size). The trade-off between egg size and fecundity was included as the last step in the multiple regression. The residual variation in fecundity being regressed against the residual egg weights after the significant affects of other variables (season and dry weight) had been removed. The degrees of freedom were corrected for the additional parameters estimated from the data.

The results are shown in Fig 42 & 43. The arrows indicate the direction of the causality, and the path coefficients (the standardised partial regression coefficients) the magnitude of the affects. The path diagrams for the two sites are found to have the same structure, with the magnitude and direction of the effects being closely similar.

Path diagrams of this sort are useful and worthwhile for a number of reasons :

a) they present explicitly an hypothesis of the causality between variables;
b) the magnitude of the effect of any variable on another can be determined statistically when experimentally this might not be possible;
c) the effect of a variable on another can be separated into several component parts;

Fig 42. Path analysis of the variation in individual fecundity and egg size at Whitby in 1981. $U_{1,2,3}$ & 4 represent unknown sources of variability in variables incorporated in the model.

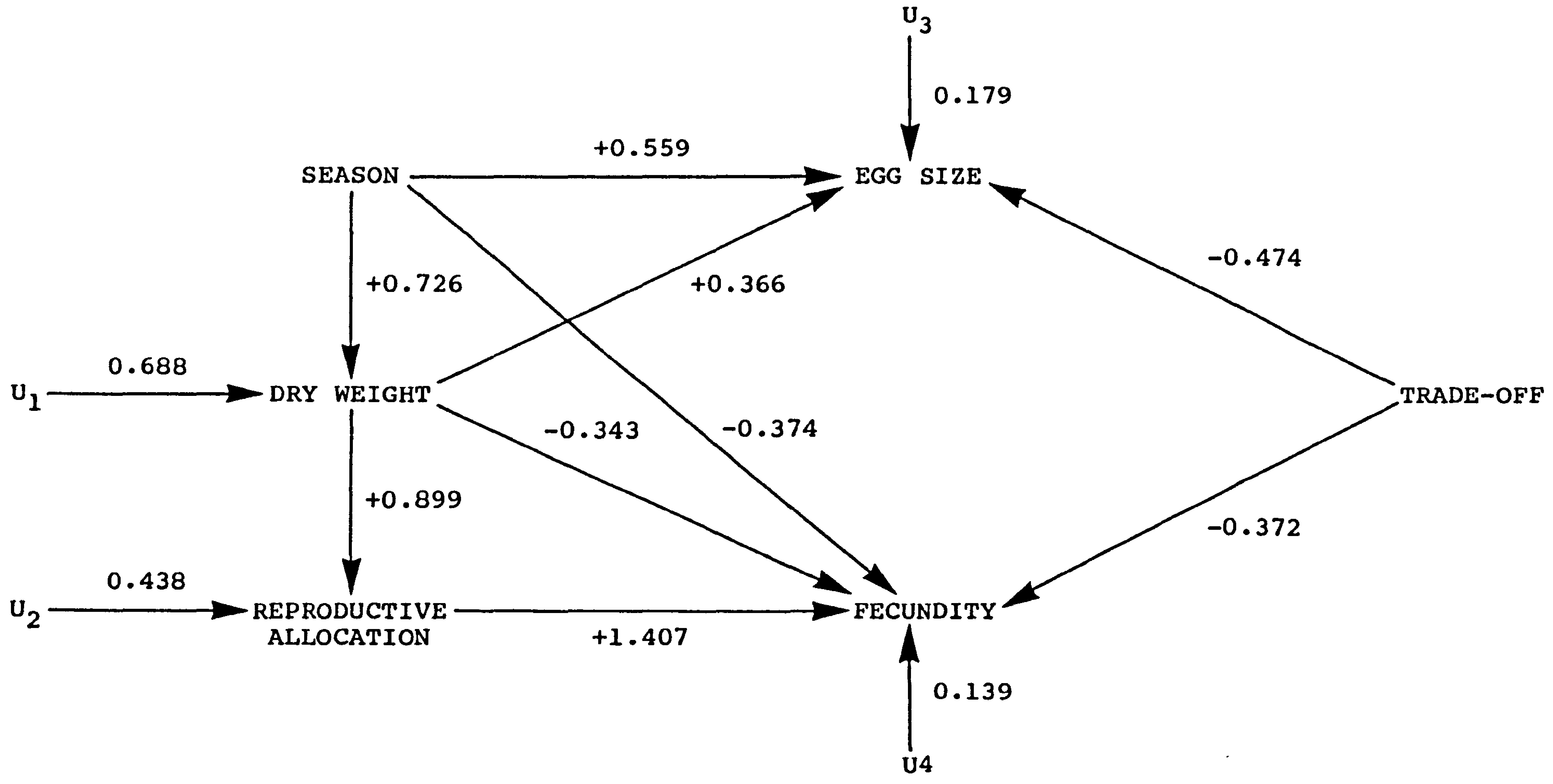
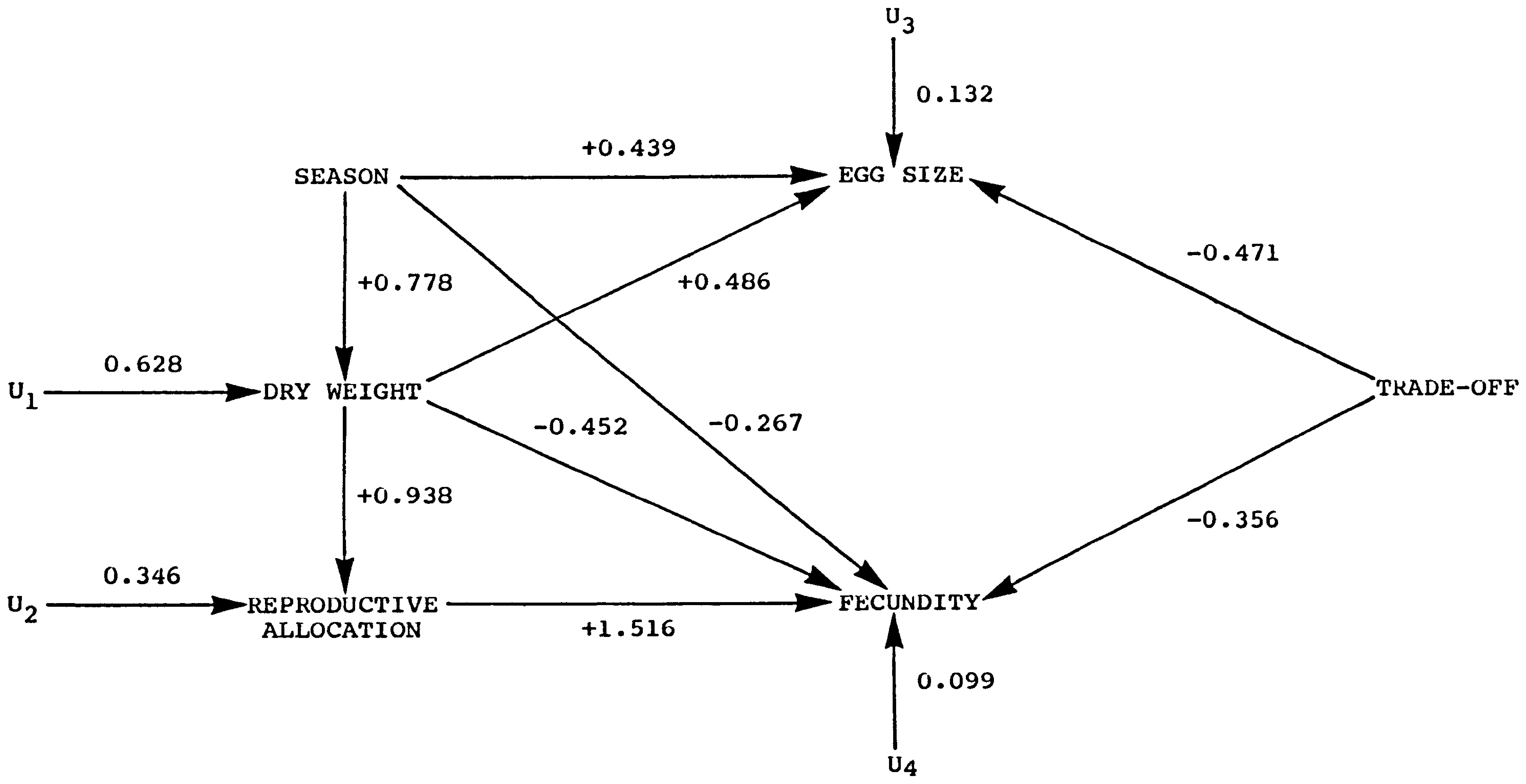


Fig 43. Path analysis of the variation in individual fecundity and egg size at R.H.B. in 1982. $U_{1,2,3}$ & 4 represent unknown sources of variability in variables incorporated in the model.



d) it allows an explicit evaluation of unknown sources of variation.

This analysis illustrates some of these advantages. For example body size is frequently, through the use of fecundity regressions, shown as being causal with respect to fecundity. If egg size were constant with respect to individual body size then fecundity would be determined by the amount of resources, the reproductive allocation, devoted to reproduction, and body size would affect fecundity only indirectly. However egg size in this species is not constant, varying both with body size and breeding season, implying an effect of body size also on fecundity. This is revealed in Fig 42. Taking the data for R.H.B., body dry weight (size) has a direct negative effect on fecundity, as indicated by the standardised partial regression coefficient (-0.452), and an indiect one via reproductive allocation (+1.422). The affect of reproductive allocation on fecundity, not caused by dry weight, is thus seen to be a small one (+0.094). This is the same factor as the partial correlation between fecundity and reproductive allocation shown earlier, but its affect on fecundity is small, explaining only 0.9% of the total variation in fecundity. The overall affect of body size on fecundity through both these routes is thus found to be +0.970.

The fourth point is illustrated here. The total amount of variation in fecundity explained by the variables in the path diagram is shown in Tables 51 & 52. Clearly this simple, linear additive model has explained the majority of the variation in these two life history variables (~98% of the variation in fecundity, and ~96% of that in egg weight). Although 12.0% of the variation in reproductive allocation is unexplained, this accounts for only 0.1% of the total variation in fecundity. Similarly a substantial part (39.4%) of the variation in female dry weight is explained by growth between breeding seasons. Similarly, the trade-off between egg weight and fecundity, which explains 22.2% of the variation in egg weight and 12.7% of the variation in fecundity, is itself totally unexplained. Hence we have only explained, albeit very successfully, in a very proximate way the variation in egg size and fecundity. However the analysis has been useful in concentrating attention on those variables whose variation we have to explain to account for the intrapopulation differences in the life history characteristics of Ligia oceanica. Of those examined it is clear that the reasons behind the trade-off between fecundity and egg size, and the variability in female size, are the most in need of further investigation.

Table 51. Analysis of the components of variation in individual fecundity at Robin Hood's Bay and Whitby.

SOURCE OF VARIATION	ROBIN HOOD'S BAY 1982					WHITBY 1981				
	d.f.	S.S.	C.D.	F	P	d.f.	S.S.	C.D.	F	P
SEASON	1	8407.94	0.295	43.20	$\ll 0.001$	1	1233.82	0.090	6.67	< 0.05
RESIDUAL	103	20046.12				67	12400.00			
REPROD. ALLOCATION	1	15463.22	0.543	344.16	$\ll 0.001$	1	10051.65	0.737	282.50	$\ll 0.001$
RESIDUAL	102	4582.90				66	2348.35			
BODY DRY WEIGHT	1	702.63	0.025	18.29	$\ll 0.001$	1	204.62	0.015	6.20	< 0.05
RESIDUAL	101	3880.27				65	2143.74			
TRADE-OFF	1	3601.31	0.127	1252.25	$\ll 0.001$	1	1880.87	0.138	436.46	$\ll 0.001$
UNEXPLAINED	97	278.96				61	262.87			
TOTAL EXPLAINED	4	28175.09	0.990	2449.26	$\ll 0.001$	4	13370.96	0.981	775.70	$\ll 0.001$
TOTAL	104	28454.06				68	13633.83			

Table 52. Analysis of the components of variation in individual egg size at Robin Hood's Bay and Whitby.

SOURCE OF VARIATION	ROBIN HOOD'S BAY 1982					WHITBY 1981				
	d.f.	S.S.	C.D.	F	P	d.f.	S.S.	C.D.	F	P
SEASON	1	0.13961	0.667	206.42	≪0.001	1	0.08823	0.680	142.40	≪0.001
RESIDUAL	103	0.06966				67	0.04151			
BODY DRY WEIGHT	1	0.01953	0.093	39.73	≪0.001	1	0.00823	0.063	16.34	≪0.001
RESIDUAL	102	0.05013				66	0.03328			
TRADE-OFF	1	0.04649	0.222	1245.73	≪0.001	1	0.02913	0.225	428.18	≪0.001
UNEXPLAINED	97	0.00362				61	0.00415			
TOTAL EXPLAINED	3	0.20565	0.983	1836.84	≪0.001	3	0.12559	0.968	615.34	≪0.001
TOTAL	104	0.20927				68	0.12974			

4. DISCUSSION : DIFFERENCES BETWEEN POPULATIONS

In choosing to compare sites varying in only a single climatic variable the intention was to study the effects of this factor on the dynamics of the populations and investigate any evolutionary response to the different environmental conditions. The philosophy behind this approach is important, for any differences found between the populations have to be interpreted with respect to this precept. Greater exposure to wave action was believed to result in different levels of density-independent mortality, a mortality factor extrinsic to the biology of the animal. Under r- and K-selection theory increased density-independent mortality, presupposed at the exposed site, should result in variations in population size and resource availability through which selection on the life history acts (MacArthur & Wilson, 1967). However there were no detectable differences between the two populations in their dynamics. As far as could be ascertained these were indistinguishable (see Chapter 3, section 4), and characteristic of equilibrium populations. Although adult mortality and longevity were less at R.H.B. than at Whitby (Chapter 3, section vi), as expected from the exposure of the sites to wave action, there is good reason to believe that exposure was not the direct cause of this difference. Winter survival at R.H.B., when death due to wave action might be expected to be greatest, was generally very good (about 80% for animals $<$ one year old), and considerably better than survival during the summer period, suggesting that exposure was not a direct cause of significant mortality. Indeed, much female adult mortality preceded the autumnal storms.

The similarities and differences between the sites and life history characteristics of their populations are summarised in Table 53 (see also Table 27). The decreased survival, increased weight specific fecundity and increased weight specific reproductive allocation manifest at the exposed site appear to agree with the predictions of r- and K-selection theory (Pianka, 1970, 1972; Menge, 1974; Stearns, 1976; Begon & Mortimer, 1981). Under this view the increased density-independent mortality, and therefore reduced adult

Table 53. Summary of the population and life history characterisics of the R.H.B. and Whitby populations.

FACTOR	R.H.B.	WHITBY	Chapter, section
Wave action	Exposed	Sheltered	2.2 & 3.2
Expected levels of density independent mortality	Higher & variable	Lower & constant	3.1
Population dynamics	Equilibrium	Equilibrium	2.3.ii.d, 2.9 & 3.4
Growth rate	Equal	Equal	3.3.v & 4.2.ii
Breeding waves	2	2	3.3.iii
Breeding proportions, sizes and ages	Equal	Equal	3.3.iii
Survivorship	Lower	Higher	3.3.vi
Weight specific fecundity	Higher	Lower	5.3.i.b & 3.3.iv.b
Reproductive allocation	Higher	Lower	5.3.ii.b
Egg weight	Equal	Equal	5.3.iii.b

survival, at the exposed site would be seen as causal in determining the observed increased fecundity and reproductive allocation. Calow (1979) has pointed out that in the reverse situation (ie Whitby) selection cannot favour a decrease in fecundity alone. There has to be an increase in fitness associated with a character linked to fecundity (Charlesworth, 1984). There was no increase in egg weight (= investment per offspring) at the sheltered site as predicted by r- and K-selection for more competitive situations. Egg weight at both sites varied with breeding group and female weight, but did not differ between sites. The increased reproductive allocation at R.H.B. goes into more eggs only, and these eggs are neither smaller nor larger than those at the sheltered site. Although there is no evidence of decreased female breeding size brought about by intraspecific competition at the sheltered site, it is conceivable that this increased competition is manifest in the smaller reproductive allocation of females at Whitby. However in my view an effect of competition is more likely to be expressed through growth, in breeding body size, than through weight specific reproductive allocation. The mechanism of selection is not supported by the influence of exposure on the dynamics of the populations. If these findings are to be accepted as support for the theory of r- and K-selection then the lack of any discernable influence of exposure on the population dynamics must be excused as due to either poor resolution of the dynamics, which seems unlikely, or due to the short timescale over which the study took place.

Other models of life history evolution say little about the adaptations of semelparous species to different mortality schedules, being more concerned with the evolution of iteroparity and semelparity to different schedules of age-specific mortality. This is perhaps one of their weaknesses. However Schaffer's (1974a) bet-hedging model suggests that, for a semelparous species variation in individual reproductive success should favour populations which exhibit polymorphic breedings pattern in which only a fraction of the individuals in the population breed in any one breeding season. While this might be the explanation for the peculiar EARLY/LATE breeding phenology (see Chapter 6) there was no evidence that this phenomenon was any more pronounced at R.H.B. than at Whitby. Under these models of life history evolution the decreased survival at R.H.B. can be interpreted as a consequence of the greater reproductive allocation at this site. Various authors have found negative correlations between rates of reproduction and lifespan (Murdoch, 1966; Tinkle, 1969; Calow & Woollhead, 1977; Snell & King, 1977; Law, 1979b, Browne, 1982). Brody et al. (1983) found that in Armadillidium vulgare, because reproduction reduces growth and because smaller sized animals are more susceptible to death, that there is a cost, in terms of survival, to reproduction early in life at smaller sizes. Higher levels of reproductive allocation at R.H.B. implies that reproductive effort at Whitby is not maximal, a conclusion supported by the limited degree of iteroparity observed at both sites. Unfortunately the numbers surviving and reproducing a second time were too small to be evaluated accurately at both sites. Although small in number and effect on the population dynamics, they might be important in terms of the evolution of the life histories exhibited by individuals in the population, if they are the fittest individuals, contributing most to future generations. Łomnicki (1980) and Begon (1984) have stressed the importance of rare but successful individuals in the evolution of life histories.

It might also be appropriate to question the legitimacy of the usual indices of reproductive effort, such as those evaluated here, in estimating the reproductive effort of woodlice. For these brooders the most important component of reproductive effort may be the use of resources while carrying the brood, rather than its initial production. The prolonged gravid intermoult and reduced growth achieved at this time (Hubbell, 1971; Chapter 6, section, 2.iii.a) may prove a significant physiological drain.

If the differences in the life history characteristics shown in Table 53 are adaptive then they must be assumed to have a genetic basis. This is possible, the isolated nature of the two populations, separated by only 10km of eroding clay and mudstone cliffs (Agar, 1960), the antiquity of the sites (> 100 years, > 60 generations), and the lack of a dispersal stage in the life history, predisposing the populations to genetic differentiation. Also the isolated nature of the sites for *Ligia oceanica* on the east coast leads me to suppose an initial colonisation of these sites by only a few individuals, and random founder effects might have been important. In addition McGill (1978) has demonstrated genetic differentiation of populations of *Ligia occidentalis*. The most likely means of gene flow between these populations of *L. oceanica* is by the transport of sea-slaters on fishing vessels.

An alternative to the evolutionary explanation would be an ecological one. It could be argued that the increased reproductive allocation, and hence fecundity, at the exposed site is a direct consequence of reduced costs associated with growth at this site. Perhaps food *per capita* is greater at R.H.B. (because of increased density independent mortality?) and animals have to forage less to achieve an equivalent growth rate, while the resources saved are devoted to reproduction. All such hypotheses are purely speculative, and the data inadequate to distinguish them.

The results of the intraspecific comparison of the two populations support to a limited extent the predictions of r- and K- theory, but the mechanism by which it occurs is not demonstrated. The association of decreased survival and increased fecundity and reproductive allocation supports the concept of a trade-off embodied in the optimality models of life history evolution. However there need be no correlation between a trade-off between phenotypic traits, as shown here, and a trade-off between genetically based traits on which evolution acts (Charlesworth, 1984).

CHAPTER 6

POPULATION BREEDING PHENOLOGY AND INDIVIDUAL FITNESS

1. INTRODUCTION

Here I take up some of the points raised in Chapters 2,3 & 5 concerning the breeding phenology of *Ligia oceanica*. This pattern of reproductive activity is apparently identical in the two populations studied. In considering the specific case of *Ligia* I will also consider the more general significance and, in doing so, I review the data for complex breeding phenologies in woodlice and similar patterns in other taxa. I believe that these complex phenologies are a widespread feature of woodlouse population biology and deserve attenton in their own right. In addition I am particularly interested in the association of different life history traits, particularly variation in egg size, with different breeding groups within populations.

In Chapter 5 I gave a justification of the proximate, ecological explanation underlying the breeding phenology of *L. oceanica* (section 3.ii.a., p.105), and will consider here ecological explanations more generally, their consequences for the stability of woodlouse populations, and attempt to reconcile these with an evolutionary explanation. In doing so I reject the possibility that such breeding phenologies are an adaptive response on the part of the populations to stabilise their numbers. Such an hypothesis requires the action of group selection which, while theoretically possible, seems unlikely to operate in the majority of natural populations (Maynard Smith, 1976).

2. BREEDING PHENOLOGIES

i. Occurrence

A common finding of studies of the population dynamics of woodlouse species has been that, within each breeding season, there are two distinct waves of brood production and natality. I define breeding season as the time between the start and finish of the release of offspring by a population into the environment within a year. The data are summarised in Table 55. I have only included work on field populations where the sampling procedure was such that the breeding phenology of the population could be determined adequately. In fifteen populations of nine species a bimodal pattern of breeding was found, whereas six populations of three species did not show this bimodality. Interestingly *Armadillidium vulgare*, which has received most study, shows a bimodal breeding phenology in some populations but not in others. With the exception of *A. vulgare* which is iteroparous, the majority of species in Table 55 are essentially semelparous, so that the two waves of breeding are not due to repeated reproduction by individuals but the result of breeding activity by different groups of individuals within the population. Lawlor (1976b) has shown that the breeding bimodality of *A. vulgare* is the result of some woodlice producing two broods within a breeding season, while others only breed once, towards the end of the season. I have already discussed the breeding phenology of various populations of *Ligia* spp. (Chapter 2, section 9) and pointed out that while some species have similar phenologies to that of *L. oceanica* at R.H.B. and Whitby (eg *L. pallasii*, Carefoot, 1973b), others have different phenologies (eg *L. oceanica* at La Rochelle, Besse *et al*. 1975) (see Fig 15).

Breeding phenologies identical to that shown here for *L. oceanica* have been described for species of prawn (Jensen, 1958b) and a shrimp which also exhibits seasonal shifts in egg size (Boddeke, 1982).

TABLE 55. Breeding phenology of field populations of woodlice

SPECIES	POPULATION SITE	NUMBER OF BREEDING GROUPS	SOURCE
Armadillidium vulgare	California, U.S.A.	2	Paris & Pitelka (1962), Lawlor (1976b)
	Texas, U.S.A.	2	Miller & Cameron (1983)
	Texas, U.S.A.	2	Miller & Cameron (1983)
	Texas, U.S.A.	1	Miller & Cameron (1983)
	Lakenheath, Norfolk	1	Al-Dabbagh & Block (1981)
	Weeting, Norfolk	1	Al-Dabbagh & Block (1981)
	Spurn Head, Yorks.	1	Sutton *et al*. (1984)
Porcellio scaber	Spurn Head, Yorks.	2	Davis (1978)
Porcellio laevis	India	2	Nair (1984)
Porcellio spinicornis	Toronto, Canada	2	McQueen (1976b)
Tracheoniscus rathkei	Toronto, Canada	2	McQueen (1976c)
Trichoniscus pusillus	Oxfordshire	2	Sutton (1968), Phillipson (1983)
	Cheshire	2	Standen (1973)
Philoscia muscorum	Spurn Head, Yorks.	2	Sunderland, Hassall & Sutton (1976)
Ligia oceanica	La Rochelle, France	2	Besse, Picaud & Mocquard (1975)
	Western Baltic, Germ.	2	Jöns (1965)
	Robin Hood's Bay, Yorks.	2	This study
	Whitby, Yorks.	2	This study
Ligia pallasii	Vancouver, Canada	2	Carefoot (1973b)
Ligia dilatata	South Africa	1	Koop & Field (1980)
Hemilepistus reaumuri	Israel	1	Shachak (1980)

ii. Population regulation

In Chapter 1 I pointed out that some investigators of field populations of woodlice have commented on the significance of complex breeding phenologies for the stability of woodlouse populations whose individuals are essentially semelparous (Sunderland *et al*. 1976; Phillipson, 1983; Al-Dabbagh & Block, 1981). Not only may the existence of two distinct breeding groups enhance population survival probability, by partitioning recruitment into more than one defined time period, but the existence of a few individuals with the ability to reproduce a second time adds an additional assurance of population persistence (Murdoch, 1966), but only if repeated breeding, due to the phenology, and individual iteroparity do not overlap. Of the two phenomena population iteroparity will be by far the most important in maintaining the population of *Ligia oceanica* if a recruitment episode should fail because so few individuals survive to produce second broods in these populations.

In my view the phenomenon of "cohort-splitting", suggested as a mechanism of population regulation in *Philoscia muscorum* (Sunderland *et al*. 1976), is a consequence of the seasonal breeding phenology of this species. This results in two cohorts (groups of evenly aged individuals) of recruits which grow at different rates. The term "cohort-splitting" is perhaps unfortunate, although there is evidence of a very similar phenomenon from a lizard population (Bradshaw, 1971).

iii. Individual patterns of brood production in L. oceanica

a. The evidence

From an examination of the data for Ligia it was apparent that females did not produce broods at random within each breeding group, but that within each group larger females produced broods earlier than smaller females. This can be shown statistically by taking the ratio :

$$\frac{\text{Mean weight of gravid females in age group}}{\text{Mean weight of all females in age group}}$$

If females become pregnant at random, independent of their size, then this ratio should equal unity. Using data from both the R.H.B. and Whitby populations, the value of this ratio for the EARLY breeding, two year old age group in samples taken up to the time of peak brood production in late May exceeded unity in every case (two-tailed sign test, $P < 0.002$, $n = 12$, Conover, 1971). Furthermore a significant negative correlation exists between this index and the percentage of the age group which have produced broods ($r_s = -0.88$, $n = 13$, $P < 0.02$). So the larger females produce broods first followed by progressively smaller individuals until all females of the age group have become pregnant. The same was true of the younger, one year old, LATE breeding group. Using all samples up to peak breeding (taken to be the middle of July), the breeding animals tended to be the largest of the age group (sign test, $P < 0.002$; $n = 13$). This result is not surprising as a substantial proportion of the LATE breeding age group are still reproductively immature. However not all those animals which are mature do produce broods. Again there was a significant negative correlation between the index of reproductive size and the percentage of the age class carrying broods ($r_s = -0.57$; $n = 13$; $P < 0.05$).

Taking the EARLY breeding age group as a whole over the period in which the animals were producing their broods, ANOVA showed that there was significant variation in mean live weight of the age group over this period ($F = 5.47$; d.f. = 12,505; $P<0.001$). Regression of the mean live weights of females in each sample on the time of year (days from March 1st) showed that the animals, as a whole, increased in weight over this period ($r^2 = 0.43$; d.f. = 11; $P<0.02$). Taking only the gravid females within each sample for analysis, there was significant variation between the mean size of animals in each sample ($F = 2.81$; d.f. = 11,183; $P<0.01$) but no significant increase in size occurred over this period ($r^2 = 0.04$; d.f. = 11; n.s.). The results for the LATE breeding group are similar. While there were highly significant differences between the average live weights of the age group in samples taken over the duration of the period of brood production ($F = 10.15$; d.f. = 11,1721; $P<0.001$) due to growth by the age group over this period ($r^2 = 0.61$; d.f. = 10; $P<0.01$), there were no differences in the size of the gravid females in samples over this period ($F = 1.61$; d.f. = 12,143; n.s.; $r^2 = 0.08$; n.s.).

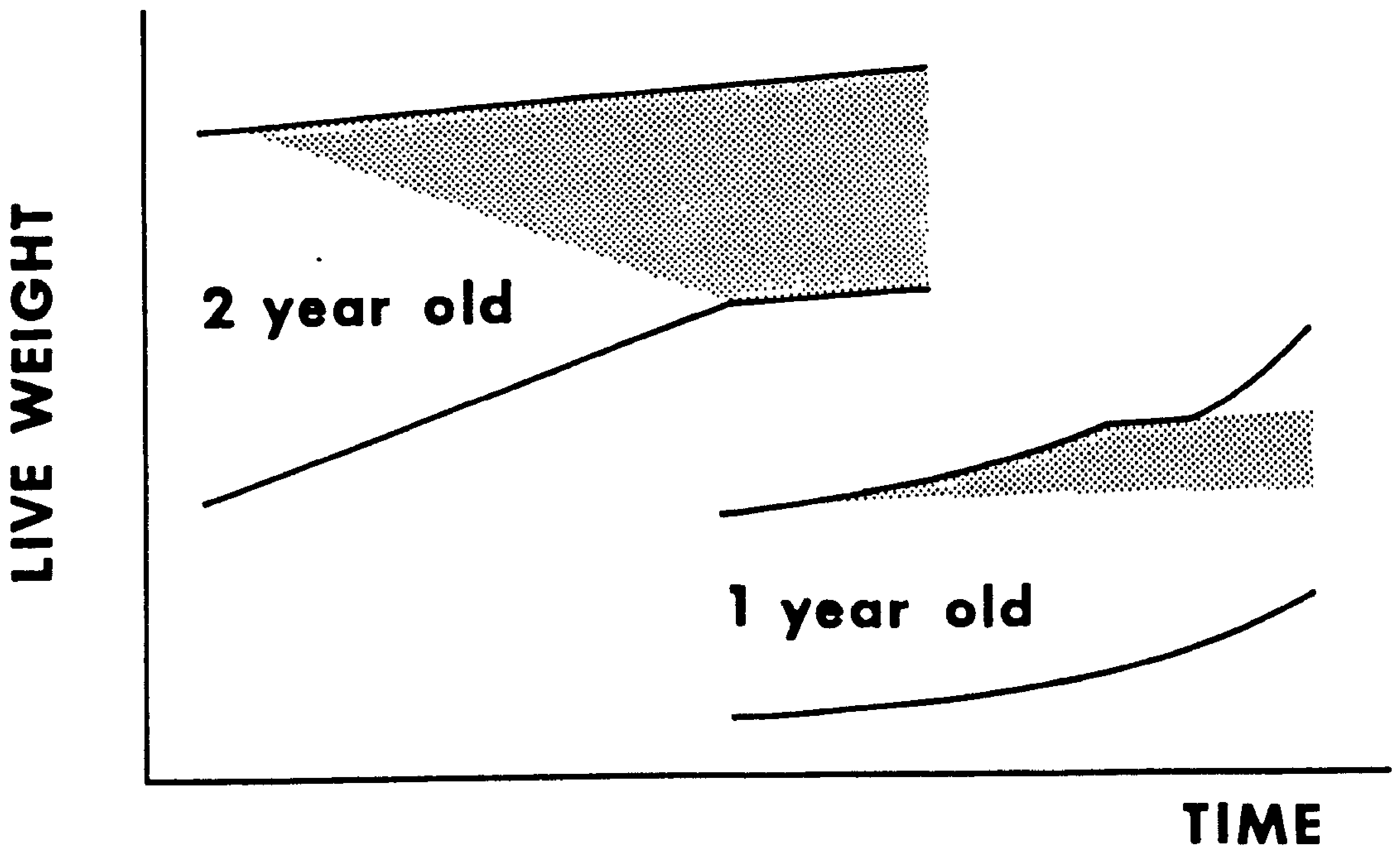
Since, in both groups, there is growth by the group as a whole but not by that sub-group which are gravid, it is clear that the majority of the growth is being achieved by those animals which have not yet produced broods. As we know that the larger animals become gravid first, any growth by the animals which are gravid will be offset by the recruitment of smaller individuals into the gravid population. The effect of this pattern of brood production and growth should be to reduce the variation in live weights of the post-breeding female population compared to the pre-breeding population. This prediction is borne out by the data for the EARLY breeding group (Table 56). In three of the five years for which there are data there was a significant reduction in variation of the post-breeding over the pre-breeding population (one-tailed variance ratio test, Sokal & Rohlf, 1981). In all five cases there was a reduction in the variance over this period (one-tailed sign test, $P = 0.03$). The prediction does not hold for the LATE breeding group because, unlike the EARLY group, only a small proportion actually produce broods at this time and the effect on the age class size variance is correspondingly slight.

Table 56. Reduction in variance in female live weight following brood release. Numbers in brackets are sample sizes.

SITE	DATE	VARIANCE s^2		F RATIO	P
		BEFORE	AFTER		
R.H.B.	1980	5634.9 (38)	1723.1 (18)	3.27	<0.01
	1981	3473.9 (75)	2543.7 (45)	1.37	n.s.
	1982	8352.9 (22)	4203.1 (14)	1.99	~0.10
WHITBY	1980	11299.7 (57)	2532.4 (36)	4.46	<0.001
	1981	6996.2 (25)	2015.3 (17)	3.47	<0.001

FIGURE 44

Diagrammatic representation of the trade-off between growth and reproduction, and the breeding phenology of Ligia oceanica at Robin Hood's Bay and Whitby. Females which have produced broods are shown stippled. These animals grow less quickly than those which have not yet produced broods, resulting in a decrease in the variation in size of the age group (see Table 56). Only a fraction of the one year old animals breed LATE, just before the end of the breeding season.


LIVE WEIGHT
2 year old
1 year old
TIME

These results are shown diagrammatically for each breeding group up to the time of brood release in Fig 44.

b. Discussion

For Ligia oceanica at Robin Hood's Bay and Whitby the bimodal pattern of brood production within a breeding season is not brought about by the synchronous repeated breeding by individuals, but rather by a complex population process in which a small proportion of animals reproduce LATE in the breeding season of their first year, while the remainder reproduce EARLY in the breeding season of their second year. It is probable that those animals born EARLY in a breeding season will be those which will achieve sufficient growth to reproduce LATE in their first breeding season, aged about fourteen months. However this does not explain why all animals do not reproduce at the same time.

The analysis of the data for each breeding group indicates a trade-off between growth and reproduction for animals differing in size within each of the two groups. In the field, over the period when females were producing their broods, non-gravid individuals showed larger increases in live weight than did their gravid counterparts. Furthermore, within each group, it was the smallest individuals which delayed reproduction the most, and therefore gained most in size. Hubbell (1971) also demonstrated that, in the laboratory, the weight of female Armadillidium vulgare remained constant over the period when they were carrying their broods. However some care should be taken in equating increase in live weight with growth because the process of growth may not be the same in the gravid and non-gravid physiological states. Non-gravid animals are able to moult and increase in physical size as well as in weight, whereas gravid animals are unable to moult until brood development is complete. Saudray (1954) has shown that, over the period of incubation of the eggs in the brood pouch, there is a gradual increase in the lipid content of the body tissue of L. oceanica until it reaches those levels found prior to the production of a brood, and this may represent a different type of growth. However Lawlor (1976b) measured growth of non-gravid and gravid A. vulgare in terms of the weight increment immediately following the moult, and also found that gravid individuals grew less than did non-gravid individuals of comparable weight. Whether or not increase in live weight can, in the longer term, be equated with growth, the effect is to reduce the variation in body size of the breeding animals within each group and, because fecundity is related to body weight this will result in a reduction in the variance in number of offspring produced by individuals in each breeding group.

Lawlor (1976b) first pointed out the existence of a trade-off between growth and reproduction in a woodlouse, A. vulgare. He showed that smaller animals will leave more offspring at the end of a breeding season if they reproduce once, towards the end of the breeding season. By foregoing early reproduction they are able to grow more and thereby enhance their fecundity. Conversely, larger animals will leave more offspring by producing two broods, one early and one late, but in doing so grow less than they otherwise would. Hence Lawlor (1976b) demonstrated a trade-off between growth and reproduction for two groups of individuals varying in size and age, and a bimodal breeding phenology due to synchronous repeated reproduction by older, larger animals. Such a trade-off may also occur in Ligia in addition to that found within each of the two breeding groups. Of the LATE breeding age group only 16% of the animals reproduce in their first year, these being the largest. Those which do not reproduce gain in size through growth and overwinter to reproduce as the EARLY group in the following spring. This retardation of growth represents, in terms of reduced potential fecundity, a measurable cost of reproduction. Brody et al. (1983) have shown that small body size in A. vulgare increases susceptibility to death by desiccation and low temperatures, an additional cost of reproduction. Hence small animals which grow rather than reproduce may gain both through increased growth and increased survivorship.

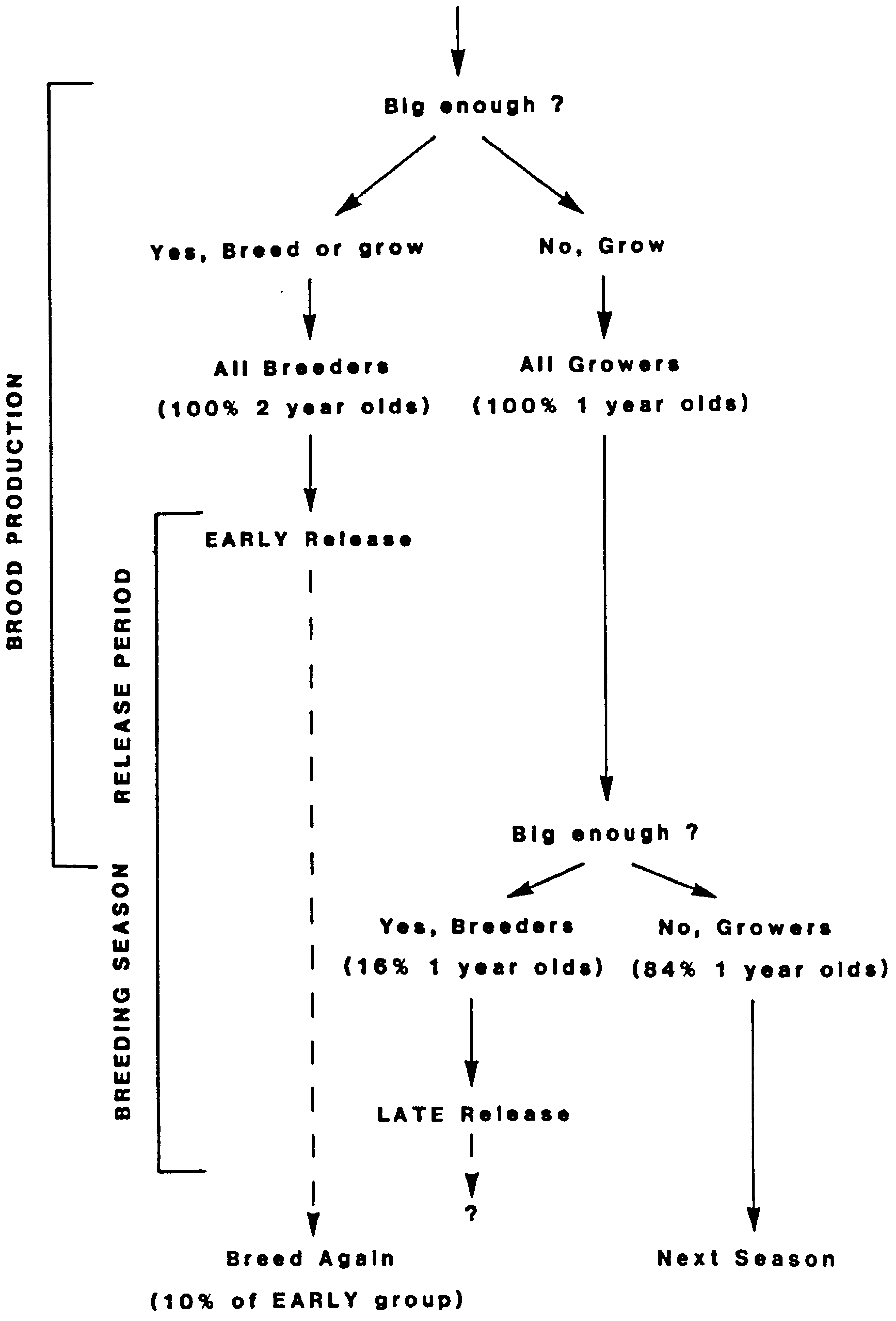
It is not known whether any of those animals which reproduce LATE in their first year themselves survive to reproduce a second time as part of the EARLY group. Although Ligia is essentially semelparous, about 10% of those animals which produce EARLY broods do manage to produce a second brood VERY LATE in the summer, in September, well after the main breeding period. One might expect that it would be those individuals which produce broods first among the EARLY group which would manage to squeeze in a second brood before the winter. However two factors act against this. While the EARLY group are producing their broods the ambient temperature is rising. Brood development time is temperature dependent, so that animals delaying reproduction are not penalised unduly. In addition, larger animals (which produce broods first) produce larger eggs than smaller individuals. Large egg size may prolong development (eg Steele, 1977; but see Kaplan, 1980b), so that the difference in time between release of the offspring will tend to be much less than the difference in time between the production of the broods. Indeed in the field the release of the offspring by each breeding group appeared to be highly synchronous, and separated by about six to seven weeks. It seems probable that the benefit accruing to large individuals producing broods earlier in the breeding season may only materialise in exceptionally mild springs.

iv. A general explanation

Using these results for Ligia, and those of Lawlor (1976b) on A. vulgare it is possible to explain why so many temperate woodlouse species have a bimodal breeding phenology. The breeding phenology of woodlice seems to depend critically on the growth rate and the length of the period when the habitat is suitable for the release of offspring. Where the breeding season is long and growth is rapid, repeated reproduction can occur in iteroparous species, for example A. vulgare (Lawlor, 1976b). For essentially semelparous species, such as Ligia, the optimum strategy may depend upon female size at the beginning and during the breeding season, and is shown diagrammatically in Fig 45.

FIGURE 45

Diagrammatic representation of the breeding phenologies of essentially semelparous woodlice. The breeding season is that period suitable for the release of offspring and follows a period of brood production. Figures in brackets refer to the population of *Ligia oceanica* at Robin Hood's Bay. For further details see text.


Big enough ?
Yes, Breed or grow
No, Grow
All Breeders
(100% 2 year olds)
All Growers
(100% 1 year olds)
BROOD PRODUCTION
RELEASE PERIOD
EARLY Release
Big enough ?
BREEDING SEASON
Yes, Breeders
(16% 1 year olds)
No, Growers
(84% 1 year olds)
LATE Release
?
Breed Again
(10% of EARLY group)
Next Season

For individuals which achieve reproductive size before the start of a breeding season the best strategy is to reproduce EARLY in that season. Within this EARLY group animals can produce broods earlier or later, depending on their size, without markedly affecting the date on which the offspring will be released. Of these about 10% will benefit from the opportunity of producing a second brood very much later in the summer. For groups of individuals which are not of reproductive size at the onset of a breeding season the best strategy is to delay reproduction until the end of the breeding season, when they have gained in size, and then to produce their broods. Hence the breeding season of woodlice does not have a single, environmental optimal time when offspring should be produced, but is continually suitable. Because both growth and survivorship vary seasonally, individuals can perhaps maximise the number of offspring they produce by reproducing at the beginning or end of the breeding season. Any alternative explanation of breeding bimodality would have to involve the unlikely premise that there is more than one environmentally determined optimum time to breed within each breeding season. As in _Oniscus asellus_ the environmental cue to the onset of reproduction is probably lengthening daylength, modified by temperature (Steel, 1980; McQueen & Steel, 1980).

The interpretation that woodlouse species breed either at the beginning or at the end of the breeding season is supported by the results for _A. vulgare_. In England this species is approaching its northern geographical limit (S.L. Sutton, pers. comm.), and breeding seasons can be expected to be short. None of the populations studied in England have shown a bimodal breeding phenology (see Table 55), yet in California and Texas, with longer breeding seasons, this is the usual case. Similarly species living in highly seasonal environments, such as _Hemilepistus reaumuri_, do not show this breeding bimodality. _Ligia dilatata_, whose populations are limited by the seasonal availability of their food resource (Koop & Field, 1980a), also have only a single peak of brood production within a season.

The only exception would appear to be that of *Porcellio laevis* in India (Nair, 1984). In this species a bimodal breeding phenology was observed in some years, associated with two climatically suitable periods for breeding activity. These periods were determined by the highly seasonal nature of the spring and monsoon rains in the Delhi region. In my view these are best regarded as two distinct breeding seasons for the animals, rather than a single breeding season within which release of the offspring is governed by the growth and reproduction of the parents.

3. DOES LIGIA HAVE A STRATEGY?

Individuals within a population rarely if ever achieve equal reproductive success. Even amongst those which breed some will be more successful than others, perhaps producing more and better offspring, more often and for longer. I have already considered some aspects of woodlouse reproductive success (Chapter 5, section 3.iv.). The explanation of the breeding phenology of woodlice presented in the previous section supposes that an individual makes a choice, in evolutionary terms, between breeding earlier in life, LATE in its first breeding season, and at a small size, or risking a winter of inactivity and possible death to reproduce later in life and at a substantially larger size. In essence the arguments are similar to those used by Lawlor (1976b) except that, in his case, the choice was between reproducing twice in a season and growing a little, or growing a lot and reproducing only once, towards the end of that season. However Lawlor (1976b) did not have the complication of differences in life history traits between breeding groups, apart from those due to maternal size. In addition he did not consider consequences of time of birth for the fitness of the offspring produced, only the future fitness of the mother.

Unfortunately I have been unable to measure the survivorship of the young resulting from EARLY and LATE breeding episodes. At R.H.B. the young were indistinguishable in the field and difficult to maintain in the laboratory. However in Germany Jöns (1965) was able to distinguish the recruits of his population into two groups by body size. Phillipson (1983) has presented survivorship curves for EARLY and LATE born *Trichoniscus pusillus*. However the methods used to distinguish the two groups in his size-frequency samples are not given, and natality estimates for the two groups were not made, and so we can learn little about the relative survival of the two groups of offspring. Earlier (Chapter 5, section 3.ii.a) I split my histograms into upper 0.16 and lower 0.84 fractions to calculate the growth of the 16.1% of animals that breed LATE. I justified the assumption that

Table 57. Coefficients of variation of egg weight and fecundities for EARLY and LATE breeding groups at R.H.B. and Whitby.

	R.H.B.		WHITBY	
	FECUNDITY	EGG SIZE	FECUNDITY	EGG SIZE
EARLY	18.0%	10.3%	19.5%	8.9%
LATE	14.1%	6.9%	15.4%	9.0%
COMBINED	20.6%	16.6%	19.1%	15.8%

these were the progeny of EARLY breeding females only, and that these progeny would always comprise the largest 16.1% of that years age class. I further assumed that the lower 83.9% comprised a mixture of both EARLY and LATE born progeny. While I have shown that the contribution of EARLY and LATE breeding females to each age class is about 0.63 : 0.37 (Chapter 2, section 6, p.39), I feel unjustified in assuming equal survivorship because of the large differences in egg size between the two breeding groups.

Here I want to consider firstly, are the different traits shown by each breeding group likely to be adaptations to promote offspring survival in different environments. Secondly I shall ask, if these features are adaptive, what sort of parameter values would we expect to find for the decision made by an individual to breed EARLY next year rather than LATE this year to be the correct decision? In essence I assume that this is an optimal strategy and, using some data, examine the model to discover if its assumptions are reasonable.

i. Seasonal tactics

a. Variation in egg size and fecundity

Brockelman (1975) and Calow (1981) regard intraspecific variation in egg size to be generally much less than the variation in fecundity. This suggests that optimal egg size has been favoured more strongly by natural selection than fecundity (Brockelman, 1975). For Ligia, within each breeding group, variability in egg weight between broods was about half that of fecundity (Table 57). Overall, because of the greater differences in egg weights between groups, compared to fecundity, this reduced variability is masked.

There seems to be plentiful evidence of substantial intraspecific and intrapopulation variation in egg size from studies in which size has been measured as weight or volume, as it should be, rather than by diameter. Substantial variation in ovum size in vertebrates is well known, especially fish (eg Bagenal, 1969; Zijlstra, 1973; Ware, 1977; Grimm, 1979; Constantz, 1979; Mann & Mills, 1979), but also in amphibia (Kaplan, 1980a,b; Berven, 1982), reptiles (review by Nussbaum, 1981) and birds (Lack, 1954). Many crustacea also exhibit such variability, for example copepods (Hutchinson, 1951; Cooney & Gehrs, 1980), cladocera (Kerfoot, 1974), cirripedes (Barnes & Barnes, 1965), and shrimp (Boddeke, 1982). This list is by no means exhaustive. In all these cases variability in egg size is either correlated with female body size or varies seasonally. Although weight specific fecundity is known to vary seasonally in at least two other woodlice, Philoscia muscorum (Sunderland et al. 1976) and Porcellio scaber (Davis, 1978), we do not know whether this is associated with seasonal changes in egg size, reproductive allocation or both. In the case of Philoscia the pattern of seasonal weight specific fecundity is the reverse of that in Ligia. Phillipson (1983), who noted a marked EARLY/LATE breeding phenology in Trichoniscus pusillus, gives no reproductive data for this species. Apart from Lawlor (1976a), egg size and reproductive allocation in woodlice have not received the attention deserved by such important life history traits.

b. Explanations

There are three types of possible explanation of the phenomenon of seasonal variation in egg size : ontogenetic, environmental and adaptive. Possible complications might arise from interactions between these factors.

The ontogenetic argument maintains that egg size is constrained, physiologically, by body size, and that bigger females have to produce bigger eggs. However the substantial residual variability in weight specific egg size for L. oceanica argues against this (see Figs 40 & 41). Data on other species suggests that egg size can be quite independent of body weight. For example, a sample of Porcellio scaber collected from outside the Bay Hotel in R.H.B., covering the entire size range of the population, shows the following relationships with body weight (x in mg DW) (methods were those of Chapter 5, section 2) :

		d.f.	r^2	P
Fecundity	$= 2.715x - 2.485$	43	0.88	<0.001
Egg weight (mgDW)	$= 0.00011x + 0.0872$	43	0.01	n.s.

Similarly Lawlor (1976a) found no relation between egg and body size for Armadillidium vulgare.

The environmental explanation would argue that egg size is a consequence of development under different seasonal conditions. Perhaps seasonal temperature or food availability affects egg numbers during embryogenesis, and the remaining reproductive allocation is partitioned accordingly during vitelligenesis. Although environment may be a proximate factor influencing the size of egg produced, the underlying reasons may be either evolutionary and adaptive, or ontogenetic and non-adaptive. Again the lack of a seasonal difference in egg size in at least some populations of other related species in seasonal environments (eg Armadillidium vulgare, Lawlor, 1976a) argues against an ontogenetic but non-adaptive explanation.

Of the adaptive explanations there are at least two. The first proposes that, under some seasonal conditions, fitness may be increased by a greater investment per offspring and producing less of them. Under other conditions parental investment may be less important in determining offspring fitness, and larger numbers may be the optimum strategy. This hypothesis was first suggested by Hutchinson (1951) and Lack (1954) who proposed that, if food abundance varies during the breeding season, then during times of shortage larger young may be competitively superior, better able to withstand starvation and ultimately fitter than a larger number of less favoured offspring. This idea has been used as the basis of a number of models of the evolution of offspring investment strategy (eg Cody, 1966; Smith & Fretwell, 1974; Brockelman, 1975). In modified form this argument has been used by various authors who have suggested that seasonal variation in predation (Kerfoot, 1974), seasonal mortality (Ware, 1975), and food particle size (Ware, 1977) might be the selective force behind the ability of some species to alter egg size seasonally.

Nussbaum (1981) rejected this as an explanation of the phenomenon in lizards and suggested that, where maternal food supply is unpredictable and fecundity is low (<15 or so), selection should favour conservatively small broods to ensure that each egg is at least minimally provisioned. If too many eggs are produced each may be substantially smaller than the minimum necessary to ensure offspring survival. In years when resources are more abundant than usual the extra resources are put into each egg, making them larger. Nussbaum (1981) reasons that if late season maternal resources are more variable than early season resources, then late broods should comprise a smaller number of larger eggs. Whatever the merits of this theory for lizards, it cannot apply to the majority of species listed above (section 3.i.a), nor to _Ligia_, because of the high fecundities shown by these species.

In my view the seasonal differences in egg size and fecundity in _L. oceanica_ are best interpreted as an adaptive response to ensure offspring survival in particular seasonal environments which are predictable from year to year. Availability of food may be the factor involved. LATE born offspring are released just at the start of the period of maximum adult growth rate, while EARLY born offspring are released substantially in advance of this period (see Figs 23 & 28) when food may be less abundant. However food availability will probably interact with specific seasonal differences in climate at the times when the two groups are released, and we might expect that a range of factors may be important in determining the optimal seasonal egg size.

ii. Breeding strategy

In section 2.iv I assume that, for females born EARLY the year before, the largest adults breed LATE this year and the smallest breed EARLY next year, and that animals sized at the choice size will be equally fit if they breed now or delay and breed the following year. This depends on the fecundities and survival probabilities, but the separate survivals of EARLY and LATE born young are not known. Here I attempt to define a model and, using the data available, try values for survival to see if a reasonable solution may be found.

We can represent the dynamics of the population of L. oceanica at R.H.B. by a simple mathematical model (see Fig 46). Define the following terms :

x = time in years
$\varnothing_A$ = non-breeding adult survival from x+1 to x+2
$\varnothing_E$ = survivorship of EARLY born progeny from x to x+1
$\varnothing_L$ = survivorship of LATE born progeny from x to x+1
F_E = average EARLY fecundity (number of female offspring)
F_L = average LATE fecundity (number of female offspring)
p = proportion of EARLY born females breeding LATE at x+1
$1-p$ = proportion of EARLY born females breeding EARLY at x+2
N_{Ex} = numbers of offspring born EARLY in year x
N_{Lx} = numbers of offspring born LATE in year x
N_{Tx} = total population size at end of breeding season (EARLY + LATE offspring, + surviving adults)

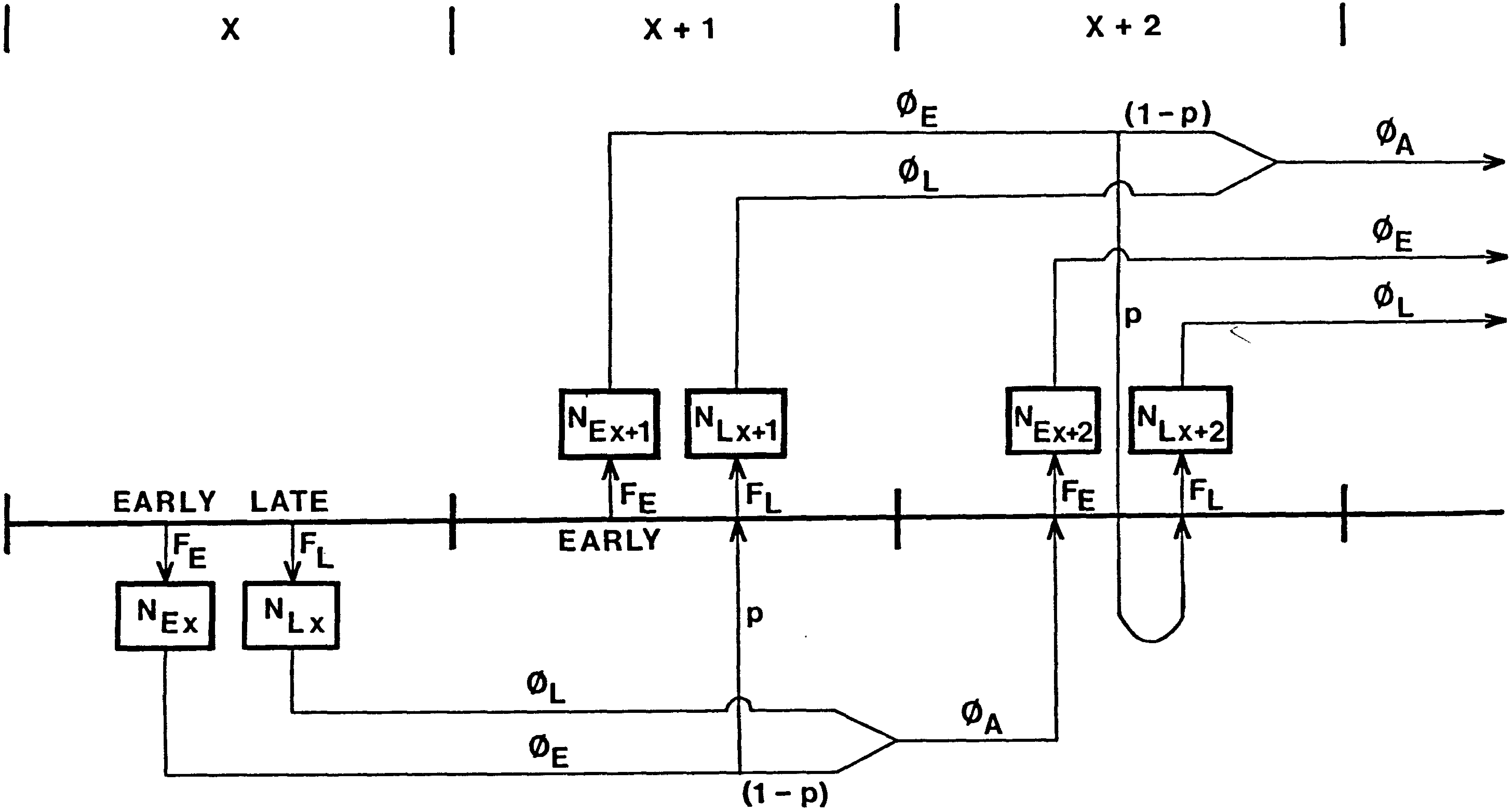
where
$$N_{Lx+2} = N_{Ex+1}\varnothing_E p F_L \quad \checkmark \tag{1}$$

$$N_{Ex+2} = (N_{Lx}\varnothing_L + N_{Ex}\varnothing_E(1-p))\varnothing_A F_E \quad \checkmark \tag{2}$$

and
$$N_{Tx+2} = N_{Lx+2} + N_{Ex+2} + N_{Lx+1}\varnothing_L + N_{Ex+1}\varnothing_E(1-p) \quad \checkmark \tag{3}$$

Animals which have reproduced are assumed to die immediately.

FIGURE 46. Diagrammatic representation of the model of the population of _Ligia oceanica_ at Robin Hood's Bay. Symbols as defined on page 134.



From Chapter 2 we have the following values :

$F_E = 36.1$ (Table 14)
$F_L = 49.2$ (Table 14)
$\emptyset_A = 0.233$ (Table 16)

and the following relations :

$$0.627\emptyset_E + 0.373\emptyset_L = 0.072 \qquad 4$$

(where 0.072 is the average survival of all juveniles from year x to x+1 in the field (Table 18), and 0.627 and 0.373 are the proportions of total natality due to EARLY and LATE breeders respectively (Table 14)),

and $$p = \frac{0.161}{0.627\emptyset_E}(0.627\emptyset_E + 0.373\emptyset_L)$$

(where 0.161 is the proportion of all female progeny surviving from x to x+1 which breed LATE in year x+1).

substitute eq 4 $$p = \frac{0.018^{488}}{\emptyset_E} \quad \checkmark \qquad 5$$

Sustituting 5 into 1 and 2 :

$$N_{Lx+2} = N_{Ex+1}0.018\overset{488}{F_L} \quad \checkmark \quad \checkmark \qquad 6$$

and $$N_{Ex+2} = (N_{Lx}\emptyset_L + N_{Ex}\emptyset_E - 0.018N_{Ex})\emptyset_A F_E \qquad 7$$

Equations 6 and 7 together describe the dynamics of the population assuming a constant proportion of EARLY born animals breed LATE. By starting with a single adult female at time x we can examine the consequences of a decision to reproduce now, LATE, and die, or a decision to reproduce EARLY at x+1 with a probability of surviving to x+1 of $\emptyset_A$. As we iterate through equations 6 and 7 the surviving females are partitioned between EARLY and LATE breeding groups. This is because LATE born offspring always breed EARLY at x+2 and EARLY born offspring partition themselves between breeding episodes LATE at x+1 or EARLY at x+2, dependent on equation 5. Initially values of N_{Ex}, N_{Lx} and N_{Tx} will fluctuate widely until a stable breeding structure is achieved (see Fig 47). By calculating, for each x, the ratio N_{Ex}/N_{Lx}, the stable breeding distribution can be determined when $N_{Ex}/N_{Lx} = N_{Ex+1}/N_{Lx+1}$. In practice this is achieved when the difference is $< 1\%$. Such is usually attained by x = 20 and, after 20 more iterations a value for the rate of increase is estimated as :

$$r = \mathrm{Ln}(N_{Tx+1}) - \mathrm{Ln}(N_{Tx}).$$

Using the mean survival value of $\phi_L = \phi_E = 0.072$ the model generates a slowly increasing population ($r = 0.056$), as would be expected from the standard life table analysis (Chapter 2, section 8).

I now ask, what values of ϕ_L and ϕ_E are needed for the choice made by a small female to breed LATE immediately, or to delay and breed EARLY the next year, to result in equivalent fitness. Following Lawlor (1976b) I shall define fitness as the eventual number of offspring that remain, but in this case only when a stationary population structure has been realised. I assume that the minimum sized LATE breeding female which decides to reproduce LATE has the potential to become one of the largest EARLY breeding females observed in the population. The respective fecundities (numbers of female offspring) are (from Fig 12) :

LATE minimum = 50/2
EARLY maximum = 120/2

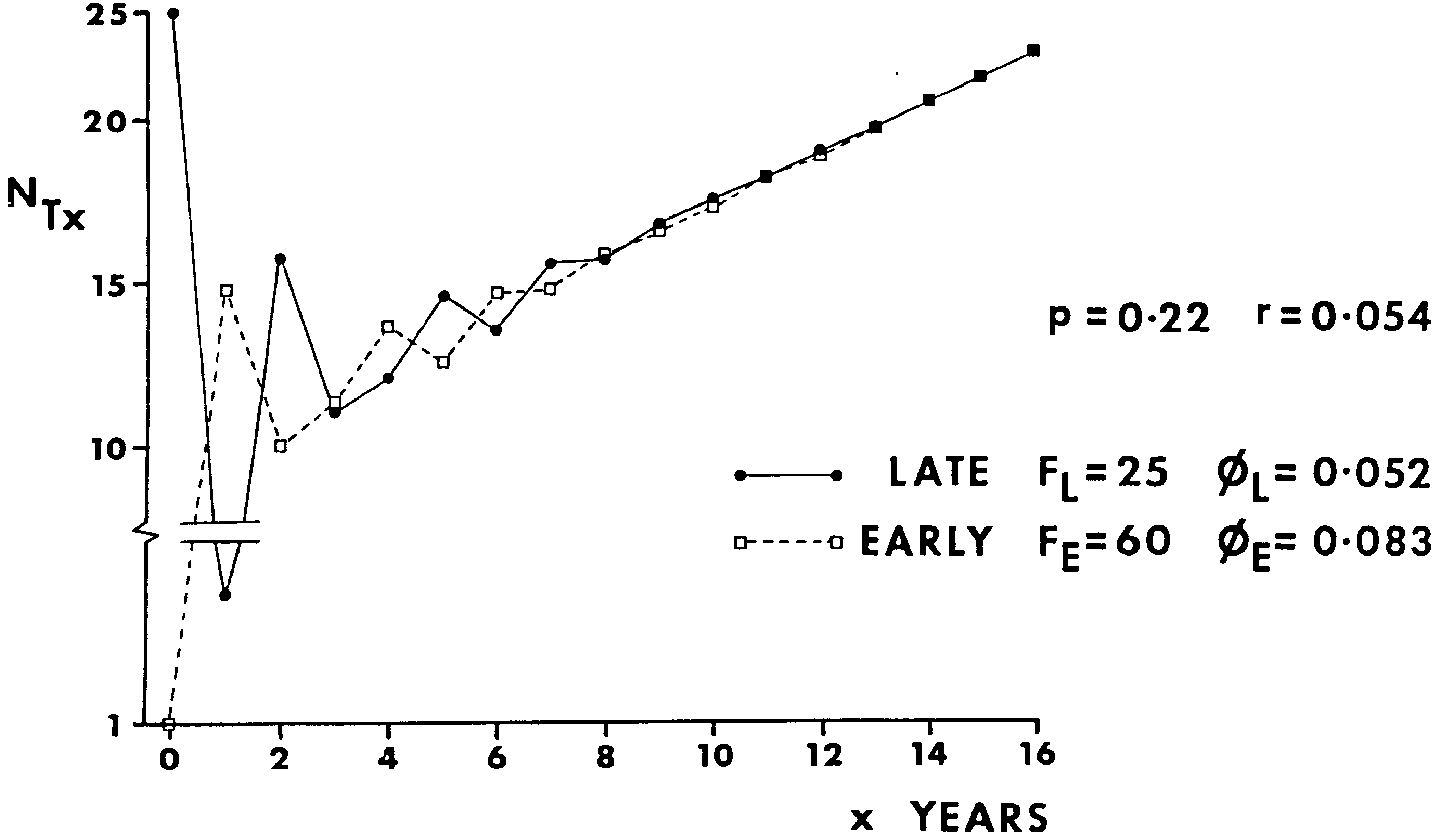
Using these values as the initial starting fecundities at time x = 0 we have :

$$N_{Tx} = N_{Lx} = 25 \qquad \text{(for a LATE decision)}$$

$$\text{and} \quad \left[\begin{array}{l} N_{Tx} = 1, \quad N_{Lx} = 0 \\ \\ N_{Tx+1} = N_{Ex+1} = 60\phi_A \end{array}\right] \quad \text{(for an EARLY decision).}$$

FIGURE 47

Results of the simulation of the breeding activities of a small, LATE breeding female producing offspring at time x=0, and a large EARLY breeding female producing offspring at time x=1. Values of ϕ_E and ϕ_L chosen to ensure equal population sizes (N_{Tx}) when a stable breeding structure has been reached.


N_{Tx}
25
20
15
10
1
0
2
4
6
8
10
12
14
16
x YEARS
$p = 0{\cdot}22$ $r = 0{\cdot}054$
LATE $F_L = 25$ $\phi_L = 0{\cdot}052$
EARLY $F_E = 60$ $\phi_E = 0{\cdot}083$

Increasing values of ϕ_E, and decreasing values of ϕ_L from the mean value are now tried (subject to the constraints of equation 4) until the population sizes N_{TX}, at the stable breeding structure, resulting from these two decisions differ by <1%. The resulting simulations are shown in Fig 47, and the necessary values of juvenile survival are found to be :

$$\phi_E = 0.0831$$
$$\phi_L = 0.0520$$

A consequence of increasing ϕ_E relative to ϕ_L is to decrease the value of r slightly from 0.056 to 0.054, even though overall juvenile survival remains unaltered at 0.072 and fecundity also remains unchanged. (This is because the value of p decreases from 0.252 to 0.217, in effect a decrease in generation time through a smaller proportion breeding in their first year.)

The above analysis does not prove, of course, that the observed phenology is a strategy, only that given the assumptions it is possible to model it as such. The model includes many unstated assumptions. It ignores the relationship between female size and egg size within each breeding group and the trade-off between fecundity and egg size. It ignores problems of sex. In essence I have examined the values necessary to ensure equal fitness of a gene deciding to breed LATE or EARLY at the given body size. I assume that the population is near equilibrium, and that the offspring of a gene breeding LATE or EARLY subsequently have only the average fitness (expectations of survival and reproduction) of the population. I do so because it would have been misleading to use Lawlor's (1976b) definition of fitness in this context. Until offspring have partitioned themselves between breeding groups in the long term, no assessment of the contribution of a parent to the future can be made. The finding that the value of ϕ_E needed to achieve equal fitness is not very much greater than ϕ_L is a reassuring feature of the model. That it is larger agrees with the contention that larger eggs may result in greater survival. However the estimated value for overall juvenile survival of 0.072 is probably highly inaccurate and is used to determine the relative survivals of EARLY and LATE born offspring only, not their absolute values.

An interesting feature of this model is that it gives an assessment of the bet-hedging potential of this phenology. The offspring of a LATE breeding female all reproduce synchronously in their second year. Should this recruitment fail a LATE breeding females fitness would be zero. However an EARLY breeding female immediately has some of its progeny breeding LATE and some EARLY, so it does not take the same risk of absolute failure. Although there are these bet-hedging consequences to the decision to breed or not to breed, I think them unlikely to be a significant component in the evolution of that decision.

The model also has consequences for the dynamics of woodlouse populations. If it is moderately unchanged by the effects of any density-dependence, then the model may represent, albeit only qualitatively, the growth of a population in a new environment. We may then expect large fluctuations in woodlouse density during the first years of population growth purely as a result of the breeding phenology. However, as growth under non-crowded conditions is likely to be greater, the value of p may increase, not because more EARLY born females survive to make the choice to breed LATE or not (as modelled here), but because more achieve the size for this choice before it has to be made.

It is clear that the population dynamics of woodlice, such as Ligia oceanica, may be a complicated consequence of quite subtle life history adaptations. The evolution of such adaptations may only be possible in environments which, although perhaps stressful, are seasonal, predictable from year to year, and durable. The ability of these animals to respond flexibly to differences in individual circumstances may help to explain the success of woodlice in terrestrial habitats.

4. POSTSCRIPT

In a recent paper Brody & Lawlor (1984) have also observed considerable seasonal variability in offspring size in a population of Armadillidium vulgare in Texas. Unlike the data presented here for Ligia oceanica, they found that smaller young were produced by females in the spring, and larger young in the summer. However these authors also suggest that large size may be important in determining initial offspring survival for, unlike R.H.B. and Whitby, food availability for A. vulgare is greater in the spring than in the summer when environmental conditions are not suitable for foraging. Hence, although the seasonal pattern of variation in egg size is reversed for A. vulgare, the adaptive explanation is the same as that reasoned here for L. oceanica. In addition Brody & Lawlor (1984) show that the environmental determinant of offspring size may be the food available to the female parent prior to production of the brood. As I have suggested for Ligia oceanica, they suggest that the "physiological ability to respond proximately to variable ecological conditions may be genetic, subject to selection, and an important reproductive adaptation".

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APPENDIX

OOSTEGITE DEVELOPMENT IN LIGIA OCEANICA (L.) AND THE BREEDING PHENOLOGY OF WOODLICE (CRUSTACEA : ONISCOIDEA)

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CONTENTS

Synopsis

A bimodal pattern of brood production within a breeding season appears to be characteristic of populations of many species of woodlice, including Ligia oceanica. In this species the females possess, throughout life, oostegites which undergo a clear developmental sequence related to the reproductive state of the females. This allows different year classes within the breeding population to be accurately differentiated. This in turn allows a detailed study of the breeding phenology of this species. A trade-off between growth and reproduction is found within each of the two breeding groups. This tends to reduce the variation in number of offspring produced by individuals within each group. The trade-off between growth and reproduction noted by Lawlor (1976) in Armadillidium vulgare might also be occurring between the two breeding groups. The bimodal brood production characteristic of woodlouse populations is the product of complex population processes which differ between populations, and may be explained by the length of the favourable period for release of the offspring. Where this period is long, mature individuals should breed at the beginning of the season, with the prospect of perhaps managing to produce a second brood later on in the season. Smaller immature animals may grow and, if achieving a minimum size for reproduction, should reproduce at the end of the season. Although the breeding season may be continually suitable for release of the offspring, offspring are released either at the beginning or end of the season, allowing females to produce the maximum number possible before death.

I Introduction

A characteristic of many populations, especially those in seasonal environments, is that reproduction is frequently confined to a distinct breeding season or period. These periods are usually located in those months when physical conditions are less severe. It is often an implicit assumption that there is an optimal time of year for the release of an individual's offspring, when the physical and biotic environment is most suitable. This optimal time may be more or less predictable from year to year, but those animals which reproduce at that time may be viewed as the most successful. Todd & Doyle (1981) made this assumption explicit in their model of the breeding strategies of marine invertebrates. They suggest that breeding by the nudibranch mollusc *Onchidoris muricata* is governed by the need of the larvae of this species to settle on the shore at the same time as one of the juvenile prey species, the barnacle *Semibalanus balanoides*.

However a common finding of studies of the population dynamics of woodlouse species has been that, within each breeding season, there are two distinct waves of brood production and natality. The data are summarised in Table 1. I have only included work on field populations where the sampling procedure was such that the breeding phenology of the population could be determined adequately. In fifteen populations of nine species a bimodal pattern of breeding was found, whereas six populations of three species did not show this bimodality. Interestingly *Armadillidium vulgare*, which has received most study, shows a bimodal breeding phenology in some populations but not in others. With the exception of *A. vulgare* which is iteroparous, the majority of species in Table 1 are essentially semelparous, so that the two waves of breeding are not due to repeated reproduction by individuals but the result of breeding activity by different groups of individuals within the population. Unless we are to accept the unlikely hypothesis that, within each breeding season, there is more than one environmentally determined optimum time for woodlice to breed, then there must be additional factors operating in these populations to produce the

TABLE 1. Breeding phenology of field populations of woodlice

SPECIES	POPULATION SITE	NUMBER OF BREEDING GROUPS	SOURCE
Armadillidium vulgare	California, U.S.A.	2	Paris & Pitelka (1962), Lawlor (1976b)
	Texas, U.S.A.	2	Miller & Cameron (1983)
	Texas, U.S.A.	2	Miller & Cameron (1983)
	Texas, U.S.A.	1	Miller & Cameron (1983)
	Lakenheath, Norfolk	1	Al-Dabbagh & Block (1981)
	Weeting, Norfolk	1	Al-Dabbagh & Block (1981)
	Spurn Head, Yorks.	1	Sutton *et al.* (1984)
Porcellio scaber	Spurn Head, Yorks.	2	Davis (1978)
Porcellio laevis	India	2	Nair (1984)
Porcellio spinicornis	Toronto, Canada	2	McQueen (1976b)
Tracheoniscus rathkei	Toronto, Canada	2	McQueen (1976c)
Trichoniscus pusillus	Oxfordshire	2	Sutton (1968), Phillipson (1983)
	Cheshire	2	Standen (1973)
Philoscia muscorum	Spurn Head, Yorks.	2	Sunderland, Hassall & Sutton (1976)
Ligia oceanica	La Rochelle, France	2	Besse, Picaud & Mocquard (1975)
	Western Baltic, Germ.	2	Jons (1965)
	Robin Hood's Bay, Yorks.	2	This study
	Whitby, Yorks.	2	This study
Ligia pallasii	Vancouver, Canada	2	Carefoot (1973b)
Ligia dilatata	South Africa	1	Koop & Field (1980)
Hemilepistus reaumuri	Israel	1	Shachak (1980)

observed breeding bimodalities. In this paper I examine in detail the breeding phenology of Ligia oceanica, and suggest a possible explanation of the bimodal breeding phenology of woodlice with particular reference to the work of Lawlor (1976) on A. vulgare.

II Methods

Samples of L. oceanica were collected approximately monthly from two sites on the north east coast of England, at Robin Hood's Bay and Whitby. Samples were stored overnight in 75 cm^3 containers at 10^oC on filter paper moistened with sea water. This allowed time for the animals to reach a standard water balance prior to weighing to 0.1 mg for size frequency analysis. The width of the size class intervals was decided after applying Scott's (1979) formula for optimal class intervals on a representative number of individual age class distributions. Females were also recorded as to their reproductive status and the stage of development of their oostegites. For further details of sampling methods and sites see Willows (1984). In addition a large group (initially $>$200) of individuals was maintained in the laboratory over eight months to study oostegite development, supplemented by observations on groups of individually marked reproductive females.

III Results

A Oostegite development.

Ligia is unusual amongst the terrestrial Isopoda in that the females develop oostegites as the juvenile animals mature and keep them throughout life, though they are only fully developed when the females are carrying broods. Several authors (Nicholls, 1931; Gebelin, 1939; Mocquard, Picaud & Besse, 1974) have noted a variety of different types or developmental stages of the oostegites of Ligia oceanica.

Male Ligia mature first, rapidly increasing in frequency until they comprise about 50% of the recently born recruits (Fig. 1). Juvenile females show no oostegite development until, at about 50-60 mg live weight, the percentage of animals with oostegites increases until, at about 120 mg, all have oostegites. These small females are still reproductively immature and two stages, based on oostegite morphology, can be distinguished (Fig. 2a,b):

Immature 1 (I1). Oostegites small, standing erect from the base of legs one to five. A small tooth present on the anterior edge of the oostegites. Mean live weight 98.7 ± 2.8 mg (95% C.I.).

Immature 2 (I2). Oostegites larger, also standing erect from the base of the legs, but lacking a tooth. Mean weight 116.2 ± 4.0 mg (95% C.I.).

From this state animals moult into the mature and prevalent state:

Mature (M). Fig. 2c. Oostegites flap-like, lying flat against the ventral surface of the sternite and extending up to half-way from the base of the leg to the mid-line of the body.

Animals can undergo an indefinite number of moults with no obvious change in the morphology of the oostegites from this immature state. However three further types can be recognised, all being associated with the production of broods by the females:

Pre-brood (PB). Fig. 2d. The intermoult preceding the production of a brood is characterised by oostegites which are rounded in cross-section, curving posteriorly from the base of the legs.

Gravid (G). Fig. 2e. Females with fully developed oostegites which overlap to form a brood-pouch containing the eggs. Following the development and release of the offspring females possess an empty but complete brood pouch. This sub-stage, the post-parturient (PP) stage, precedes the next moult and is of greatly varying duration (a few days to two to three weeks). It is of sufficient length for substantial numbers of animals to occur in field samples.

Post-reproductive (PR). Fig. 2f. Following the post-parturient moult the oostegites become greatly reduced in size, standing erect from the base of the legs, with a small anterior projection or tooth. Animals moult from this stage back to the prevalent mature (M) non-reproductive state.

B. Age structure

From samples taken in mid-winter two distinct age classes could be identified in the population based on the bimodality in the live weights of the females. By April these two age groups have just started to merge (see Fig. 3), but could still be separated by size. However by July the two groups had merged so as to be indistinguishable by size alone (Fig. 4). This figure also shows how the female population at this time breaks down into clearly defined groups based on oostegite development. The reason this is possible is that the older animals, in their second year, start to produce broods much earlier in the year than the smaller animals in their first year. In April only the larger, two year old animals are gravid, and those which are not have oostegites of the pre-brood type (Fig. 3). Hence, for samples taken in early spring, oostegite development reinforces the analysis of population structure based solely on size because very few of the smaller, one year old animals have oostegites further developed than the immature states.

Oostegite development becomes particularly important in the separation of the age classes in samples taken during the summer. The substantial overlap in size between the one and two year old animals (Fig. 4) is principally due to the loss of weight by the two year old animals which have released their broods. In laboratory studies the weight lost on release of a brood was 22.2 ± 1.7% (95% C.I.) of the females live weight immediately preceding release. In the sample shown in Fig. 4 the majority of the two year old animals are post-reproductive (PR), having released their broods and moulted. A smaller proportion have released their broods but not yet moulted (PP). A yet smaller proportion are still gravid (G). These can be distinguished from the smaller, younger animals which have recently produced broods of yellow eggs, by the advanced stage of embryonic development of the broods of the older animals. The majority of the one year old animals have mature (M) oostegites at this time, and a few two year old animals have already passed through the post-reproductive moult. No animals with pre-brood (PB) oostegites were taken in this sample because, by July, all the one year old animals which are going to become gravid during a season have done so. However 10% of the two year old animals produced second broods in September, well after the main periods of brood release.

The use of oostegite development and reproductive state as a means of assigning an individual female to a particular age group is to be preferred to the available graphical (Harding, 1949; Cassie, 1954) and statistical (Hasselblad, 1966; Schnute & Fournier, 1980) methods because of its biological reality. In addition it avoids making many assumptions, such as the nature of the underlying distributions and the form of the growth curve, which are unlikely to hold in practice.

C. Brood production

The two waves of brood production are shown in Fig. 5. Females of the first wave, which I term the "early" group, start to become gravid at the beginning of March, and 100% of the year class have become pregnant by the end of May. There was little variation in the pattern of breeding phenology of the early group either between years or between the two sites. There was greater variation in the pattern of breeding of the second wave, the "late" group, which usually commenced towards the end of May and peaked in mid-July, when about 16% of the year class were found to be gravid. Of the initial, early breeding group, about 40% survive to the end of the summer, and of these survivors about 25% produce a second brood at this time (Willows, 1984). *Ligia oceanica* is essentially semelparous, less than 10% of females will produce more than a single brood in the field.

Closer examination of the data shows that animals do not produce broods at random within each of the two groups. From Fig. 3 it is apparent that it is the larger of the females within this age class which have produced broods. The smaller females, although reproductively mature (that is above the minimum size at which reproduction can occur) have not yet produced their broods. If the females within an age class become pregnant at random, independent of their size, then the ratio:

$$\frac{\text{Mean weight of gravid females in age group}}{\text{Mean weight of all females in age group}}$$

should average unity. However the value of this ratio for the early breeding, two year old age group in samples taken up to the time of peak brood production in late May exceeded unity in every case (two-tailed sign test, $P < 0.002$, $n = 12$, Conover, 1971). Furthermore a significant negative correlation exists between this index and the percentage of the age group which have produced broods ($r_s = -0.88$, $n = 13$, $P < 0.02$). So the larger females produce broods first followed by progressively smaller individuals until all females of the age group have become pregnant. The same was true of the younger, one year old, late breeding group. Using all samples up to peak breeding (taken to be the middle of July), the breeding animals tended to be the largest of the age group (sign test, $P < 0.002$, $n = 13$). This result is not surprising as a substantial proportion of the late breeding age group are still reproductively immature. However not all those animals which are mature do produce broods. Again there was a significant negative correlation between the index of reproductive size and the percentage of the age class carrying broods ($r_s = -0.57$, $n = 13$, $P < 0.05$).

Taking the early breeding age group as a whole over the period in which the animals were producing their broods, ANOVA showed that there was significant variation in mean live weight of the age group over this period ($F = 5.47$, d.f. = 12,505, $P < 0.001$). Regression of the mean live weights of females in each sample on the time of year (days

Table 2. Reduction in variance in female live weight following brood release. Numbers in brackets are sample sizes.

SITE	DATE	VARIANCE s^2 BEFORE	VARIANCE s^2 AFTER	F RATIO	P
R.H.B.	1980	5634.9 (38)	1723.1 (18)	3.27	<0.01
	1981	3473.9 (75)	2543.7 (45)	1.37	n.s.
	1982	8352.9 (22)	4203.1 (14)	1.99	~ 0.10
WHITBY	1980	11299.7 (57)	2532.4 (36)	4.46	<0.001
	1981	6996.2 (25)	2015.3 (17)	3.47	<0.001

from March 1st) showed that the animals, as a whole, increased in weight over this period ($r^2 = 0.43$, d.f. = 11, $P < 0.02$). Taking only the gravid females within each sample for analysis, there was significant variation between the mean size of animals in each sample ($F = 2.81$, d.f. = 11,183, $P < 0.01$) but no significant increase in size occurred over this period ($r^2 = 0.04$, d.f. = 11, n.s.). The results for the late breeding group are similar. While there were highly significant differences between the average live weights of the age group in samples taken over the duration of the period of brood production ($F = 10.15$, d.f. = 11,1721, $P < 0.001$) due to growth by the age group over this period ($r^2 = 0.61$, d.f. = 10, $P < 0.01$), there were no differences in the size of the gravid females in samples over this period ($F = 1.61$, d.f. = 12,143, n.s.; $r^2 = 0.08$, n.s.).

Since, in both groups, there is growth by the group as a whole but not by that sub-group which are gravid, it is clear that the majority of the growth is being achieved by those animals which have not yet produced broods. As we know that the larger animals become gravid first, any growth by the animals which are gravid will be offset by the recruitment of smaller individuals into the gravid population. The effect of this pattern of brood production and growth should be to reduce the variation in live weights of the post-breeding female population compared to the pre-breeding population. This prediction is borne out by the data for the early breeding group (Table 2). In three of the five years for which there is data there was a significant reduction in variation of the post-breeding over the pre-breeding population (one-tailed variance ratio test, Sokal & Rohlf, 1981). In all five cases there was a reduction in the variance over this period (one-tailed sign test, $P = 0.03$). The prediction does not hold for the late breeding group because, unlike the early group, only a small proportion actually produce broods at this time and the effect on the age class size variance is correspondingly slight.

These results are shown diagrammatically for each breeding group up to the time of brood release in Fig. 6.

IV Discussion

For Ligia oceanica at Robin Hood's Bay and Whitby the bimodal pattern of brood production within a breeding season is not brought about by the synchronous repeated breeding by individuals, but rather by a complex population process in which a small proportion of animals reproduce late in the breeding season of their first year, while the remainder reproduce early in the breeding season of their second year. It is probable that those animals born early in a breeding season will be those which will achieve sufficient growth to reproduce late in their first breeding season, aged about fourteen months. However this does not explain why all animals do not reproduce at the same time.

The analysis of the data for each breeding group indicates a trade-off between growth and reproduction for animals differing in size within each of the two groups. In the field, over the period when females were producing their broods, non-gravid individuals showed larger increases in live weight than did their gravid counterparts. In addition, within each group, it was the smallest individuals which delayed reproduction the most, and therefore gained most in size. Hubbell (1971) also demonstrated that, in the laboratory, the weight of female Armadillidium vulgare remained constant over the periodwhen they were carrying their broods. However some care should be taken in equating increase in live weight with growth because the process of growth may not be the same in the gravid and non-gravid physiological states. Non-gravid animals are able to moult and increase in physical size as well as in weight, whereas gravid animals are unable to moult until brood development is complete. Saudray (1954) has shown that, over the period of incubation of the eggs in the brood pouch, there is a gradual increase in the lipid content of the body tissue of L. oceanica until it reaches those levels found prior to the production of a brood, and this may represent a different type of growth. However Lawlor (1976) measured growth of non-gravid and gravid A. vulgare in terms of the weight increment immediately following the moult, and also found that gravid individuals grew less than did non-gravid individuals of comparable weight. Whether or not increase in live weight can, in the longer term, be equated with growth, the effect is to reduce the variation in body size of the breeding animals within each group and, because fecundity is clearly related to body weight (Willows, 1984), this will result in a reduction in the variance in number of offspring produced by individuals in each breeding group.

Lawlor (1976) first pointed out the existence of a trade-off between growth and reproduction in a woodlouse, A. vulgare. He showed that smaller animals will leave more offspring at the end of a breeding season if they reproduce once, towards the end of the breeding season. By foregoing early reproduction they are able to grow more and thereby enhance their fecundity. Conversely, larger animals will leave more offspring by producing two broods, one early and one late, but in doing so grow less than they otherwise would. Hence Lawlor (1976) demonstrated a trade-off between growth and reproduction for two groups of individuals varying in size and age, and a bimodal breeding phenology due to synchronous repeated reproduction by older, larger animals. Such a trade-off might be occurring in Ligia in addition to that found within each of the two breeding groups. Of the late breeding age group only 16% of the animals reproduce in their first year, these being the largest. Those which do not reproduce gain in growth and overwinter to reproduce as the early group in the following spring. This retardation of growth represents, in terms of reduced potential fecundity, a measurable cost of reproduction. Brody, Edgar & Lawlor (1983) have shown that small body size in A. vulgare increases susceptibility to death by desiccation and low temperatures, an additional cost of reproduction. Hence small animals which grow rather than reproduce may gain both through increased growth and increased survivorship. It is not known whether any of those animals which reproduce late in their first year themselves survive to reproduce a second time as part of the early group. Although Ligia is essentially semelparous, about 10% of those animals which produce early broods do manage to produce a second brood very late in the summer, in September, well after the main breeding period. One might expect that it would be those individuals which produce broods first among the early group which would manage to squeeze in a second brood before the winter. However two factors act against this. While the early group are producing their broods the ambient temperature is rising. Brood development time is temperature dependent, so that animals delaying reproduction are not penalised unduly. In addition, larger animals (which produce broods first) produce larger eggs than smaller individuals (Willows, 1984). Large egg size prolongs development (e.g. Steele, 1977), so that the difference in time between release of the offspring will tend to be much less than the difference in time between the production of the broods. Indeed in the field the release of the offspring by each breeding group appeared to be highly synchronous, and separated by about six to seven weeks. It seems likely that the benefit accruing to large individuals producing broods early in the breeding season may only materialise in exceptionally warm springs.

Using these results for Ligia, and those of Lawlor (1976) on A. vulgare it is possible to explain why so many temperate woodlouse species have a bimodal breeding phenology. This pattern is particularly well documented and interesting in L. oceanica. Two independent studies of populations in the western Baltic (Jöns, 1965) and at La Rochelle, France (Mocquard et al., 1974; Besse et al., 1975) have both described two waves of brood production. Both studies recorded the time of year when births occur as June and July/August, exactly those determined in this study, even though the populations cover a substantial geographical range. The similarity is particularly striking because the bimodal pattern of breeding by the French population is brought about in quite a different way to that at Robin Hood's Bay and Whitby. At La Rochelle each breeding wave is made up of individuals aged twelve months, and those animals which are born early reproduce early, and those born late reproduce late. The maximum longevity of females in the French population was only 15-18 months, compared to 30-36 months at Robin Hood's Bay and Whitby, and again the majority of animals died after the production of a single brood (Besse et al., 1975).

The breeding phenology of woodlice seems to depend critically on the growth rate and the length of the period when the habitat is suitable for the release of offspring. Where the breeding season is long and growth is rapid, repeated reproduction can occur in iteroparous species, for example A. vulgare (Lawlor, 1976). For essentially semelparous species, such as Ligia, the optimum strategy depends upon female size at the beginning and during the breeding season, and is shown diagrammatically in Fig. 7. For individuals which achieve reproductive size before the start of a breeding season the best strategy is to reproduce early in that season. Within this early group animals can produce broods earlier or later, depending on their size, without markedly affecting the date on which the offspring will be released. Of these about 10% will benefit from the opportunity of producing a second brood very much later in the summer. For groups of individuals which are not of reproductive size at the onset of a breeding season the best strategy is to delay reproduction until the end of the breeding season, when they have gained in size, and then to produce their broods. Hence the breeding season of woodlice does not have a single, environmental optimal time when offspring should be produced, but is continually suitable. Because both growth and survivorship vary seasonally, individuals can maximise the number of offspring they produce by reproducing at the beginning or end of the breeding season. Any alternative explanation of breeding bimodality would have to involve the unlikely premise that there is more than one environmentally determined optimum time to breed within each breeding season. As in Oniscus asellus the environmental cue to the onset of reproduction is probably lengthening daylength, modified by temperature (Steel, 1980; McQueen & Steel, 1980).

The interpretation that woodlouse species breed either at the beginning or at the end of the breeding season is supported by the results for A. vulgare. In England this species is approaching its northern geographical limit (S.L. Sutton, pers. comm.), and breeding seasons can be expected to be short. None of the populations studied in England have shown a bimodal breeding phenology (see Table 1) yet in California and Texas, with longer breeding seasons, this is the usual case. Similarly species living in highly seasonal environments, such as Hemilepistus reaumuri, do not show this breeding bimodality. Ligia dilatata, whose populations are limited by the seasonal availability of their food resource (Koop & Field, 1980), also have only a single peak of brood production within a season.

The only exception would appear to be that of Porcellio laevis in India (Nair, 1984). In this species a bimodal breeding phenology was observed in some years, associated with two climatically suitable periods for breeding activity. These periods were determined by the highly seasonal nature of the spring and monsoon rains in the Delhi region. In my view these are best regarded as two distinct breeding seasons for the animals, rather than a single breeding season within which release of the offspring is governed by the growth and reproduction of the parents.

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Figure Legends

Figure 1. Percentage of animals which can be sexed from external characteristics as females (black), males (stipple) or juveniles whose sex cannot be determined (white). Data from Robin Hood's Bay includes all animals < 150 mg live weight taken in samples over a period of three years.

Figure 2. Ventral view of the right side of the third perionite showing the oostegite development stages. The base of the leg is shown cross-hatched.
a. Immature 1; b. Immature 2;
c. Mature; d. Pre-brood; e. Fully-formed oostegite of the gravid state;
f. Post-reproductive.

Figure 3. Female population size-structure, 19 April 1981. The 1980 and 1979 year classes are still distinct, the 1979 year class having oostegites of the gravid (G) and pre-brood (PB) types.

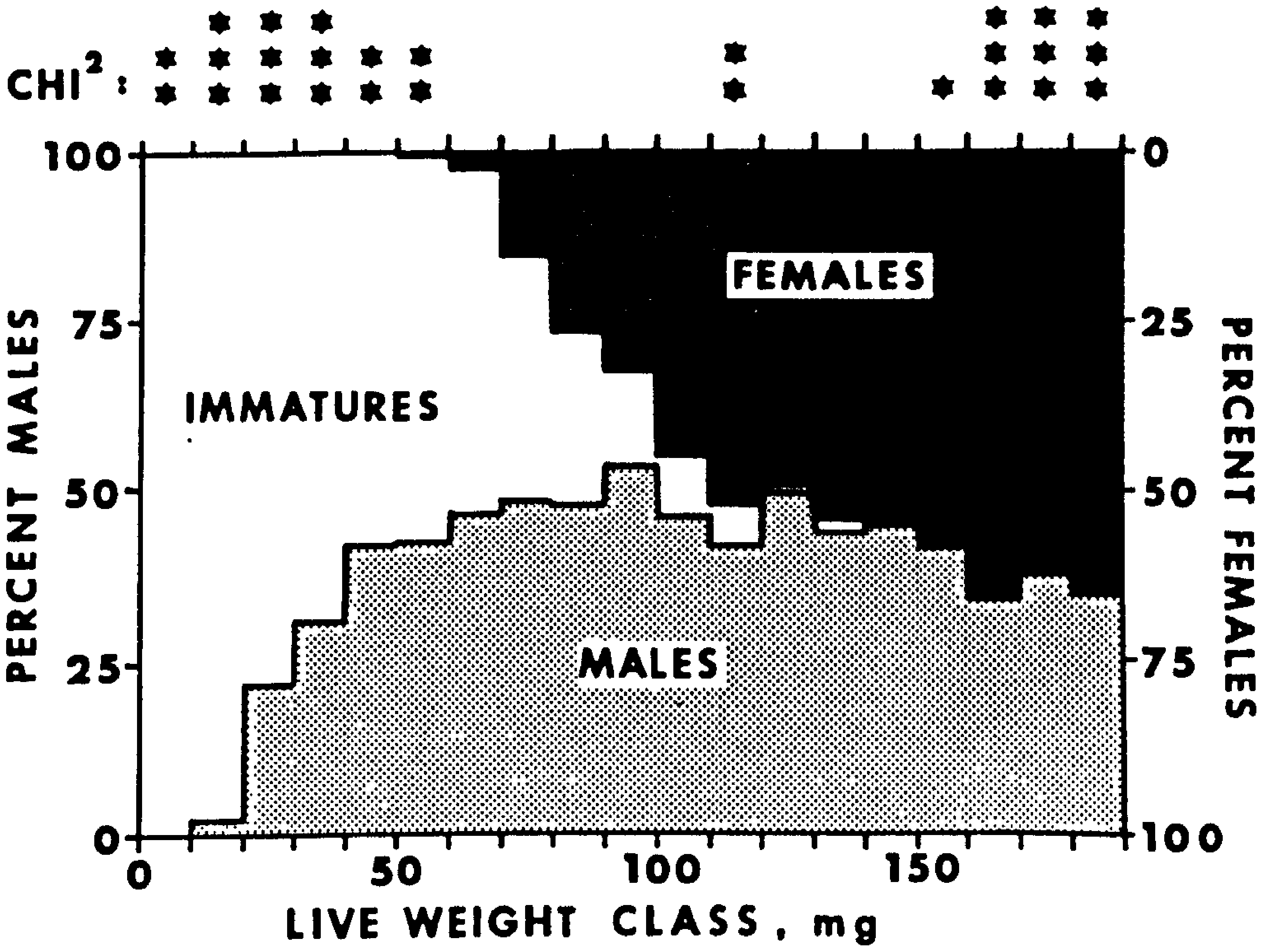
Figure 4. Female population size-structure, 15 July 1981, showing the distribution of oostegite types amongst the 1980 (white) and 1979 (black) year classes. For further details see text.

Figure 5. Proportion of animals of each age group found gravid in samples. ○ Robin Hood's Bay early (two year old) group, ● Whitby early group. ▲ Robin Hood's Bay late (one year old) group, △ Whitby late group.

Figure 6. Diagrammatic representation of the trade-off between growth and reproduction, and the breeding phenology of L. oceanica at Robin Hood's Bay and Whitby. Females which have produced broods are shown stippled. These animals grow less quickly than those which have not yet

produced broods, resulting in a decrease in the variation in size of the group. Only a fraction of the one year old animals become gravid before the end of the breeding season.

Figure 7. Diagrammatic representation of the breeding strategies of essentially semelparous woodlice. The breeding season is that period suitable for the release of offspring, and follows a period of brood production. Figures in brackets refer to the population of *Ligia oceanica* at Robin Hood's Bay. For further details see text.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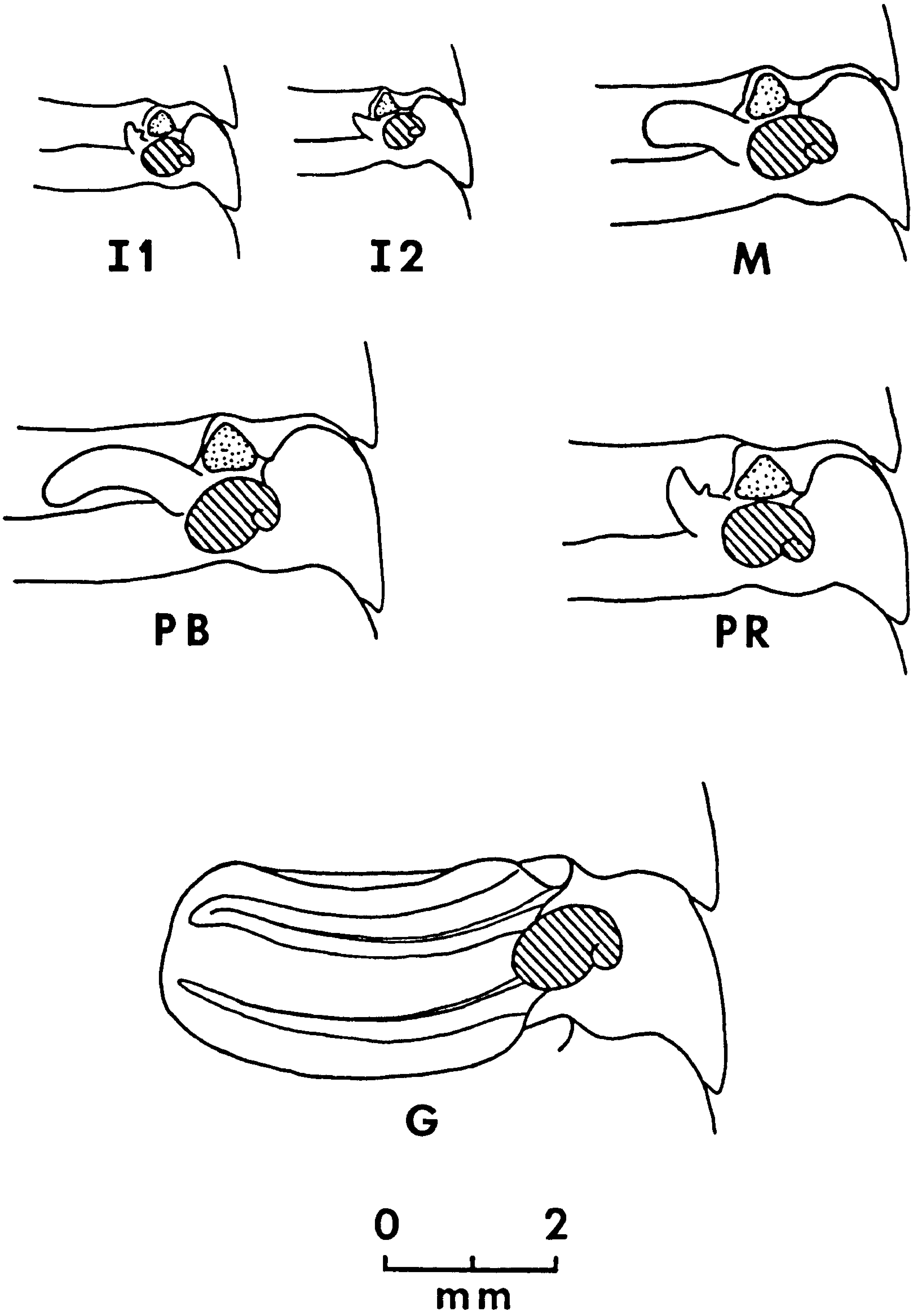
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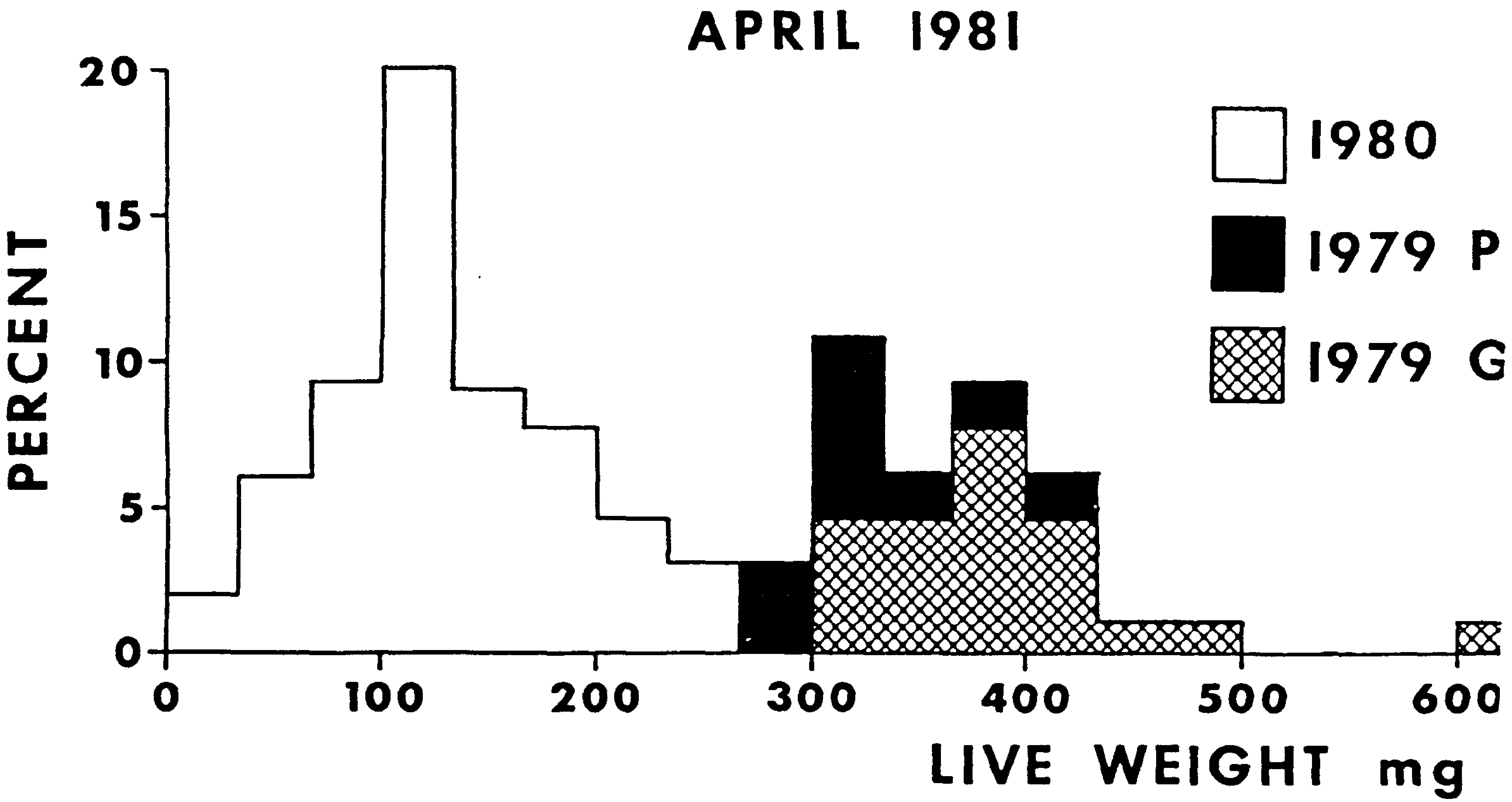
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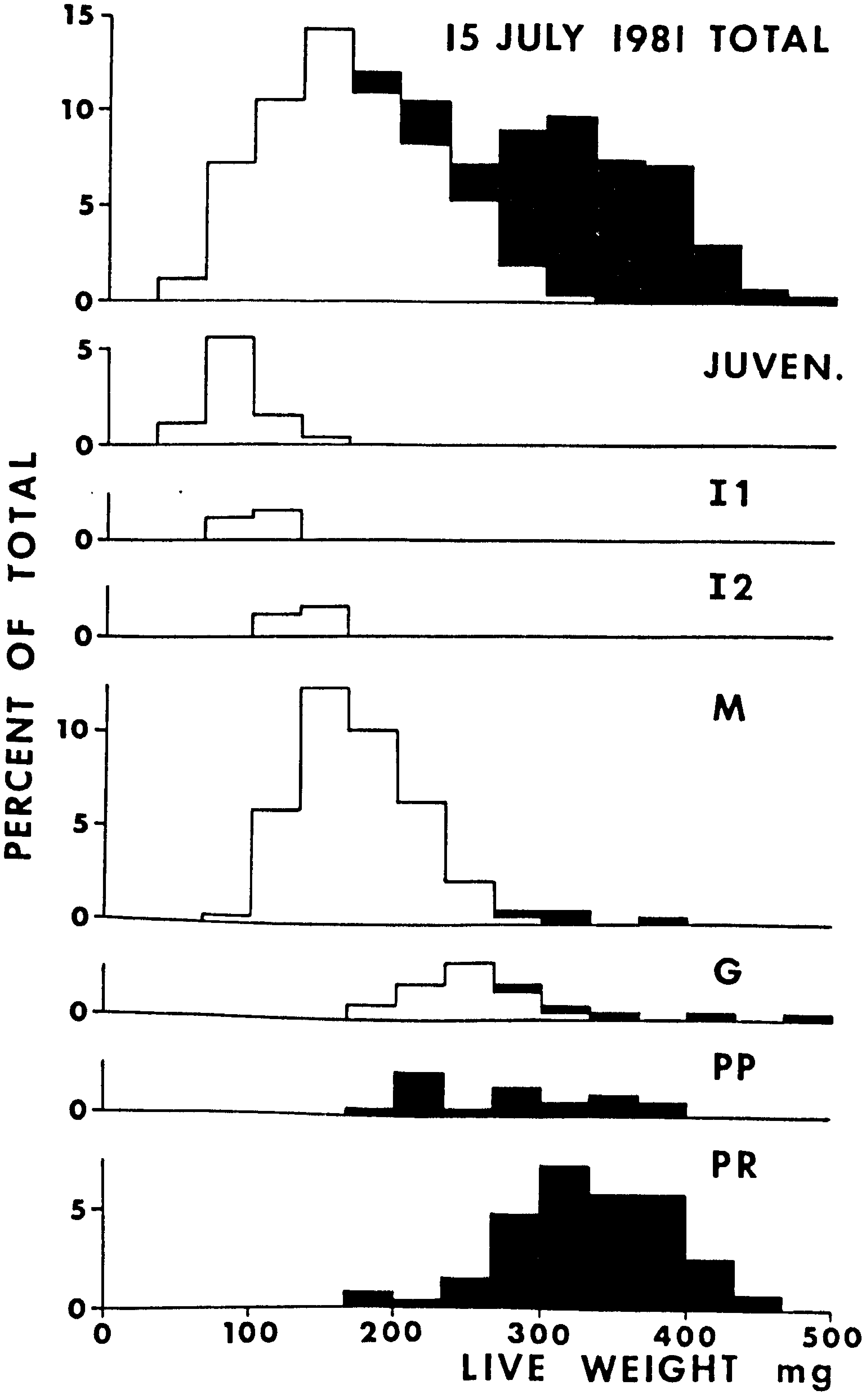
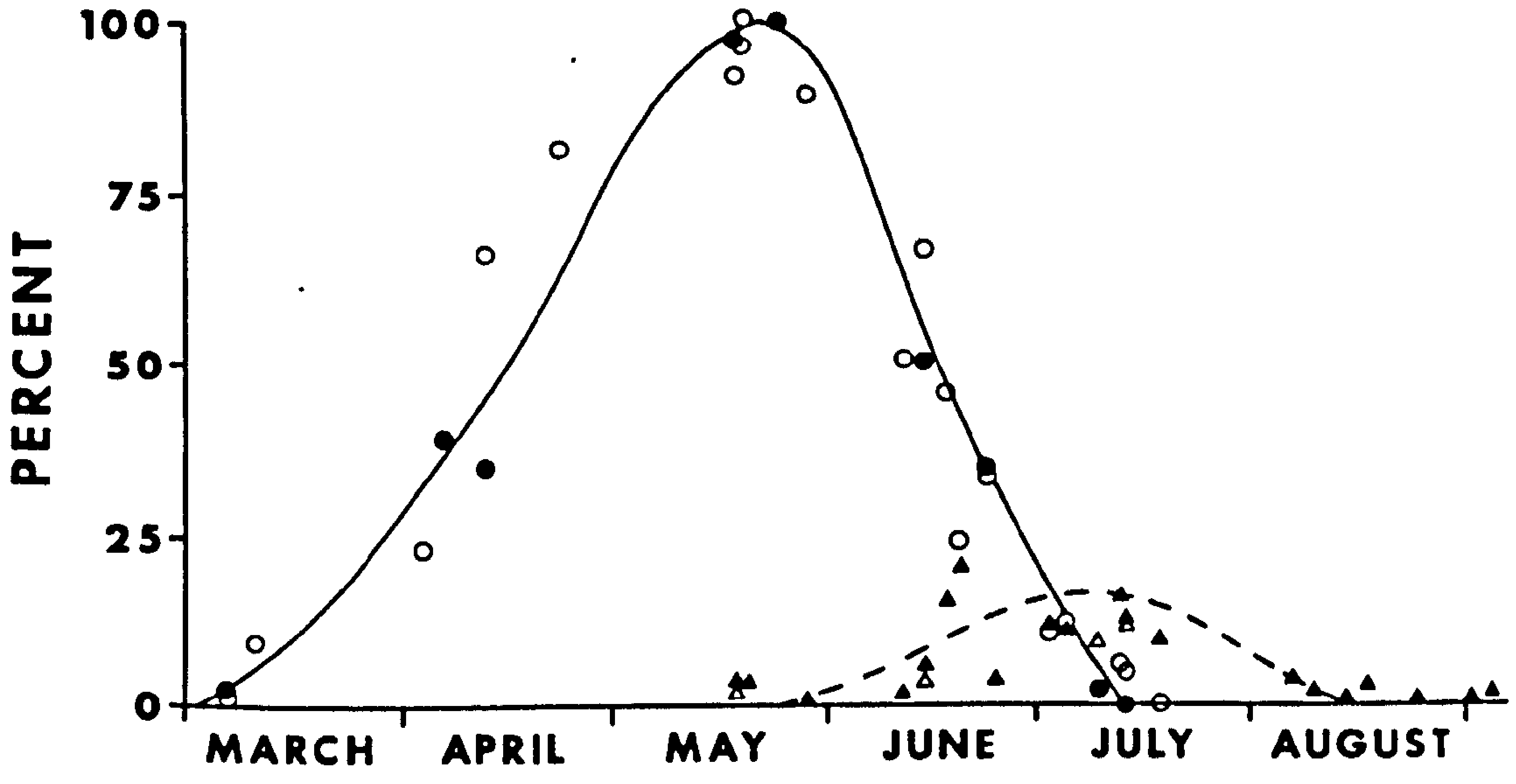
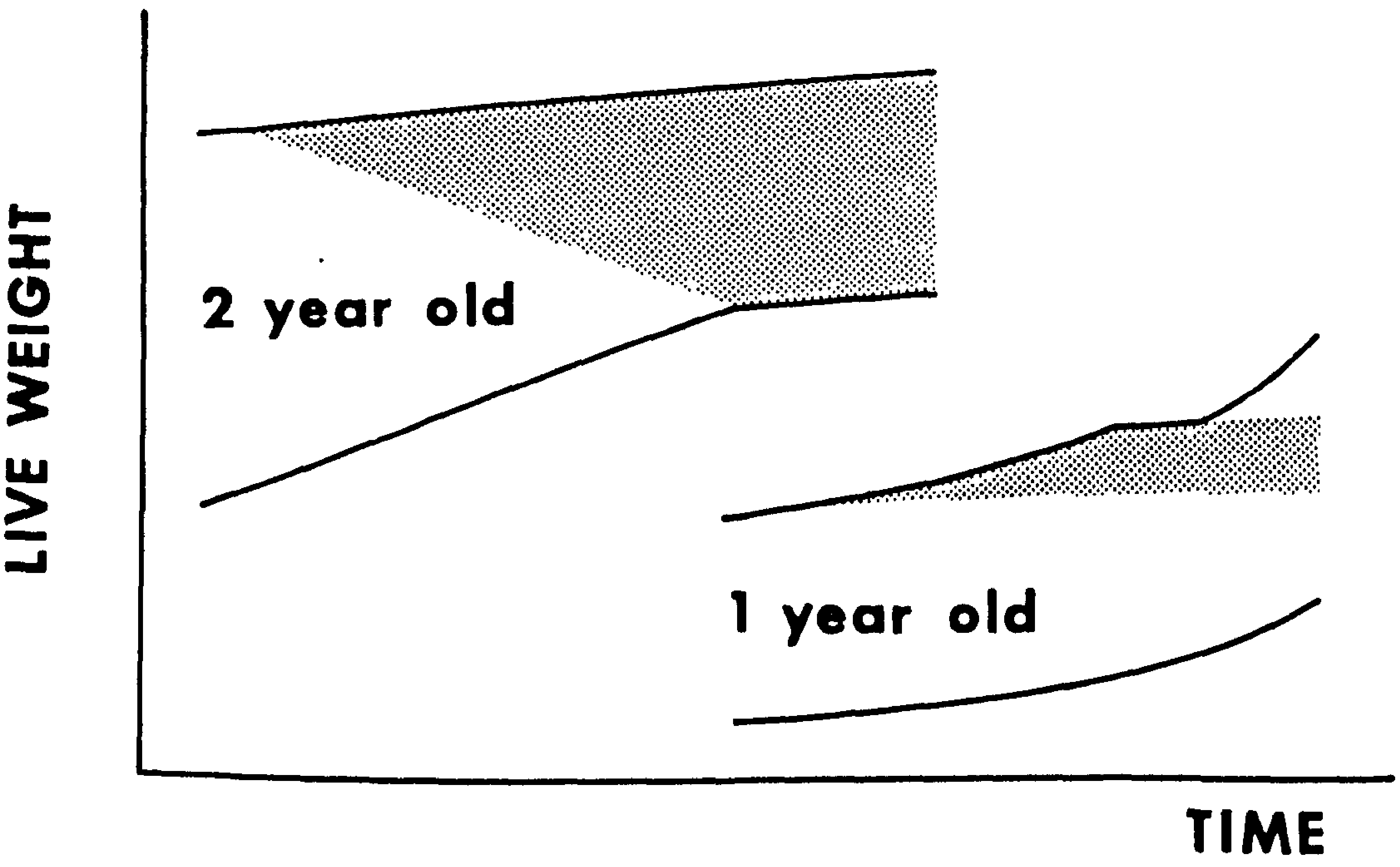
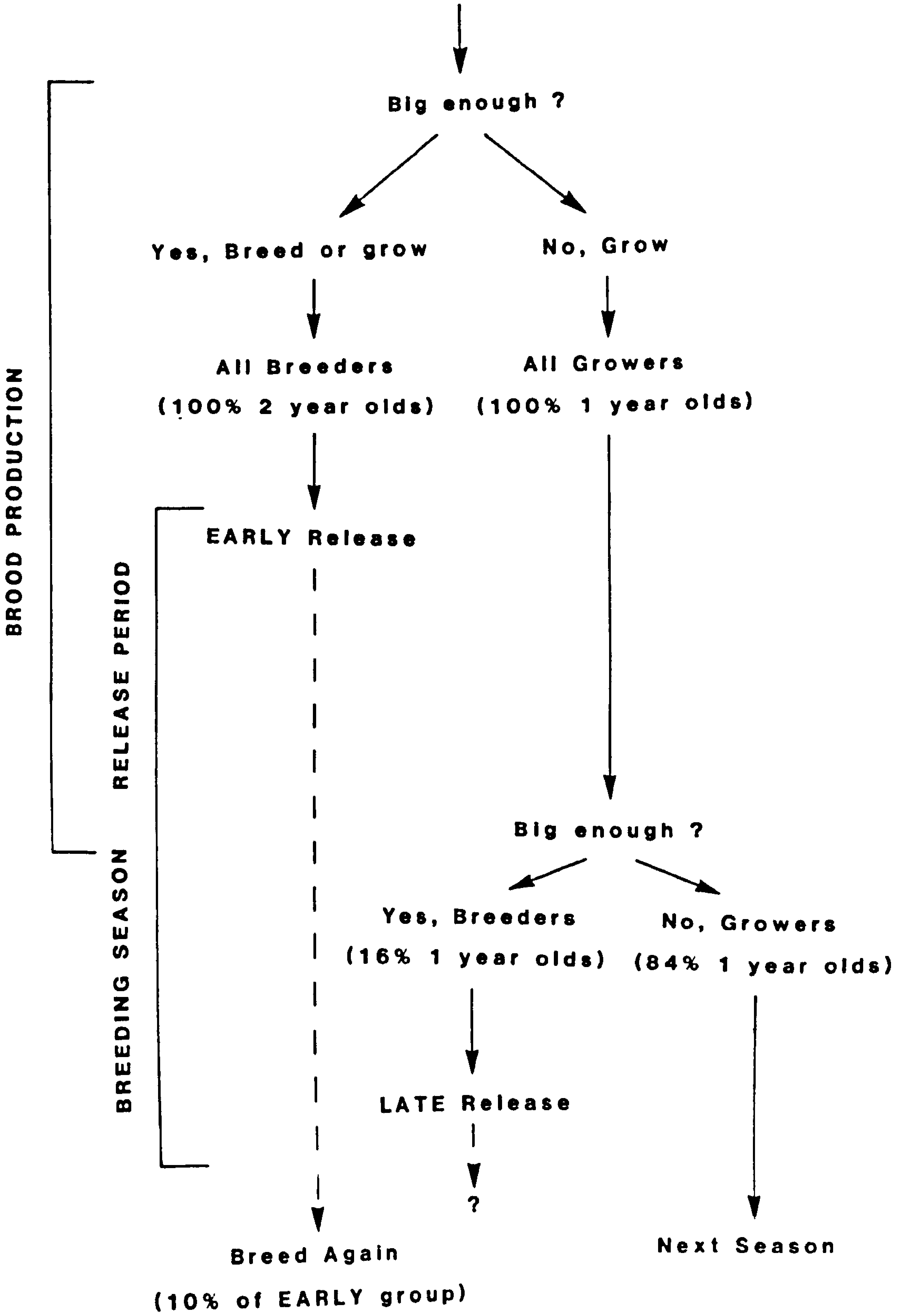
1979 P
1979 G


15 JULY 1981 TOTAL
JUVEN.
I1
I2
M
G
PP
PR
PERCENT OF TOTAL
15
10
5
0
0
100
200
300
400
500
LIVE WEIGHT mg


PERCENT
100
75
50
25
0
MARCH
APRIL
MAY
JUNE
JULY
AUGUST


LIVE WEIGHT
2 year old
1 year old
TIME


Big enough ?
Yes, Breed or grow
No, Grow
All Breeders
(100% 2 year olds)
All Growers
(100% 1 year olds)
EARLY Release
Big enough ?
Yes, Breeders
(16% 1 year olds)
No, Growers
(84% 1 year olds)
LATE Release
?
Breed Again
(10% of EARLY group)
Next Season
BROOD PRODUCTION
RELEASE PERIOD
BREEDING SEASON

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