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M. Sheader

Factors influencing egg size in the gammarid amphipod *Gammarus insensibilis*

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Abstract Developmental and seasonal changes in egg volume were examined in a population of the amphipod *Gammarus insensibilis* Stock occurring on the south coast of England, towards its northern limit of distribution. Results showed a marked increase in egg volume during development (2.9 times by Egg Stage V), resulting from water uptake and from the conversion of yolk reserves into structural elements. The maximum rate of increase coincides with the period of organ and limb development. At hatching, after initial rupture of the egg membrane by urosome spines, egg volume increases rapidly over a short period (15 to 20 min) by a further 30% (uptake rate 3.6×10^{-5} $mm^3 s^{-1}$), followed by a post-hatching decrease in juvenile volume. Increase in size at hatching is the result of drinking by embryos, although changes in body-wall permeability may contribute. Females carrying eggs in an advanced stage of development exhibit egg-collecting behaviour. This is seen as an adaptation to an increased likelihood of egg loss with increase in volume of the brood as hatching approaches. Seasonal changes in Stage I (early) egg size are marked in this species, with winter eggs as much as 60% greater in volume than summer eggs. Egg size is inversely related to the temperature during oocyte development. A simple model has been derived to account for the observed seasonal pattern in egg size. The consequences of seasonal variation in egg and juvenile size are considered.

Introduction

Amphipods are useful subjects for the study of reproductive biology and egg production in that the eggs are held by the female within a ventral brood pouch or marsupium during development and are therefore readily accessible for study. Information is available in the literature on aspects of the reproductive biology of many gammarid amphipods, chiefly littoral and shallow-water species, and a number of reviews have been written bringing together the published data and attempting to detect and interpret patterns (Steele and Steele 1975, 1991; Nelson 1980; Van Dolah and Bird 1980; Kolding and Fenchel 1981; Wildish 1982; Skadsheim 1984; Sainte-Marie 1991). Gammarid amphipod species exhibit diverse life-history strategies, allowing adaptation to a wide range of environments by variation in reproductive parameters such as egg size and number, the duration of embryonic development, the size of hatched young, and the body length of adults at maturity (Sheader 1983; Steele and Steele 1991). Although relationships between reproductive parameters are evident across the broad mass of gammarid species (Steele and Steele 1991), relatively few studies have considered the within-species variability of these parameters in any detail (Doyle and Hunte 1981 a, b; Sheader 1983). Such studies have demonstrated that temporal (seasonal) and spatial (latitudinal/geographic) changes in reproductive parameters can occur. These changes, although relatively small in comparison with the differences observed between species, nevertheless show that individual species can be reproductively flexible. In addition, such studies provide additional and essential information for the interpretation of the observed larger scale patterns described across the Gammaridea.

In the present study, factors influencing a single reproductive parameter, egg size, are considered. Many published studies on amphipod reproduction have used preserved material, which may be suitable for gross comparisons between species but is unsuitable for within-species studies since preservation techniques greatly affect egg size (Sheader and Chia 1970).

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M. Sheader
Department of Oceanography, University of Southampton,
Southampton SO17 1BJ, Hants, England

The species used in this study, *Gammarus insensibilis* Stock, breeds throughout the year at the study site, with peak reproductive activity in the warm summer months. Once mature, females produce a succession of broods. This type of life history subjects reproductive individuals to change in a wide range of environmental parameters during the course of a year. Species respond by exhibiting seasonal patterns in reproductive parameters (Sheader 1978, 1983), resulting from seasonal changes in energy budgets and evolutionary selective pressures optimising reproductive output.

The amphipod *Gammarus insensibilis* is recorded from the Black and Mediterranean Seas to the Atlantic coast of Europe, extending as far north as England (Stock 1967). The species is generally found sublittorally in sheltered brackish sites down to 15 m, although in the Mediterranean it can be found in fully marine conditions. In England, *G. insensibilis* is recorded from saline lagoons and ponds in central southern England and on the east coast as far north as Lincolnshire (Sheader and Sheader 1985, 1987). The English population studied is therefore towards the northern distributional limit of the species.

Materials and methods

Gammarus insensibilis Stock was collected monthly from Fort Gilkicker Lagoon at Gosport (Hampshire) on the south coast of England (see Sheader and Sheader 1985 for site description). The amphipod is common throughout the lagoon, and, as at other sites in England, it is associated with floating mats of the green filamentous alga *Chaetomorpha linum*, which forms the major component of its diet (Sheader and Sheader 1985, 1987; Bamber et al. 1992).

The amphipods were separated from the weed using a fine sieve (0.5 mm aperture), and on return to the laboratory eggs were removed from the marsupium of mature females (for the purposes of this study, all pre-hatching marsupial stages are referred to as eggs, and all ovary stages are considered as oocytes). All eggs in each brood were placed in seawater (salinity 34 psu), and their dimensions were measured (diameter of three axes: length, width and height) under a stereomicroscope. The live eggs were then staged using the system described by Sheader and Chia (1970), whereby early (newly fertilized) eggs are Stage I, and eggs close to hatching are Stage V. Egg volume (V) was calculated assuming their shape to be ellipsoidal. Females were fixed in buffered seawater formalin (10%) for several days before dissection to remove the ovaries and measure the oocytes. The body length of adults and juveniles was measured as the distance from the tip of the head to the distal end of the telson.

Adults and juveniles were maintained in the laboratory in temperature-controlled aerated seawater. The green alga *Chaetomorpha linum* was used as a food source. Marsupial eggs removed from females were maintained in gently moving temperature-controlled aerated seawater. Eggs were measured daily.

Results

Change in egg volume during embryonic development of *Gammarus insensibilis*

Once females are mature, eggs are produced at each moult. Males carry females in precopula for a relatively short period (~3 to 4 h at summer temperatures) and for a short time after sperm transfer. In the absence of males, females are able to delay moulting for up to 2 d (at 15 °C) and, if mating does not occur, the oocytes are resorbed following the moult.

After the female moults, the male places a bundle of spermatozoa around the opening of each of the two oviducts (sited at the base of Pereiopods 5). Shortly after sperm transfer, eggs are deposited in the marsupium, but at this stage they are retained in two membranous sacs, each produced by one of the two oviducal glands and representing the contents of a single ovary. These sacs remain attached to the oviducts. As the eggs are laid, the spermatozoa are activated and become distributed over the surface of each sac. Small pores in the sacs permit the sperm heads to pass through the membrane and to fertilize the eggs. The membranous sacs disintegrate within a few hours, and the eggs become distributed within the marsupium. It appears that the sacs serve to confine the eggs until fertilization has occurred.

The timing of egg development within the marsupium is temperature-dependent. Fig. 1 shows changes in the mean egg volume of a single brood of 84 eggs which developed in vitro at 15 °C. Fig. 1 excludes volume changes during the 30 min prior to hatching. During the first 6 d, egg volume increased slowly, but thereafter more rapidly as yolk reserves were converted into structural components (Sheader 1983). The increase in

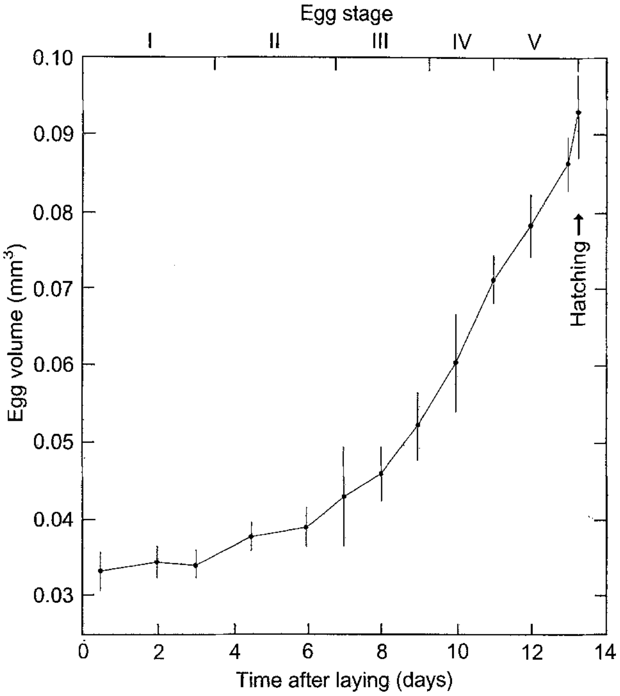

Fig. 1 *Gammarus insensibilis*. Change in mean egg volume during development of a single brood ($n = 84$), relative to time and egg stage (temperature = 15 °C)

egg volume during development (excluding changes during the immediate pre-hatching period) was calculated as 178% for this brood [mean value for all broods studied ($n = 12$) 188.3% ± 12.7% (SD)].

Egg size was found to vary seasonally (see Fig. 4), but in any month, increase in egg volume during development remained at ~190%, irrespective of season or temperature. As hatching approaches therefore, the brood volume is ~2.9 times the initial Stage I brood volume.

Eggs within a single brood developed almost synchronously, all eggs hatching within a period of 3 to 4 h. Also, single broods showed little variation in egg size; Stage I broods ($n = 93$) had a mean range in egg volume of ± 7.74%. The between-brood variation in Stage I egg size range was greater than the within-brood range on each sampling occasion; in monthly samples, between-brood ranges were recorded as low as ± 8.9% ($n = 17$), and as high as ± 17.5 ($n = 14$).

In culture, individual females at a given temperature showed little variation in Stage I egg volume between successive broods (mean Stage I egg size did not differ significantly between broods). However, at a given temperature, there were consistent differences in mean Stage I egg volume between certain females, probably the result of genetic variation within the population. As is the usual case for amphipods, egg size and female size were not correlated (Sheader 1977, 1978, 1983).

Changes in volume at hatching

At Stage V, the embryo possesses the full complement of segmented limbs, the heart is beating and the eyes are pigmented. The embryo is curled ventrally within the egg so that the urosome is close to the head. During the last hour of this stage, embryonic activity increases. Changes during the final minutes of a single Stage V egg are shown in Fig. 2. The changes depicted are typical and representative of all hatching eggs observed in the study, although the exact timing of events is temperature-dependent.

Increased movement of the abdomen causes hatching spines on the urosome (Le Roux 1933) to pierce the egg membranes. Some 10 min later, the telson and uropods extend through the breach, and repeated flexion of the abdomen causes the hole to enlarge. The urosome withdraws into the egg membranes and the egg begins to swell rapidly, increasing by 30.3% in volume over 13 min (an uptake of 0.041 mm^3, at a mean rate of 5.26×10^{-5} $mm^3 s^{-1}$). During this period of rapid increase the head is sited close to the hole in the egg membranes, and movements of the midgut, foregut and mouthparts suggest that this rapid size increase is achieved, at least in part, by drinking. In the final stages of hatching, the head emerges from the egg membranes, followed by the pereion, pleon and finally the urosome. The egg membranes remain attached to the urosome of the newly hatched juvenile for some minutes (or hours) until they are consumed by the juvenile. At all stages of development, up to and including hatching, the embryo completely fills the egg membranes which, as hatching approaches, are stretched and under tension. After hatching, the egg membranes contract.

Stage I eggs differ in size according to season and temperature, and this in turn controls the size of Stage V eggs. Fig. 3 shows changes at hatching in a brood of smaller summer eggs ($n = 8$). The volume increase after the egg membrane is broken is similar to that seen in Fig. 2 (volume increase = 30.7%) and the

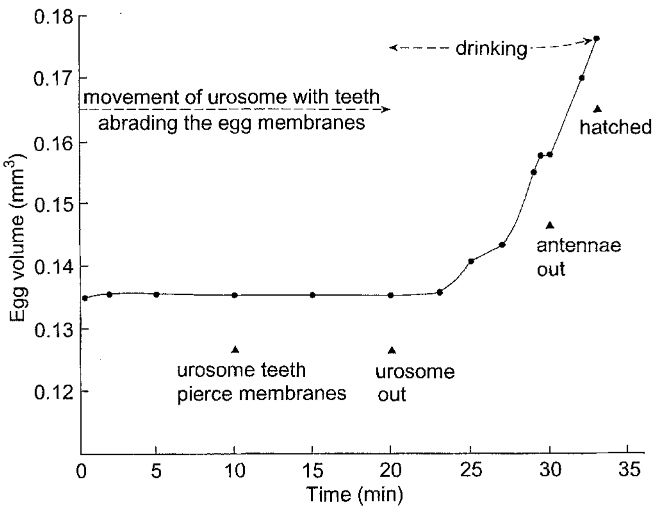

Fig. 2 *Gammarus insensibilis*. Change in volume of a single egg during period immediately prior to hatching. Main events during hatching are noted

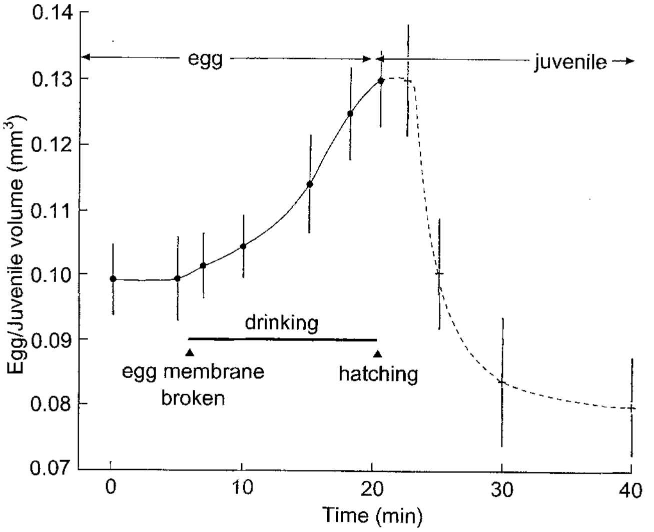

Fig. 3 *Gammarus insensibilis*. Change in egg and juvenile volume (means ± SD) of a brood ($n = 8$) immediately prior to and after hatching, respectively. Main events during hatching are noted

rate of volume increase (3.27×10^{-5} mm^3 s^{-1}) is of the same order of magnitude. Similar values were recorded for changes at hatching for egg sizes over the seasonal range. By measuring the pereion length of embryos just prior to hatching (L_t) and relating this to changes in pereion length post-hatching (L_{t+1}), an indication of juvenile volume (JV) change was determined [$JV = (L_{t+1} \times E_t)\ L_t$, where E_t is the egg volume just prior to hatching/pereion length^3 just prior to hatching] (Fig. 3). Juveniles decrease in size rapidly after hatching, after 20 min achieving a body volume equivalent to ~80% of their pre-hatching Stage V volume. The mechanism controlling this rapid loss of volume by newly-hatched juveniles was not determined.

Seasonal changes in egg volume

Mean Stage I egg volume was determined for females collected in monthly samples between October 1980 and August 1982. Stage I egg volume was measured to allow between-month comparisons, since eggs increase in size considerably during development but show relatively little size increase during Stage I. Also, the dimensions of recently produced early eggs are more likely to relate to ambient environmental parameters than would the dimensions of older later-stage eggs.

The results (Fig. 4) show a clear seasonal cycle in Stage I egg size, with small eggs in the warmer summer months and large eggs in winter. The maximum winter value of egg volume (~0.054 mm^3) is ~ 60% greater than the minimum summer value (0.034 mm^3). Midday temperature values when sampling are also given in Fig. 4, and mirror the seasonal pattern found for egg volume. The shallow lagoon shows marked diurnal fluctuations in temperature, and the midday values are therefore only a rough guide to environmental temperature.

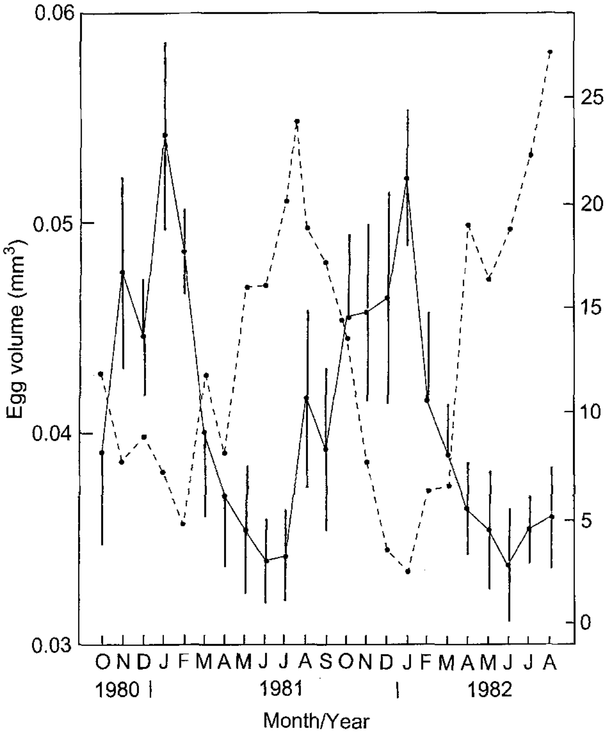

Fig. 4 *Gammarus insensibilis*. Seasonal cycles in temperature (*dashed line*) and egg volume (*continuous line*) (means ± SD)

To test the hypothesis that temperature controls egg size, 74 females were maintained in the laboratory over at least one complete intermoult period and allowed to pair, and the resulting Stage I eggs were measured. Each female was maintained at a temperature within the range 2.5 to 27.0 °C, and food was provided in excess of requirements. Stage I egg volume ($\log_{10}$ volume) and temperature ($\log_{10}$ temperature) were significantly negatively correlated ($r = -0.849$, $df = 73$, $p < 0.001$), with a predicted Stage I volume of 0.049 mm^3 at the minimum winter temperature recorded (2.5 °C), and a predicted Stage I volume of 0.036 mm^3 at the maximum summer temperature (27.0 °C).

The observed seasonal differences in egg size are the result of differences in the quantity of yolk laid down in the egg, and this in turn is reflected in the size of marsupial juveniles. Juveniles hatched from eggs produced by females maintained over the temperature range in the above experiment show that Stage I egg volume and juvenile length are significantly positively correlated ($r = 0.7235$, $df = 34$, $p < 0.01$). Juvenile length (L, mm) can be related to Stage I egg volume (V, mm^3) by the following equation:

$$L = 9.336\, V^{0.333} - 1.614\,.$$

Winter eggs of 0.049 mm^3 and summer eggs of 0.036 mm^3 would give rise to juveniles of 1.81 and 1.47 mm, respectively. The difference between these lengths is of the same order as observed growth-factor values, and is equivalent to the expected change in body length between juvenile instars. This may therefore give rise to an additional juvenile instar for summer-produced eggs.

Control of egg volume

Egg volume in *Gammarus insensibilis* is temperature-controlled both in the laboratory and in the field. This gives rise to a clear seasonal pattern in egg size in the population studied (Fig. 4). A simple model is put forward below to explain the observed relationship between temperature and egg volume.

In those amphipods where oogenesis has been studied, oocytes have been shown to develop over two intermoult periods (Hartnoll and Smith 1978; Sheader 1983), and the same pattern was found to occur in

Gammarus insensibilis (Fig. 5). During the first intermoult, the oocytes grow very little, but during the latter half of the second intermoult period growth increases markedly as yolk is deposited within the oocytes. Rapid oocyte growth continues up to the point where the oocytes are deposited into the marsupium for fertilisation. As oocytes are growing rapidly up to the point of laying, it is suggested that any factor acting to delay or precipitate an early moult would increase or decrease oocyte size, respectively (Fig. 5).

This hypothesis was tested in the laboratory by manipulating the time of the moult. In *Gammarus insensibilis*, the male carries the female in precopula for a relatively short period (~4 h at 15to 20 °C). If newly formed pairs are separated and the females isolated, each female is able to delay moulting for up to 2 d. An experiment was carried out using females raised in the laboratory from a single brood (thus reducing experimental variability in egg size resulting from genetic differences between females). The experiment was conducted at a temperature of 15 °C. Males and females in precopula were separated. Males were returned to females after 0, 0.5, 1.0, 1.5 or 2.0 d of initial pairing. Eggs were produced by females in the first three experiments (0 to 1.0 d), but not in the last two experiments (1.5 and 2.0 d). Marsupial juveniles resulting from these crosses were measured: Experiment I, pairing after 0 d - juvenile length 1.48 mm (SD ± 0.03) ($n = 125$); Experiment II, pairing after 0.5 d – juvenile length 1.52 mm (SD ± 0.03) ($n = 80$); Experiment III, pairing after 1.0 d – 1.58 mm (SD ± 0.05) ($n = 52$). Using the Fisher–Behrens test to compare data from the three experiments, differences in means between Experiments I and II, between II and III and between I and III were found to be significant at the 0.1% level ($P < 0.001$). Juvenile length therefore changed significantly between Experiments I, II and III, with an observed trend of increase in juvenile (and hence egg) size with progressive delay in moulting. The results therefore support the hypothesis that intermoult length determines egg size.

Assuming therefore that the length of the intermoult period is important in determining the size of oocytes, a simple model can be used to explain the observed relationship between temperature and egg volume (Fig. 6). As with other gammarids studied, the intermoult period is temperature-dependent. The model proposed assumes that oocyte growth and the moult cycle vary in their degree of synchrony at different points on the temperature scale. At low temperature, mean Stage I egg volume (for this population = 0.04 mm^3) is achieved well before the moult, allowing the oocytes additional time for yolk deposition, and therefore giving rise to large eggs. At high temperature, the moult occurs before the oocytes reach mean Stage I egg volume, resulting in the production of small eggs. This proposed model accounts for the observed seasonal changes in Stage I egg volume, with temperature as the controlling parameter.

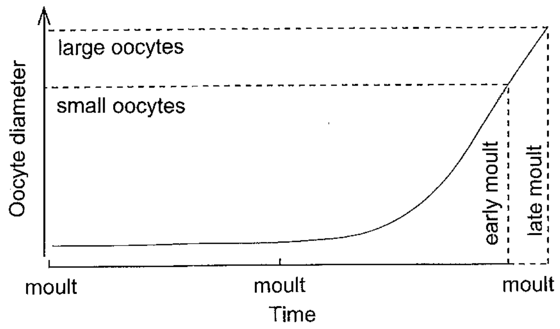

Fig. 5 *Gammarus insensibilis*. Diagrammatic representation of oocyte growth, indicating process by which timing of moult may determine Stage I egg size

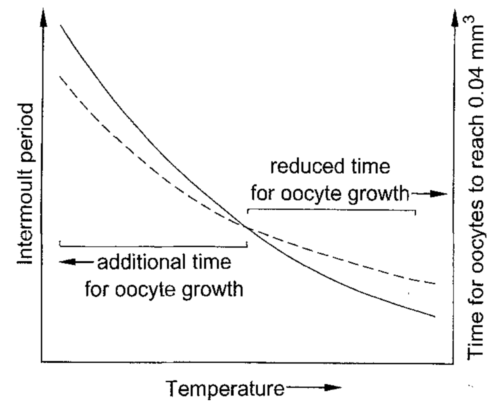

Fig. 6 *Gammarus insensibilis*. Model explaining observed changes in egg size with temperature [*Continuous line* intermoult period; *dashed line* time for oocytes to reach 0.04 mm^3 (mean egg diameter)]

Discussion

Most studies dealing with reproduction in amphipods utilise preserved material, and whilst this is generally acceptable for determining egg numbers per brood, it can give rise to spurious results if egg dimensions are required (Sheader and Chia 1970; Sheader 1983). Preserved material provides egg-size data which are sufficient for between-species comparisons, but only if preservation/fixation techniques are standardised (Steele and Steele 1991). However, within-species variation in egg volume occurs over a smaller size range than does between-species variation, and requires the use of living material. The use of living eggs also provides a realistic picture of developmental and seasonal changes, which can be related more readily to environmental and life-history parameters (Sheader 1983).

The eggs of amphipods generally increase in size during development. In *Gammarus insensibilis*, late (Stage V) eggs are ~2.9 times greater in volume than early eggs (Stage I). The data (Sheader unpublished) for a number of amphipods (gammarids and hyperiids) given in Fig. 7 indicate that the percentage increase in size during development is, to some extent, related to Stage I egg volume. At 0.19 mm diam, the eggs of *Eupronoe* sp. are the smallest amphipod eggs recorded, and hardly increase in size (by ~10%) during development. *Eupronoe*, *Phronima* and *Streetsia* are hyperiid genera in which the eggs hatch as "larvae", with abdominal appendages reduced or absent, whereas the hyperiid genera *Themisto* and *Primno* and all gammarids have direct development, hatching with the full complement of appendages. Eggs of gammarids and of hyperiid species with direct development increase in volume by 140 to 200%. Although there are between-species differences within this group, there is no apparent relationship between egg size and the percentage increase during development. However, within the hyperiids, the few results suggest that egg volume and the percentage increase are related. The results also suggest that, within certain gammaridean species, egg size and developmental increase may be correlated.

An increase in egg volume during development is a common feature of many crustacean eggs (Davis 1981). Gammarid eggs generally show an increase in volume of the order of 140 to 200% during development (Sheader and Chia 1970; Sheader 1978, 1983; Moore 1981). Although few studies have been conducted, it seems that this change in volume is the result of water uptake (Sheader and Chia 1970; Bregazzi 1973) together with the conversion of yolk reserves into structural components (Sheader 1983). In *Gammarus insensibilis*, the maximum volume increase occurred during Egg Stages III to V, and was associated with the formation of the major body regions (head, pereon, pleon and urus) and with the development of major organs and appendages.

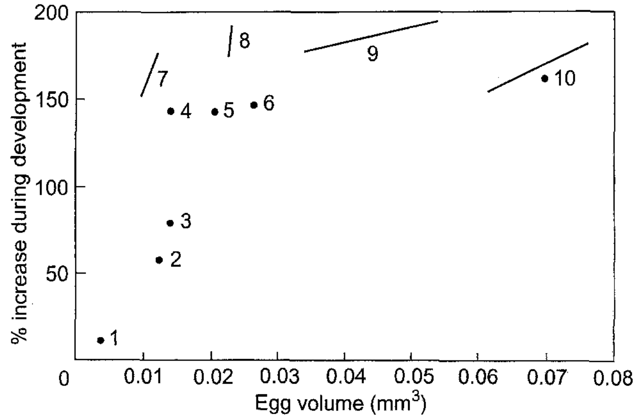

Fig. 7 Relationship between egg volume and percentage increase in volume during development of gammarids and hyperiids (*1, Eupronoe* sp.; *2, Phronima sedentaria*; *3, Streetsia challengeri*; *4, Primno johnsoni*; *5, Themisto compressa* (Biscay); *6, Ampelisca tenuicornis*; *7, Corophium insidiosum*; *8, T. compressa* (North Sea); *9, Gammarus insensibilis*; *10, G. duebeni*)

Although a few studies have followed changes in egg volume during amphipod development, none have described volume changes associated with the hatching process. In crustaceans, the egg is enclosed by three membranes, which in most groups (but not the Amphipoda) are readily distinct. Hatching in many crustacean groups seems to occur by a change in the permeability of the inner membrane, causing the outer and inner membranes to split, although the exact nature of the hatching process varies greatly (Davis 1981). In some crustaceans, including the Amphipoda, breaking of the membranes is, in part, mechanical (Sheader and Chia 1970; Fish 1975; Sheader 1977; Fish and Mills 1979). In *Gammarus insensibilis*, hatching spines on the urosome are used to pierce the membranes, and this is followed by a rapid increase in egg volume of ~30%, brought about by drinking and possibly by changes in permeability of the embryo. This is followed by a post-hatching decrease in body size of the newly hatched juvenile. Drinking has been observed in *G. obtusatus* embryos (Sheader and Chia 1970: referred to therein as *Marinogammarus obtusatus*), and a similar rapid increase in egg volume (20 to 40%) just before hatching has been reported for the brachyuran *Rhithropanopeus harrisi*, although in this species the membranes are not pierced mechanically prior to the increase (Davis 1981).

Change in the total volume of the brood during development and hatching has implications for the brooding female. In *Gammarus insensibilis*, the marsupium must be capable of retaining the brood during development, as the brood volume increases to 2.9 times its Stage I volume. Further, at hatching there is a sudden increase in volume to 3.8 times the Stage I brood volume by Stage V. In laboratory experiments done during the present study, eggs (of any stage) presented to females carrying Stage V eggs in the marsupium were quickly collected and pushed into the marsupium using Pereiopods 1 and 2. Females carrying other egg stages (I to IV) do not show egg-collecting behaviour, which seems to be limited to the critical period of maximum brood volume when accidental spillage of eggs from the marsupium is most likely. During the productive summer months, brood volumes are close to the limits imposed by marsupium morphology, and, in laboratory experiments at this time the collection of relatively few eggs by females carrying Stage V eggs results in a simultaneous loss of eggs from the posterior region of the marsupium. It would be expected that the many hyperiid species, producing small eggs with relatively little volume increase during development, would be able to brood a relatively greater Stage I brood volume than would gammarids, an advantage to species with semi-parasitic life histories necessitating an increased reproductive output.

Although individual females showed little variation in egg size within a brood, there was a greater range of Stage I egg sizes apparent within groups of females collected together in any month. These differences between females may be the result of genetic variation within the population, as occurs in *Gammarus lawrencianus* (Doyle and Hunte 1981a,b). Differences between females might also be generated by any factors acting to increase or decrease the intermoult period. A semilunar rhythm of egg production has been recorded for a range of littoral and shallow-water amphipod species, although the degree of synchrony is not always high and varies between species (Fish 1975; Sheader 1978, 1983; Fish and Mills 1979; Moore 1981). *G. insensibilis* exhibits synchronous egg production, especially during the summer months (Sheader unpublished observation) and it is suggested that this is achieved by females adjusting the length of their intermoult so that the population approaches (although never fully achieves) synchrony (Sheader 1983), thus potentially causing variation in egg size between females whose reproductive cycles are not perfectly synchronised.

Seasonal changes in egg volume are evident in *Gammarus insensibilis* (winter eggs as much as 60% greater in volume than summer eggs), but are not as great in *G. duebeni* (winter eggs 24% greater in volume than summer eggs: Fig. 7). The population of *G. insensibilis* studied is towards the northern limit of its distributional range and therefore experiences a broader temperature range relative to its distributional centre in the Mediterranean. Conversely, *G. duebeni* in the south of England is close to its southern limit, and the population experiences a reduced annual temperature range relative to its centre of distribution.

The model put forward to explain the observed variation in egg volume in relation to season and temperature was tested by manipulating intermoult length, and the results of these experiments supported the hypothesis. Egg size appears to be controlled by differences in the relative growth rates of the oocytes and soma at different points on the seasonal temperature scale. As temperature influences other reproductive parameters of this population, the highest rates of egg output occur in the warmest summer months and are associated with the production of small eggs giving rise to small juveniles. In winter, egg output is low and eggs/juveniles are large. A similar pattern has been recorded for *Gammarus duebeni* (Sheader 1983). Large young are often considered to have a better chance of survival than small young (Thorson 1959; Skadsheim 1984; Rabalais and Gore 1985), although there is no direct evidence to support this within the Amphipoda (Steele and Steele 1991). Indirect evidence from population size-frequency data of many amphipod species suggests that mortality is highest at juvenile stages, falling as the amphipods grow. Although there is relatively little published data on seasonal changes in egg size of gammarids, the pattern of large winter and small summer eggs seems to be a feature of many littoral and shallow-water species that breed over the greater part of the year. For this pattern to persist in a number of species, it might be expected that similar selection pressures are involved. Large eggs, requiring a longer development period, may be a means of extending the period of marsupial protection in winter. Large juveniles may have reduced mortality relative to small juveniles in winter; in *G. insensibilis*, winter juveniles may achieve a size equivalent to the second instar of summer juveniles. Juvenile size, together with temperature during growth, will influence the number of instars and the time taken for individuals to reach maturity.

In winter or early spring, populations of many short-lived (~1 yr or less) gammarid amphipods are at their lowest abundance. The adult stock usually continues breeding into spring and early summer, and juveniles produced from winter eggs often begin to breed as food resources become plentiful in early summer. The large winter eggs are therefore required to have relatively low mortality, and serve to boost the small overwintered adult generation. Small summer eggs are produced in mid- to late summer when egg-production rates are at their highest. Females at this time grow rapidly, mature at a small body size and produce a rapid succession of broods. As temperatures fall, the rate of egg production declines and population numbers fall to winter levels. The observed seasonal variation in egg volume, common to many species, is probably related to seasonal patterns of size-dependent growth and mortality. A fuller understanding of reproductive strategies can only be achieved by detailed autecological studies of gammarid populations, including not only reproductive parameters but also measures of size-specific growth and mortality rates.

References

Bamber RN, Batten SD, Sheader M, Bridgwater ND (1992) On the ecology of brackish lagoons in Great Britain. Aquat Conserv: marine Freshwat Ecosystems 2: 65–94

Bregazzi PK (1973) Embryological development in *Tryphosella kergueleni* (Miers) and *Cheirimedon femoratus* (Pfeffer), (Crustacea: Amphipoda). Br Antarct Surv Bull 32: 63–74

Davis CC (1981) Mechanisms of hatching in aquatic invertebrate eggs. II. Oceanogr mar Biol A Rev 19: 95–123

Doyle RW, Hunte W (1981a) Genetic changes in "fitness" and yield in a crustacean population in a controlled environment. J exp mar Biol Ecol 52: 147–156

Doyle RW, Hunte W (1981b) Demography of an estuarine amphipod (*Gammarus lawrencianus*) experimentally selected for high "r": A model of the genetic effects of environmental change. Can J Fish aquat Sciences 28: 1120–1127

Fish JD (1975) Development, hatching and brood size in *Bathyporeia pilosa* and *B. pelagica* (Crustacea: Amphipoda). J mar biol Ass UK 55: 357–368

Fish JD, Mills A (1979) The reproductive biology of *Corophium volutator* and *C. arenarium* (Crustacea: Amphipoda). J mar biol Ass UK 59: 355–368

Hartnoll RG, Smith SM (1978) Pair formation and the reproductive cycle in *Gammarus duebeni*. J nat Hist 12: 501–511

Kolding S, Fenchel TM (1981) Patterns of reproduction in different populations of five species of the amphipod genus *Gammarus*. Oikos 37: 167–172

Le Roux ML (1933) Recherches sur la sexualite des gammariens. Bull biol Fr Belg 16: 1–138

Moore PG (1981) The life-histories of the amphipods *Lembos websteri* Bate and *Corophium bonnellii* Milne Edwards in kelp holdfasts. J exp mar Biol Ecol 49: 1–50

Nelson WG (1980) Reproductive patterns of gammaridean amphipods. Sarsia 65: 61–71

Rabalais NN, Gore RH (1985) Abbreviated development in decapods. In: Wenner AM (ed) Larval growth. A.A. Balkema, Rotterdam, pp 67–127 (Crustacean Issues)

Sainte-Marie B (1991) A review of the reproductive bionomics of aquatic gammaridean amphipods: variation of life history traits with latitude, depth, salinity and superfamily. Hydrobiologia 223: 189–227

Sheader M (1977) Breeding and marsupial development in laboratory-maintained *Parathemisto gaudichaudi* (Guerin) (Amphipoda). J mar biol Ass UK 57: 943–954

Sheader M (1978) Distribution and reproductive biology of *Corophium insidiosum* (Amphipoda) on the north-east coast of England. J mar biol Ass UK 58: 585–596

Sheader M (1983) The reproductive biology and ecology of *Gammarus duebeni* (Crustacea: Amphipoda) in southern England. J mar biol Ass UK 63: 517–540

Sheader M, Chia F-S (1970) Development, fecundity and brooding behaviour of the amphipod *Marinogammarus obtusatus*. J mar biol Ass UK 50: 1079–1099

Sheader M, Sheader AL (1985) New distribution records for *Gammarus insensibilis* Stock, 1966, in Britain. Crustaceana 49: 101–105

Sheader M, Sheader AL (1987) The distribution of the lagoonal amphipod, *Gammarus insensibilis* Stock, in England. Porcupine Newsl, Edinburgh 3: 220–223

Skadsheim A (1984) Coexistence and reproductive adaptations of amphipods: the role of environmental heterogeneity. Oikos 43: 94–103

Steele DH, Steele VJ (1975) The biology of *Gammarus* (Crustacea, Amphipoda) in the northwestern Atlantic. XI. Comparison and discussion. Can J Zool 53: 1116–1126

Steele DH, Steele VJ (1991) Morphological and environmental restraints on egg production in amphipods. In: Wenner A, Kuris A (eds) Crustacean egg production. A.A. Balkema, Rotterdam, pp 157–169 (Crustacean Issues 7)

Stock JH (1967) A revision of the European species of the *Gammarus locusta*-group. Zool Verh, Leiden 90: 1–56

Thorson G (1959) Reproductive and larval ecology of marine bottom invertebrates. Biol Rev 25: 1–45

Van Dolah RF, Bird E (1980) A comparison of reproductive patterns in epifaunal and infaunal gammaridean amphipods. Estuar cstl mar Sci 11: 593–604

Wildish DJ (1982) Evolutionary ecology of reproduction in gammaridean Amphipoda. Int J Invert Reprod 5: 1–19