

REPRODUCTION IN *GAMMARUS* (CRUSTACEA, AMPHIPODA): FEMALE STRATEGIES

DAVID W. SUTCLIFFE

*(Dr D. W. Sutcliffe, c/o Freshwater Biological Association,
The Ferry House, Far Sawrey, Ambleside, Cumbria LA22 0LP, England)*

Introduction

Although a "hen" and its egg are two completely separate entities, each has a profound influence on the development of the other. The size *of* the hen, and her general nutritional state, determine (partly) the size and nutritional content of her egg(s). This in turn determines (partly) the size *of* the hatchling, its subsequent development and growth to sexual maturity and, possibly, the size of its own egg(s). These interactions are sometimes overtly noticeable, as in the production of ephippial eggs by certain Cladocera, but mostly they involve small, subtle changes that may occur unnoticed unless carefully looked for. Detailed research on some saltwater species of *Gammarus*, examined in this review, has revealed seasonal and other changes in the sizes of eggs laid in successive clutches, altering the "reproductive effort" that is a central part of life-history strategies and variation in fecundity within and between species. My aim here is to review the literature on *Gammarus* and draw attention to some gaps in our knowledge of freshwater species. The subject is somewhat complex, and it may be helpful to introduce below some principal points and put them briefly into perspective for the general reader. Sainte-Marie (1991) reviews reproduction in a wider spectrum of gammaridean amphipods (most of them brackish-marine) and Southwood (1988) examines general concepts relating particular life-history strategies of plants and animals to characteristics of the habitat.

This review examines how *Gammarus* allocates its internal resources when producing eggs. There is an extensive literature on the fecundity (i.e. numbers of eggs per brood) of freshwater species but almost nothing is known about the natural counterpart of fecundity, i.e. the sizes (volume and mass) and energy contents *of* the eggs. More is known for saltwater species, in which the mean number of eggs per brood is inversely proportional to mean egg size and directly proportional to the female's body size.

The partitioning of resources in egg-yolk between the numbers of eggs and their sizes at ovulation, termed "reproductive effort", is a variable reproductive strategy that is exploited in several ways by saltwater species and is expressed in the number of broods and generations

produced annually. Most of the common species have breeding seasons lasting for some 6-10 months of the year. Except in far-northern latitudes, more than one generation of sexually mature females is usually produced, each having several broods of young. In some populations of some species, breeding (i.e. precopula, copulation and fertilisation of eggs) occurs throughout the year. Nevertheless, within the breeding season or year the proportions of ovigerous females that are present each month in local populations vary considerably. Normally one or more peak periods of breeding occur at times which may vary according to species, locality and type of habitat but, in general, breeding markedly increases during the late winter and spring. This anticipates an increased supply of food for the large numbers of young that hatch in spring and early summer.

Breeding activity is also concentrated into recognisable periods by the occurrence of a resting period in the reproductive cycle, when the females stop ovulating (see Sutcliffe 1992). Evidence from saltwater species indicates that *Gammarus* readily adapts its basic life cycle to accord with local environmental conditions, especially in relation to temperature, salinity, the peak availability of food, and also to reduce interspecific competition between coexisting species. However, the annual resting period appears to be induced by changing daylengths and this restricts the total number of broods produced in a year.

As before (Sutcliffe 1992), specific names only are used in the following text. Text-figures have been redrawn and modified from sources acknowledged in the text.

Simple theoretical aspects of egg size, numbers and reproductive effort

Before laying a clutch of eggs, the female accumulates a store of precursor materials that will be used to form the egg-yolk. These materials (proteins, carbohydrates and fats) are moved into the developing oocytes during vitellogenesis, shortly before ovulation. The total amount of egg-yolk deposited in a clutch of eggs represents the female's "reproductive effort" for that particular brood.

Options for partitioning reproductive effort per brood

From a given amount of egg-yolk accumulated in time f , an ovulating female can theoretically produce a clutch of one or a few large eggs, or numerous small eggs, so her fecundity can be varied by altering the size of her eggs (solid lines in Fig. 1). Alternatively the female may ovulate after a shorter period of time, for example after $0.5f$. If the accumulation rate of precursors remains constant, as above, the amount of yolk available for egg production is halved at $0.5f$ and the theoretical

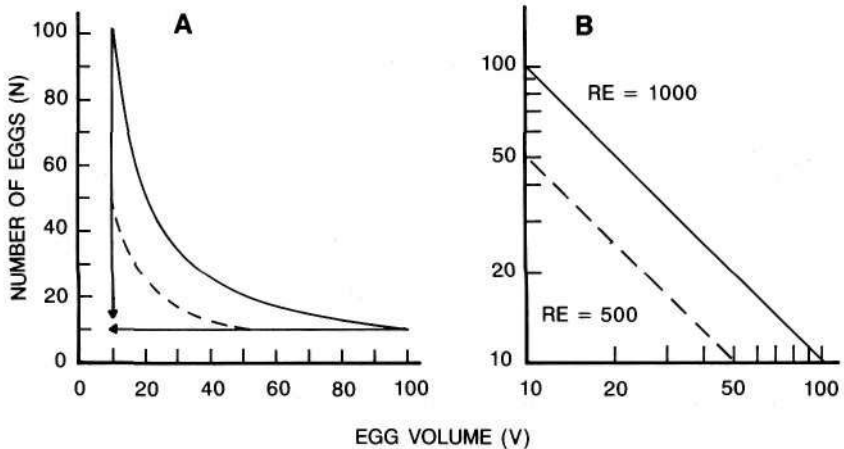


FIG. 1. Theoretical numbers of eggs (N) and volumes (V) related to reproductive efforts (RE), where $N \times V = 1000$ units (solid lines) and $N \times V = 500$ units (broken lines). The relationships are plotted on arithmetic scales (A) and logarithmic scales (B); the units are arbitrarily numbered on a scale of 0 to 100. In (B) the diagonal lines have a slope of -1.000 .

numbers of eggs and their sizes will be proportionally reduced (broken lines in Fig. 1).

Options for partitioning reproductive effort between broods

Most species of *Gammarus* produce more than one brood. If two clutches of eggs are produced at intervals of $0.5f$ and each clutch contains 500 units of yolk, the female's total reproductive effort is the same as when 1000 units of yolk are produced in a single larger clutch of eggs after an interval of $1.0f$. The production of two or more smaller clutches in the same time interval might be an important strategy to adopt when the *mortality* of hatchlings is completely independent of their initial body size at birth. (The *size* of hatchlings at birth is itself dependent on the size of the newly-laid egg.) On the other hand, if mortality of the young is partly but not wholly dependent on the initial size of the eggs, a better strategy to adopt over a longer period of time, say $3.0f$, might be to produce four broods at intervals of $0.75f$ rather than three broods (from larger eggs) at intervals of $1.0f$ or six broods (from smaller eggs) at intervals of $0.5f$, assuming the total amount of egg-yolk available for each clutch of eggs remains the same in all cases.

Various combinations of these theoretical options do in fact occur in *Gammarus*, sometimes within a single species (e.g. *duebeni* and

mucronatus) where egg size varies seasonally and also may vary between winter and summer generations, and between populations in different localities. Examples are given later. Differences in reproductive effort in successive broods of a particular female may also result from internal and external factors altering the *accumulation* rates of egg-yolk precursors. This might be important, and measurable, when considering the animal's "scope for growth", which is briefly discussed in the penultimate section of this review.

Selection and maintenance of specific egg sizes

Some species always lay large eggs whereas others have relatively small eggs (for examples see Fig. 3). The characteristic *interspecific* differences in egg size could have evolved and might be maintained by size-dependent mortality (or survival) of juveniles (Fig. 2). In this model (Kolding & Fenchel 1981) the survival of juveniles is assumed to be

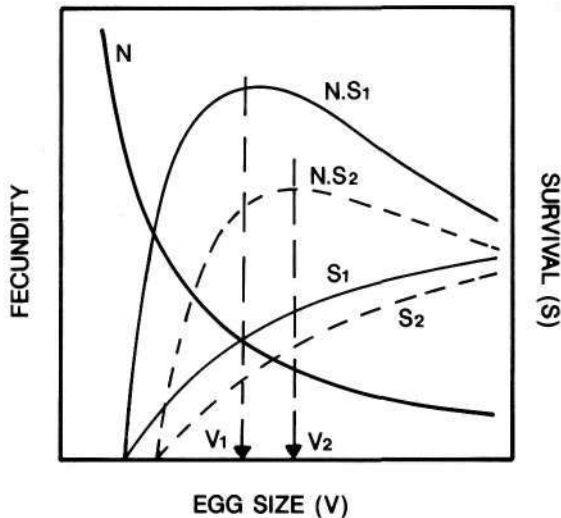


FIG. 2. A theoretical model (drawn on arithmetic scales) for increase in egg size (from V_1 to V_2) as survival of juveniles falls from S_1 to S_2 and net fecundity (the number of juveniles surviving to sexual maturity = $N \times S$) declines; N is the number of eggs per brood, inversely proportional to egg size. The model assumes that reproductive effort (RE) is constant, $N = RE/V$, and juvenile survival (S) is a convex function of size (V), i.e. increments in the probability of survival tend to decrease with larger eggs, and survival is zero at a minimum egg size. (After Kolding & Fenchel 1981 and Fenchel 1987).

partly dependent on the size of the eggs. The probability of survival (5, Fig. 2) also depends upon the availability of food and length of the juvenile growth period. When growth is slow, as at low temperatures and poor availability of food, the probability of survival decreases. Natural selection presumably will then tend to favour the production of fewer, larger eggs (V_2) in response to poor survival (S_2) and lower fecundity ($N \times S_2$). The model has been extended (Skadsheim 1984a) to show how *intraspecific* variation in egg size might respond to increased survival of juveniles, favouring the production of numerous small summer eggs. On the other hand reduced juvenile survival, in autumn and winter, might favour the production of fewer, larger winter eggs. Sibly & Calow (1986) consider how these aspects of reproductive biology fit into more general theories of reproductive strategies and adaptive evolution.

A cautionary note about models of reproductive effort

The above models are simplistic and it must be noted that information on survival/mortality rates, a central feature of these models, is almost nonexistent for natural populations of *Gammarus*. Additional factors may also have an important bearing on the variation of egg size and numbers, for example the body size of the female (big females produce large eggs) and her size at sexual maturity. Species with small eggs usually attain sexual maturity at a small body size, after a relatively short period of growth, and small eggs develop faster, allowing the female to have more broods per unit of time. Some of these aspects are considered further in the following sections.

Despite the caveats raised above, the models shown in Figs 1 and 2 are nevertheless important because they focus attention on some basic aspects of fecundity that need to be examined in greater detail, especially for freshwater species where very little is known about egg size and reproductive effort within and between populations or in different species. Doyle & Hunte (1981) have shown that growth to sexual maturity, survival, and fecundity, all progressively altered in a relatively short time (3 years) when a laboratory population of saltwater *lawrencianus* was examined through 26 generations.

Sizes of eggs, broods (clutches) and female body size

Egg size

The mean size (volume) of eggs is largest in species where the female attains sexual maturity at a relatively large body size, for example in saltwater species living in the cold waters of northern latitudes. Egg size

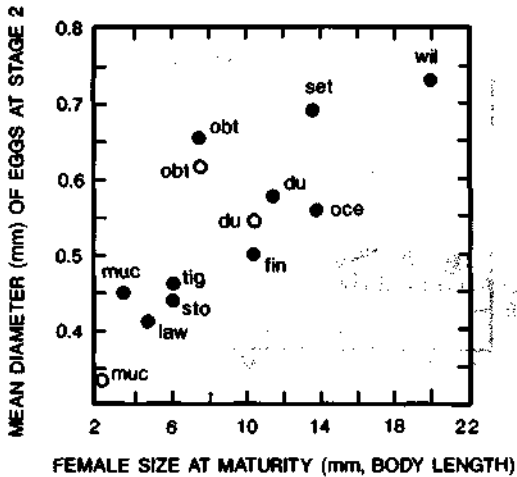


FIG. 3. Large species usually have large eggs, and eggs are larger in the winter generations (●) compared with the summer generations (○) of the same saltwater species on the east coast of North America. du, *dubeni*; fin, *finmarchicus*; law, *lawrencianus*; muc, *mucronatus*; obt, *obtusatus*; oce, *oceanicus*; set, *setosus*; sto, *stoerensis*; tig, *tigrinus*; wil, *wilkitzkii*. (Based on sources cited in Table 1).

also varies seasonally within populations of the same species, being larger in winter when low temperatures prevail (Figs 3-5, and also see Figs 7, 8). For comparative work, eggs are measured at stage 2 of development, before the eggs absorb large quantities of water and swell (see Sutcliffe 1992).

Number of eggs per brood related to size of the eggs

For a series of species, the mean number of eggs in a clutch or brood is inversely proportional to the mean size of the eggs. Thus a female of a particular body length may produce a few relatively large eggs or many small eggs, depending on the species. For ten saltwater species compared at a body length of 16 mm, the proportional relationship is approximately described by the equation:

$$\text{mean number of eggs per brood} = -197 X + 152,$$

where X is the mean egg diameter (in mm) for the range 0.35 to 0.72 mm (Fig. 7 in Steele & Steele 1975b).

Fecundity and body length of females

The above relationship was calculated for a particular body length

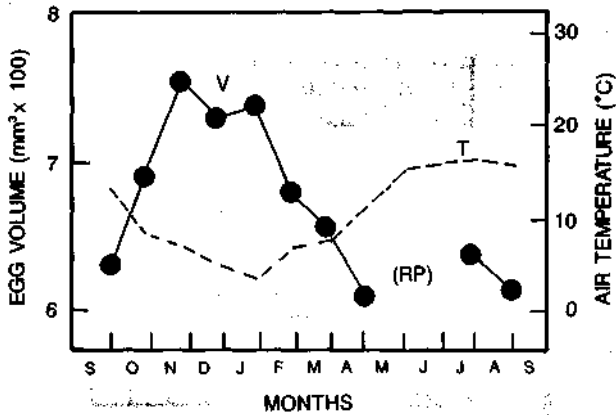


FIG. 4. The mean size of *duebeni* eggs (V, for stage 2 eggs), alters seasonally; small eggs are produced in summer by small females, when mean air temperatures (T) and water temperatures are high. (RP) is the resting period for breeding. (After Sheader 1983, for *duebeni* in the Test estuary, southern England).

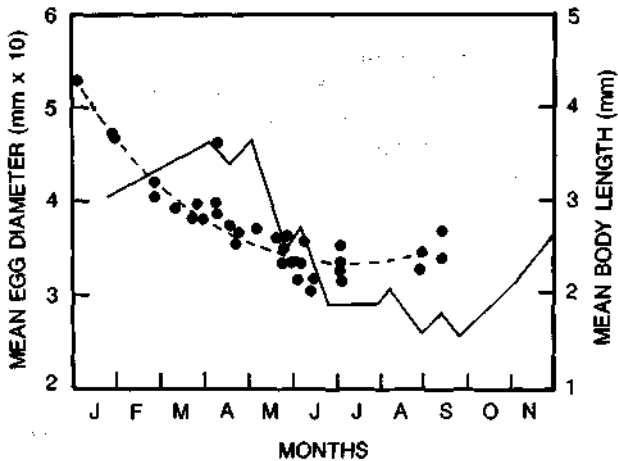


FIG. 5. The mean size of *mucronatus* eggs, in stage 2 (• and broken line), and the mean body length of ovigerous females (solid line) alter seasonally. Small females tend to produce small eggs when water temperatures are high (up to 33°C) in May - September. Larger females produce bigger eggs when temperatures are low (down to 0°C) in winter, January - March. (After Fredette & Diaz 1986, for *mucronatus* in a warm, temperate estuary, York River, Virginia, USA.).

because each female's body size, as well as the size of her eggs, affects the number of eggs in a brood (Figs 5, 6). As the female grows bigger at each moult, she normally lays a larger number of eggs in each subsequent brood, except in very big (old) females where the last brood may contain a smaller number of eggs. In the freshwater species studied by Hynes (1955), the mean brood of *pulex* increased from 6 eggs, in 6-7 mm females, to 29 eggs in 11-12 mm females. Similar mean numbers also occur in *lacustris* but *tigrinus* has more, 11 to 52 eggs per brood over the same range of body sizes. *Crangonyx pseudogracilis*, a smaller freshwater amphipod that is common in parts of Britain, western Europe and North America, has much larger broods than most if not all species of *Gammarus* (Fig. 6).

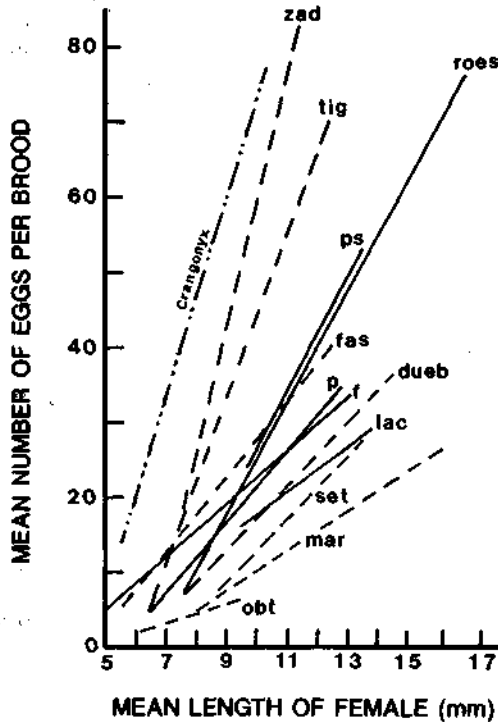


FIG. 6. Fecundity of *Gammarus* (and *Crangonyx*) is related to the mean body length of females. The lines are drawn from linear regressions on data obtained from numerous sources for: dueb, *duebeni*; f, *fossarum*; fas, *fasciatus*; lac, *lacustris*; mar, *marinus*; obt, *obtusatus*; p, *pulex*; ps, *pseudolimnaeus*; roes, *roeseli*; set, *setosus*; tig, *tigrinus*; zad, *zaddachi*.

Usually there is a direct proportional relationship between the number of eggs and embryos per brood (E), and body length of the female (L). This can be expressed by the simple linear equation: $E = bL - a$, where a and b are numerical constants. However, the relationship is often slightly curved (on arithmetic scales) and it may be more precisely modelled as a power function ($E = aL^b$) or occasionally as an exponential function ($E = ae^{bL}$). The relationship is also directly proportional between E and L^3 (or some other estimate of body "volume") or body weight.

By combining the results of several authors into a single linear regression, mean brood sizes were calculated for *pulex* of varying body lengths (Fig. 6). Results on other species, taken from numerous sources in the literature, were similarly treated to show the range of fecundity that occurs in *Gammarus*, summarised in Fig. 6.

A cautionary note about comparisons of brood size

Caution is needed when comparing brood size in natural populations of different species because, apart from the effects of egg size and body size on the numbers of eggs per brood, the numbers may also vary with water temperature, salinity and season of the year. For example, brood sizes of *duebeni* were maximal at a temperature of about 14°C in the Kleiner Kiel (Kinne 1959), they were halved in *obtusatus* kept in 25% seawater (Pinkster & Broodbakker 1980), they vary seasonally in all species that have been studied, and Marchant & Hynes (1981) found differences between years in the brood sizes (per standard body length) of *pseudolimnaeus* from the Credit River, Ontario.

Reproductive effort of saltwater species

In order to compare directly the results from species and individuals of varying sizes, the numbers of eggs per brood have been calculated here for a "standard" female of 10 mm body length, usually from regressions. This has not been done for very large species (e.g. *wilkitzkii*) or very small species (e.g. *mucronatus*) where extrapolation to 10 mm body length would not be appropriate. Where possible a distinction is drawn between winter and summer broods.

Winter broods of some North American saltwater species

There is a marked inverse relationship between egg size and the number of eggs per brood. The log - log regression line drawn through the mean data points for eight species on the Atlantic seaboard of North America (solid line in Fig. 7A) has a slope of -0.703, significantly lower than the value of -1.000 expected for a constant reproductive effort (RE)

irrespective of egg size, when $N \times V = RE$ on log - log scales (compare Figs 1 B and 7). However, closer inspection of Fig. 7 A suggests that the large winter eggs of *obtusatus*, *oceanicus*, and possibly *setosus*, are produced in *relatively* large numbers (for females of standard body length). When these data points are excluded from the regression the slope alters to -0.995 (broken line in Fig. 7A), suggesting that reproductive effort is almost constant in the species with smaller eggs. In these, further analysis shows that the mean volume of a brood (i.e. reproductive effort, $N \times V$) tends to decrease a little with increasing egg size, when plotted on arithmetic scales (Fig. 8A) but this decrease is compensated for by producing a greater number of eggs (Fig. 8B). The northern species, *obtusatus*, *oceanicus* and *setosus*, are clearly distinct in having relatively large numbers of large eggs, thereby effectively doubling the reproductive effort of a standard-sized female. This also applies to *wilkitzkii* (see later).

The decrease in mean size of eggs and body size of the female at maturity, which is correlated with latitude (Table 1), is an adaptive life-history tactic for maximising reproductive success. The correlation with latitude is partly a correlation with temperature, where small eggs, small size at maturity, high fecundity and numerous generations per year all occur at relatively high temperatures. But another important environmental factor is likely to be the long daylight hours throughout much of the year at lower latitudes, supporting high primary productivity in the habitats and thus increasing the availability of food for gammarids.

Winter broods of some West European saltwater species

Large eggs occur in species that breed in winter and spring: *oceanicus*, *duebeni* and (in the Limfjord) *salinus*. The smallest and most numerous eggs occur in species that breed in the summer and autumn: *locusta*, *zaddachi* and (in the Baltic) *salinus*. These have two generations each year, in early summer and late autumn, and they produce more broods than the first group with larger eggs, which have only one generation and fewer broods.

The mean numbers of eggs per brood of a "standard" female (10 mm body length) are inversely proportional to the mean egg sizes (volumes) of individual eggs from each species (Fig. 7B). The slopes of the lines drawn through the mean values are almost -1.00; a regression of the twelve means has a slope of -0.960, close to the value of -1.000 for a perfect proportional relationship (on log - log scales) between mean numbers of eggs and their sizes (see Fig. 1B). Thus reproductive effort apparently is constant in *duebeni*, *locusta*, *oceanicus*, *salinus* and *zaddachi* from the coastal areas of northwest Europe, ranging from 1.02 to 1.44 mm³ per brood in specimens from the Baltic Sea, and from 1.06

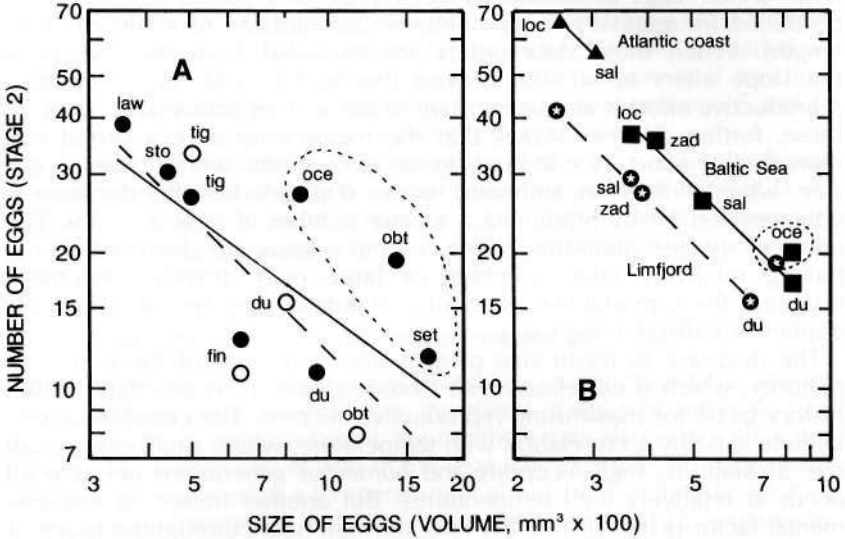


FIG. 7. The mean number of eggs per brood (in females of 10mm body length) decreases with increasing egg size of saltwater species from (A) the east coast of North America and (B) western Europe. (A), species on the Atlantic seaboard of North America (see Table 1); ●, winter broods; ○, summer broods. The solid diagonal line represents a regression of $\log Y = -0.703 \log X + 0.489$ ($r = 0.726$). The broken diagonal line represents a regression of $\log Y = -0.995 \log X + 0.096$ ($r = -0.865$). (B), species from the Atlantic coastline of southern France north to Holland (▲), the Limfjord, Denmark (⊕), and the Baltic Sea (■); diagonal lines fitted by eye, excluding the relatively high values for *oceanicus*. (After Kolding & Fenchel 1981). du, *duebeni*; fin, *finmarchicus*; law, *lawrencianus*; loc, *locusta*; obt, *obtusatus*; oce, *oceanicus*; sal, *salinus*; set, *setosus*; sto, *stoerensis*; tig, *tigrinus*; zad, *zaddachi*.

FIG. 8. (Opposite, on p. 37) The mean total volume of eggs in a brood (stage 2 eggs in females of 10mm body length, drawn on arithmetic scales) tends to decrease with increasing egg size (A) but increases with the number of eggs per brood (B) in saltwater species on the east coast of North America. Symbols and abbreviations are as in Fig. 7. In (A) the broken line represents a regression of $Y = -2.828 X + 1.419$ ($r = -0.423$) excluding the encircled data points. In (B) the broken line represents a regression of $Y = 0.023 X + 0.711$ ($r = 0.833$) excluding the encircled data points.

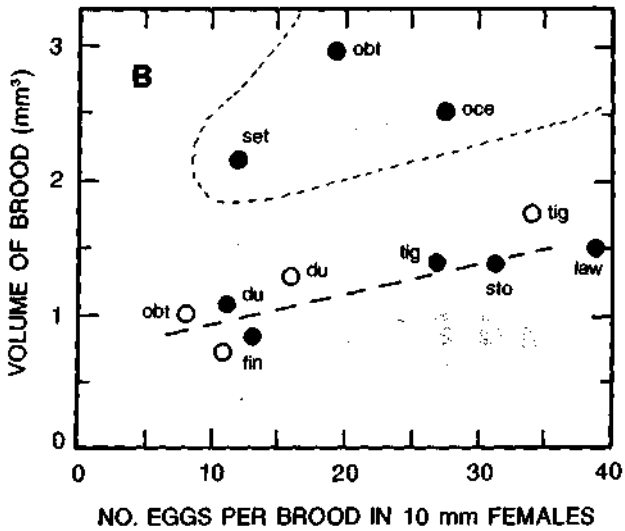
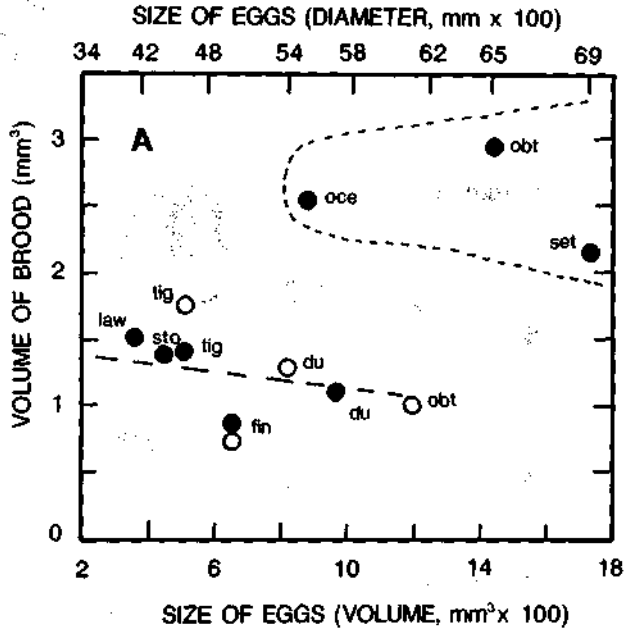


Table 1. Ranges of latitude occupied by eleven saltwater species on the Atlantic coastline of North America, and some reproductive variables for sexually mature females (Diameter of stage 2 eggs; Ranges of female body lengths; Number of generations per year; Maximum numbers of broods per year; Mean numbers of eggs per brood, calculated for the ranges of body lengths shown in the fourth column; Reproductive resting periods, when most or all are not breeding). Values are approximate, for illustrative purposes. (W) winter and (S) summer generations. Based on data from a series of papers by D. H. Steele and V. J. Steele, listed by Steele & Steele (1975a, b, c, 1986a, b), and from VanDolah et al. (1975), Gable and Croker (1977), VanDolah & Bird (1980).

Species	Lat. (°N)	Diam. (mm)	Length (mm)	Generations	No. broods	Mean no. eggs	Resting period
<i>wilkitzkii</i>	85 to 47	0.73	20-33	1 or less?	1	70-265	Nov - Jul
<i>setosus</i>	80 to 45	0.69	11-26	1	1	5-75	Nov - Jul
<i>oceanicus</i>	65 to 40	0.55	10-30	1	3	10-175	Aug - Nov
<i>obtusatus</i>	50 to 41	0.65 (W) 0.61 (S)	7-15	1	3	5-20	Sep - Nov
<i>duebeni</i>	52 to 43	0.57 (W) 0.54 (S)	11-18 (W) 10-17 (S)	1 2	5	10-30	Aug - Nov
<i>finmarchicus</i>	47 to 42	0.50	10-19	1	8	10-30	Sep - Nov
<i>tigrinus</i>	50 to 30	0.46	6-14	2+	10	10-50	Sep - Nov
<i>stoeensis</i>	45 to 42	0.44	5-7	2+	9	10-20	Sep - Mar
<i>lawrencianus</i>	55 to 41	0.41	5-10	2 or 3+	10	5-40	Sep - Dec
<i>micronatus</i>	47 to 30	0.45 (W) 0.33 (S)	2-7 (W) 1-4 (S)	2+	10	5-30*	?
<i>palustris</i>	43 to 30	?	4-10	2	5?	5-20	Oct - Feb

* Fredette & Diaz (1986) record 15-105 eggs per brood for 2-4 mm females of *micronatus* at latitude 37°N, Chesapeake Bay.

to 1.64 mm³ per brood for specimens from the Limfjord, northern Denmark. Slightly higher values for reproductive effort were calculated for the Atlantic coastline of Europe (Table 2). Excluding the relatively high values for *oceanicus* (Fig. 7B), it appears that reproductive effort is highest in localities along the main Atlantic coastline and lowest in the Limfjord (Kolding & Fenchel 1981). In fact the total volume of eggs produced by the winter generation is also remarkably similar in all five species, ranging from 3.6 to 5.2 (mean 4.4) mm³ in the Baltic and ranging from 1.8 to 4.1 (mean 3.5) mm³ in the Limfjord (Table 2). Reasons for this relative constancy of reproductive effort in each locality are not known but the different amounts of reproductive effort may reflect the availability of food and the effects of different salinity regimes on metabolism.

Table 2. Reproductive effort of five saltwater species in the Baltic sea and the Limfjord, Denmark. Values are calculated means for females of 10 mm body length. (After Kolding & Fenchel 1981*).

Species	Locality	Volume of eggs per brood (mm ³)	Number of broods per generation and year		Total egg volume per generation (mm ³)	
			winter	summer	winter	summer
<i>oceanicus</i>	Baltic	1.64	3.2	-	5.2	-
	Limfjord	1.44	2.5	-	3.6	-
<i>duebeni</i>	Baltic	1.39	2.7	-	3.8	-
	Limfjord	1.02	1.8	-	1.8	-
<i>salinus</i> **	Baltic	1.06	3.4	7.4	3.6	7.8
	Limfjord	1.36	3.0	-	4.1	-
<i>zaddachi</i>	Baltic	1.45	3.4	7.4	4.9	10.7
	Limfjord	1.05	3.8	7.8	4.0	8.2
<i>locusta</i> **	Baltic	1.34	3.5	7.4	4.7	9.9
	Limfjord	1.05	3.8	7.8	4.0	8.2

* The original tabulated values contain some errors and the egg volumes appear to be erroneously high. Here they have been divided by 10 to agree with estimated volumes and measurements of egg size given by others (e.g. Table 1.).

** The calculated mean volume of eggs per brood for specimens from Atlantic coast localities (see Fig. 7B) is 1.70 mm³ *salinus* and 1.66 mm³ for *locusta*.

These results from European species are strikingly similar to those obtained from their counterparts on the other side of the Atlantic, including the relatively high reproductive effort of *oceanicus* (Fig. 7).

Summer broods of West European saltwater species

In summer generations of *locusta*, *salinus* and *zaddachi* the calculated total reproductive effort is twice that of the winter generations (Table 2, last two columns), due to an increase in the number of broods per generation.

Reproductive effort of *duebeni* from the Test estuary, southern England

The population of *duebeni* studied by Sheader (1983), at a latitude just below 51 °N, is close to the southern limits of the geographical range of this species. In the Test estuary, breeding occurs throughout most of the

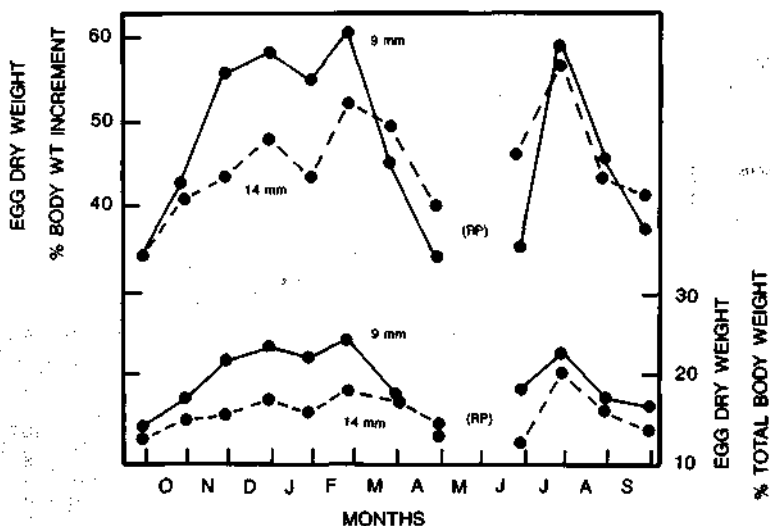


FIG. 9. In *duebeni*, the estimated mean production of eggs (brood dry mass), expressed as a percentage of total production (body dry mass), is relatively higher in small females (mean length 9 mm) than it is in large females (mean length 14 mm). Lower values show egg dry weight per brood, expressed as percentages of the female's body dry weight before moulting and ovulation. Upper values show egg dry weight per brood, expressed as percentages of the weight increment (i.e. growth in dry mass) during the previous intermoult. (RP) is the resting period for breeding. (After Sheader 1983, for *duebeni* in the Test estuary, southern England).

year and some 10-12 broods are produced by two overlapping generations. This is twice the number of broods found in cooler and more northerly populations (e.g. Tables 1 and 2). Nevertheless a "standard" 10 mm female produced a mean volume of 1.15 mm^3 eggs per brood, averaged over the year from data on egg volumes at stage 2 (Fig. 4) and clutch sizes given by Sheader. This reproductive effort per brood is remarkably similar to that of 10 mm females in other populations (Fig 8; Table 2). On the other hand the *total* annual reproductive effort is relatively high, about 20-30 mm^3 per year for 1.5 female generations, because a larger number of broods is produced each year.

Sheader (1983) calculated the net production of the total population of breeding females, from intermoult growth in body mass for all size groups of mature females. He found that up to 60% is expended on the production of eggs, being highest in spring and again in the late summer (Fig. 9). Although the number of eggs per brood is greatest in winter, the "instantaneous" (daily) rates of egg production are largest in late summer, coinciding with high water temperatures. Sheader concluded that egg size and the rates of egg production are dependent on temperature, whereas the proportion of production that is utilised to produce eggs, and the numbers of eggs per brood, are influenced by temperature but are controlled by the availability of food and the body size of the females. The latter variable is a function of generation times and the proportions of different cohorts of breeding females (and hence differing size-classes) that are present month by month throughout the year.

Reproductive effort of full-sized females of saltwater species

In the preceding sections, comparisons are based on females of a "standard" body size because fecundity increases markedly as the female grows to her full size. But this important natural phenomenon must be taken into account when considering the overall reproductive strategy of each species. As an extreme example, in the very large circumpolar Arctic species *wilkitzkii*, females do not become sexually mature until they are about 20 mm in length. At this size the females of some other large species, e.g. *locusta* and *marinus*, can be fully mature (although in some northern localities *locusta* grows to more than 30 mm length) whereas *wilkitzkii* grows to at least 33 mm in length and produces a calculated mean brood of 236 eggs at 32 mm length. Despite "considerable mortalities during embryonic development" (Steele & Steele 1975a) the potential reproductive effort *per brood* of a fully mature, large specimen of *wilkitzkii* is obviously much greater than that of other species, especially as it also lays the biggest eggs (Fig. 3). Thus a

single clutch of stage 2 eggs can represent a reproductive effort of some 50 mm³. This very high productivity, per brood, is related to the breeding strategy of *wilkitzkii*, in which a single brood is produced each year. In contrast the annual productivity of a small southern species is probably less than half and may be only a quarter (12-15 mm³ per year) that of *wilkitzkii*, even when as many as 10 broods are produced by 2 or 3 generations in a year.

Breeding cycles of saltwater species

Breeding cycles of North American saltwater species

Eleven common coastal marine and brackishwater species on the Atlantic seaboard of North America have been studied (Table 1). The most northerly (Arctic) species, *wilkitzkii* (which lives under permanent sea-ice) and *setosus*, are relatively large animals producing large eggs. The ovarian diapause (see review by Sutcliffe 1992) appears to be obligatory and the reproductive resting stage lasts for most of the year. Both species produce a single large brood each year; release of the young in April to July is timed to coincide with a plentiful supply of food in the short Arctic summers, when growth is relatively rapid. Because the growing season is relatively short in northern waters, reproduction is restricted to a single annual brood. Reproductive effort is therefore maximised by growing to a large size at sexual maturity (large females produce many large eggs) and by strict timing of ovulation and annual production of young. As slow growth to a large size at low temperatures requires more time, the life-span of northern species is relatively long, probably more than 2 years.

The other species listed in Table 1 occur at lower latitudes and have different breeding cycles. The ovarian diapause and resting periods are relatively short, occurring in the autumn. Eggs are deposited in the broodpouch in winter and the first generation of the new year is hatched in early spring, again coinciding with availability of a plentiful supply of suitable food (Vassallo & Steele 1980). A succession of broods then usually follows throughout the late spring and summer before the resting period intervenes. By this time, at low latitudes in warmer waters, the first generation has matured and started to produce a second generation. The number of broods (and generations) produced each year is partly governed by environmental temperatures, which determine the rates of development for each brood. Life-spans are shorter; summer generations may live for less than a year.

Breeding cycles of European saltwater species

The common saltwater species in northwestern Europe have reasonably well-defined life cycles. A few, e.g. *oceanicus* and *stcerensis*, have only

one generation each year whereas most species have two or more generations, with overlapping cohorts. However the breeding periods show considerable intraspecific variation between localities, depending at least partly on latitude and temperature. In the Netherlands and northern France, *marinus* breeds throughout the year, whereas in the cooler waters of Norway and Denmark *marinus* breeds only in spring and summer (Skadsheim 1982; Leineweber 1985). Similarly, in the southern part of its range *duebeni* breeds more or less throughout the year, with overlapping generations each comprised of several cohorts. In more northerly localities, on both sides of the Atlantic, *duebeni* breeds only in spring and summer, producing one generation (with overlapping cohorts) each year (Naylor et al. 1988). Although it stops breeding in winter, *tigrinus* (introduced from North America) is the most prolific species in western Europe, resembling *lawrencianus*, another North American saltwater species. In the slightly brackish and fresh waters of the Netherlands, *tigrinus* breeds from spring to autumn. In this period some 12-16 broods could theoretically be produced by a single female attaining sexual maturity in April, and 3-4 generations are probably produced each year (Chambers 1977; Pinkster et al. 1977).

Geographical variation in the breeding periods of *marinus*, *salinus*, *stoerensis* and *oceanicus*, including North American populations of the last two species, is summarised by Skadsheim (1982, 1984b).

Reproductive effort and the breeding cycles of saltwater species

The sizes (volumes) of the eggs and availability of food are also important factors determining the frequency of ovulation, number of eggs per brood and the time required for development. Apart from immediate, individual acclimation responses to changes in these variables, seasonal and longer-term adaptive responses occur within populations of the same species, and there are differences between species. In the latter case, for example, egg size decreases markedly from north to south (Table 1, column 3). There is also evidence for intraspecific latitudinal clines in egg sizes of *mucronatus*, *obtusatus* and *palustris*, a feature found in other coastal amphipods (VanDolah & Bird 1980). A similar cline may occur in *locusta* on the west coast of Europe (Kolding & Fenchel 1981). This species produces smaller numbers of larger eggs in its more northerly populations (Fig. 7B). Evidence for possible clines in *salinus* and *oceanicus* is discussed by Skadsheim (1989).

Winter and summer eggs of saltwater species

Eggs produced in summer are usually smaller than those produced by the same species in winter (Figs 3-5; Table 1). Irrespective of

temperature, small eggs develop more quickly (Fig. 7 in Sutcliffe 1992) and are produced by females which attain sexual maturity at a small body size (Figs 3, 5). Thus summer-breeding animals produce large numbers of small eggs which develop very rapidly at high temperatures and hatch into offspring that also develop rapidly to sexual maturity. Reproductive effort is therefore maximised in a short "summer" burst of production (Fig. 9) although the total production of eggs may be just as high over a longer period in winter.

Breeding cycles of coexisting saltwater species

It has been suggested that sibling species which coexist in the same habitat have responded to natural selection pressure by displacement or separation of their breeding periods (Fenchel & Kolding 1979; Kolding & Fenchel 1981). Evidence for this is shown in Fig. 10, where species with a conspicuous zonation and separation of niches down a salinity gradient have seasonal breeding periods that differ between adjacent species populations. Separation is maintained by pronounced differences in the timing of precopulatory activity (Fig. 10B). Thus interspecific pairing, which results in sterile matings, is kept to a minimum. Because the major periods of breeding occur at different times of the year, interspecific competition between juveniles for food and space is also minimised. Where salinity gradients do not occur, the separation of coexisting species that usually have overlapping breeding periods (e.g. *oceanicus*, *salinus* and *zaddachi*, Fig. 10A) may be achieved by becoming sexually mature at different times and by shortening the breeding periods in spring and summer (Kolding 1981). Some populations of *locusta* and *oceanicus* appear to be restricted to a narrow range of salinities, having lost the ability to reproduce at salinities higher than those of their particular zonal regions in the Danish Limfjord (Kolding 1985).

A temporal separation of seasonal development into mature males and females, cued by photoperiod as in *duebeni* (Naylor et al. 1988; Fig. 7 in Sutcliffe 1993) might also be part of the reproductive strategy for separating the annual breeding periods of coexisting species.

Fecundity and breeding cycles of freshwater species

There is a voluminous literature on life cycles and population dynamics of some common freshwater species in western Europe (particularly *pulex*, *fossarum*, *lacustris*, *roeseli* and *tigrinus*) and in North America (*lacustris*, *pseudolimnaeus*, *fasciatus* and *minus*). Much of this work is cited and very briefly summarised by Gledhill et al. (1993). Some of the studies include detailed analyses of fecundity in relation to female body

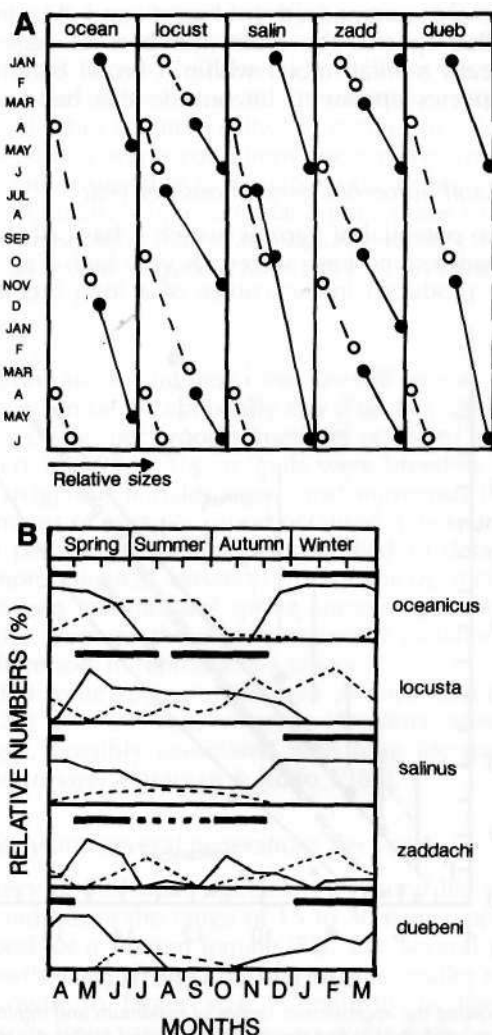


FIG. 10. Life cycles and breeding periods of five saltwater species in the Limfjord, Denmark (Latitude 57°N), where salinity gradients are occupied sequentially by *oceanicus* (highest salinities), *locusta*, *salinus*, *zaddachi* and *duebeni* (lowest salinities). In adjacent populations of each species the breeding periods tend to alternate seasonally; *oceanicus*, *salinus* and *duebeni* breed mainly in winter and spring, whereas *locusta* and *zaddachi* breed in spring through to autumn. (A), ●—●, females with eggs; ○—○, juveniles and females without eggs. Growth in size of each generation is represented across the columns. (B), relative proportions of females with eggs (solid lines) and juveniles (broken lines). Horizontal bars show the main periods for precopulatory amplexus between couples of each generation. (After Kolding & Fenchel 1981).

size and these are summarised in Figs 6 and 11. In most of the commonly-studied species the mean numbers of eggs per clutch or brood are basically similar, albeit within a broad band of values (Fig. 11), but two species appear to lie outside this band and are briefly considered first.

High fecundity and numerous generations per year

The reproductive potential of *tigrinus* (which is basically a brackishwater species that invades some fresh waters) is very high (Fig. 11); numerous generations are produced in the course of a long breeding season, as

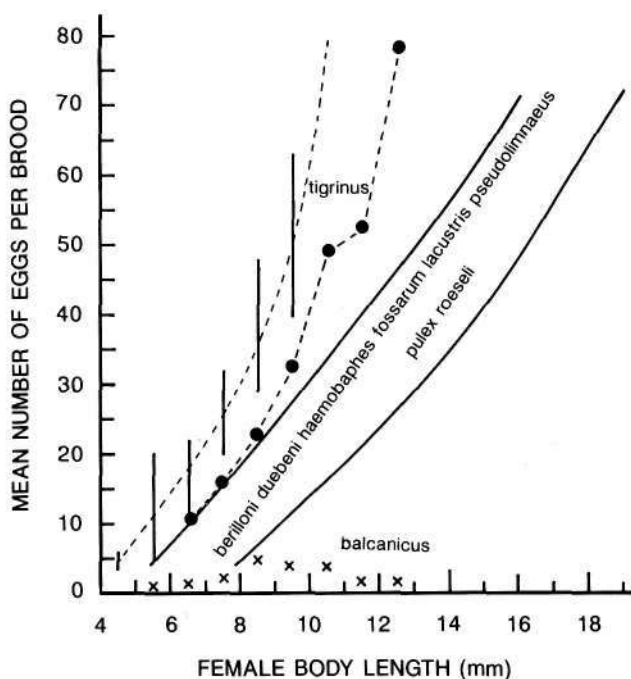


FIG. 11. Curves showing the approximate ranges of maximum and minimum values for the mean number of eggs per brood in females of several named freshwater species from Europe and North America. (Based on data from Clemens 1950; Hynes 1954, 1955; Kinne 1959; Straskraba 1966; Hynes & Harper 1972; Jazdzewski 1973; Nilsson 1977; Brzezinska-Blaszczyk & Jazdzewski 1980; Goedmakers 1981a, b; Marchant 1981; Marchant & Hynes 1981; Miller 1982; Teichmann 1982; Muskó 1990). Plotted separately are mean values for *balcanicus* (Jankovic 1983) and *tigrinus* (data from Hynes 1955 (●)). Vertical bars are also for *tigrinus*, showing the seasonal ranges of mean brood sizes found between 31 March and 6 November 1970 in the Tjeukemeer, Netherlands (Chambers 1977).

indicated above in the section on breeding cycles of European saltwater species. The reproductive strategy of this species is to produce numerous relatively *small* eggs (Figs 3, 7; Table 1), with short development times, throughout much or all of the year. This strategy, resembling that of *lawrencianus* and other southern saltwater species (see Table 1), may be related to the relatively warm conditions encountered in its geographical range and the rather unstable or variable salinity regimes of brackish-water/estuarine habitats, where populations increase explosively when conditions are favourable, but crash equally rapidly in unfavourable circumstances, as reviewed by Sutcliffe (1991) and Pinkster et al. (1992).

Low fecundity

In complete contrast to *tigrinus*, the overall mean brood size of *balcanicus* appears to be exceptionally low (Fig. 11), although maximum numbers of 21-30 eggs per brood sometimes occurred in the population studied by Jancovic (1983). The animals were breeding throughout the year although ovigerous females were most numerous in winter, when the highest numbers of eggs per brood occurred. Life-spans and numbers of generations per year have not been studied in detail, but there is considerable morphological variation in *balcanicus*, including seasonal differences between autumn and spring-summer generations (Karaman & Pinkster 1987). Perhaps these morphological variations are matched by seasonal differences in reproductive strategy?

It is known that some epigeal niphargid shrimps have relatively small numbers (ca. 20) of small eggs whereas interstitial species have even fewer large eggs, possibly associated with long life-spans - some 10 years in *Niphargus virei* (Karaman & Ruffo 1986).

Medium fecundity and several generations per year

The usual strategy of freshwater species is a natural life-span of about 1 to 2 years, fecundities in the range of 15 to 30 eggs (approximate mean values) per brood for a 10-mm female (Fig. 11), several generations per year, faster growth to reach sexual maturity at a smaller size in summer, and slower growth to larger size at maturity in the winter-spring generation. Results from various studies on *pulex* (Figs 12-14) are typical for the species listed in the central band of Fig. 11.

In most populations of *pulex*, recruitment of newly-hatched juveniles occurs daily throughout much of the year and it is not possible to determine accurately the growth in size (and hence determine survival) of cohorts representing juveniles of the same age. Therefore most workers have attempted to delineate cohorts by enumerating size-classes

in samples taken at (approximately) monthly intervals, and the growth of these "cohorts" is then interpreted in the light of laboratory studies (see references listed in the legend to Fig. 11).

Where growth from birth to sexual maturity occurs at times of rising temperatures in spring and early summer, a female may produce 2 or 3 broods in her first year and another 2 or possibly 3 broods in the following year. At the same time her first-brood daughters will have

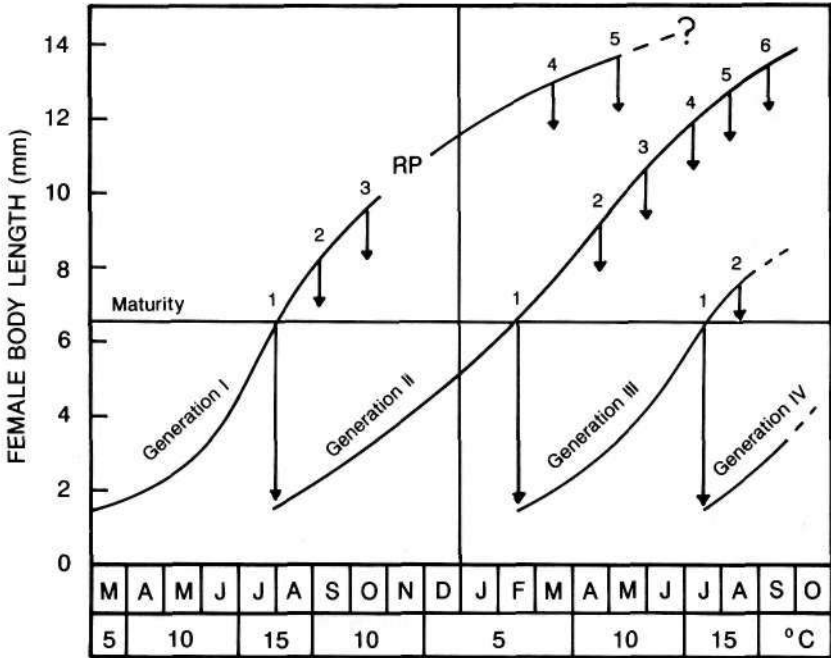


FIG. 12. Theoretical growth curves for females of the freshwater species *pulex*, based on mean monthly temperatures of 5, 10 and 15°C and data given in Table 3. Generation I is a female born in March and reaching sexual maturity in mid summer. She produces 3 broods in her first year before entering the resting period (RP), continues to increase in body size and has another 2 or possibly 3 broods before she dies in her second summer; each successive brood contains a larger number of eggs (Fig. 11). At the same time her daughters from the first brood have matured during the winter (Generation II) and produce the first granddaughters of the third generation. A fourth generation may hatch before the original female dies, especially if mean monthly temperatures in summer rise much above 15°C and/or winter temperatures are well above 5°C. Growth, and the development of eggs, is then faster and each generation may have 1–2 broods more than is shown on the text-figure (e.g. Welton 1979). Only two generations may reproduce at the same time in summer-cool waters (e.g. Iversen & Jessen 1977).

Table 3. Data used to calculate the theoretical growth and development times depicted in Fig. 12. Approximate durations (weeks) are given for incubation of eggs to hatching and release from the broodpouch, and subsequent growth to sexual maturity at 6.5 mm body length, for *pulex* kept at four constant temperatures (T, °C) in the laboratory. Based on experimental work by Nilsson (1977), Pinkster et al. (1977), Welton & Clarke (1980), Sutcliffe & Carrick (1981) and Sutcliffe et al. (1981).

T (°C)	Egg incubation	Growth to sexual maturity
5	10	52
10	5	22
15	4	17
20	3	11

reached sexual maturity and begin reproducing themselves, and some of this second generation may produce a third breeding generation in this second year of the first-generation parent (Fig. 12 and explanation in the legend). The potential for population growth and expansion is therefore relatively high but, under most conditions, high juvenile mortality (including high natural mortality when moulting, and associated cannibalism by adults) apparently keeps the population in check, unless large-scale emigration from the sampled population is invoked or occurs (Goedmakers 1981b; Goedmakers & Pinkster 1981).

Speculative ideas on reproductive effort and strategies in freshwater species

From the results on saltwater species, considered earlier, it is supposed that *pulex* and other freshwater species may similarly show variation in the sizes (volumes) and numbers of eggs laid at different times of the year. In fact seasonal variation in the brood sizes of *pulex* is well documented, with a pronounced tendency for higher numbers of eggs in winter - spring, declining to lower numbers in mid summer and autumn (Figs 13, 14). It is not known, however, how reproductive effort varies (if at all) in successive broods produced by each female, but I suggest that the following scenario could form the basis of an adaptive strategy for *pulex* and other species inhabiting temperate fresh waters.

A hypothetical scenario for reproductive effort in pulex

The annual die-back and leaf-fall of aquatic and riparian vegetation is a major food-source for *Cammarus* in the autumn and early winter, affording an opportunity for maximising the storage of precursors for egg-

yolk. Some well-fed females attain sexual maturity in the late autumn and produce a brood of relatively *large* numbers of large "winter" eggs. These slowly develop at low winter temperatures and hatch at a relatively large size in spring. The juveniles (Generations I and III in Fig. 12) utilise the spring outburst of diatoms and other algae that is a common feature of streams and lakes, and then grow rapidly to a relatively large size at sexual maturity in mid summer. These females then produce one or two broods of relatively small numbers of *small* eggs before the autumn resting period intervenes, during which they "fatten up" ready to produce a large brood of large "winter" eggs. Meanwhile, broods that are produced during the summer months (i.e.

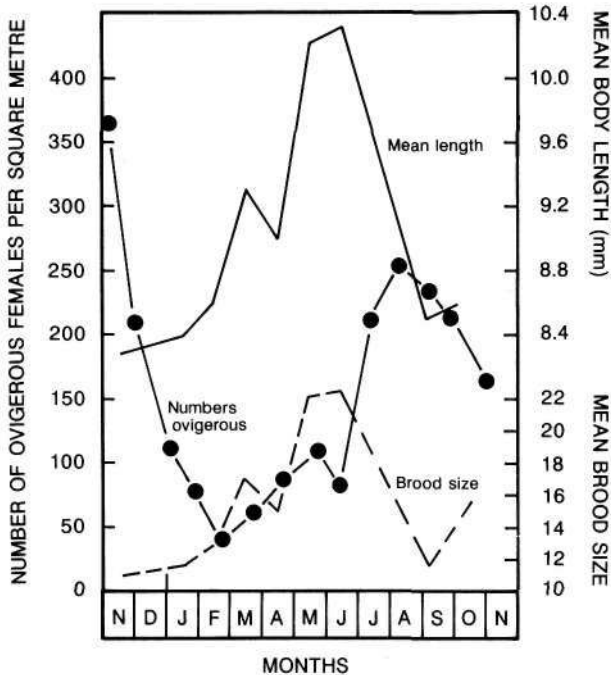


FIG. 13. In freshwater *pulex* the mean numbers of ovigerous (egg-bearing) females decrease in autumn and rise in spring – summer (●—●, numbers per square metre). The largest females occur in May – June and mean body length of the adult female population then decreases as the large (old) females die (solid line, body length in millimetres). Mean brood size in the population (broken line, numbers per brood) fluctuates in time with the population mean body length of adult females, as expected from the relationship shown in Fig. 11. (After Welton 1979 for *pulex* in Tadnoll Brook, southern England).

broods 2 to 6 in Fig. 12) may successively consist of smaller numbers of smaller eggs, in order to maximise reproductive effort when the cycles of moulting, growth and oogenesis in mature animals are inevitably shortened at high summer temperatures.

Additionally, natural populations consist of younger (small) and older (large) ovigerous females which may adopt different reproductive strategies in response to local conditions, such as the availability of suitable food and its nutritional quality, population densities affecting competition for food, and fluctuations in physical - chemical characteristics of the environment. Ideally, therefore, variation in fecundity and size of eggs, related to different cohorts of reproducing females, should be examined separately rather than "lumping" together all results from a sample or series of samples. In practice this is not always easy or possible to do, and some aspects of reproductive effort could be studied more easily in the laboratory; these are briefly considered in separate sections below.

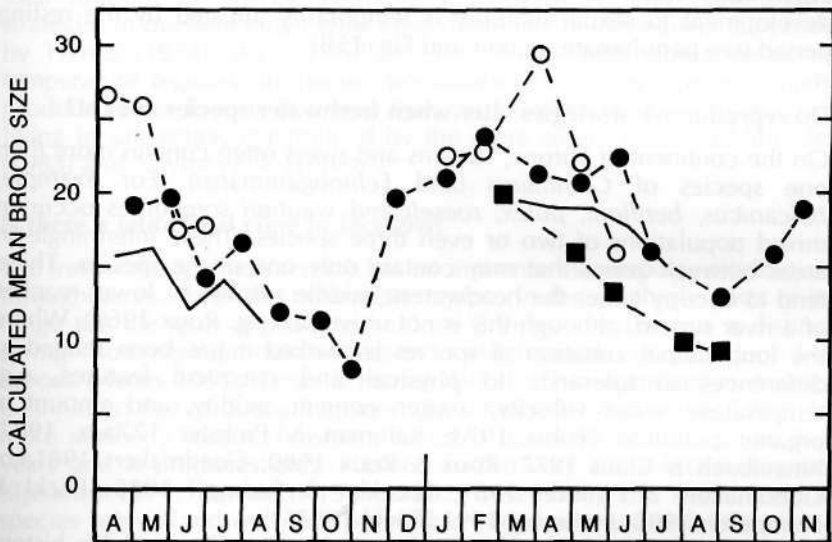


FIG. 14. In freshwater *pulex* the mean number of eggs per brood at a standard body length of 10 mm is highest in spring and tends to decline through the summer. Based on data from a pond (○) in northwest England and a stream (●) in North Wales (Ward 1986), streams in Schlitzlerland, Germany (■, Teichmann 1982) and a stream at Outgate, English Lake District (solid lines, personal observations).

An explanation for the resting period in Gammarus

The hypothetical scenario outlined above for *pulex* may also provide additional explanations for the presence of a resting period in the reproductive cycle, serving two important functions in most or all species of *Gammarus*. The cessation of the ovulation cycle for a quiescent intermoult period of some 2-3 months in autumn would enable females to feed and accumulate a relatively large store of materials before these are translocated into developing oocytes. At the same time, physiological changes associated with the control of oogonia production and vitellogenesis could occur, "switching" from a state where small numbers of oogonia containing a limited amount of yolk occurs during the summer months, to a new state in the late autumn - winter when more numerous and large-yolked oocytes are produced. Steele & Steele (1986a) have already suggested that, apart from ensuring the production of young at a time (season) favourable for their subsequent growth, the resting period may increase survival of adults and also permit their growth to a larger body size, so that large broods are produced when breeding recommences. Under experimental conditions, there is also an increased survival of adults whose development to sexual maturity is temporarily arrested by the resting period (see penultimate section and Fig. 15B).

Do reproductive strategies alter when freshwater species coexist?

On the continent of Europe, streams and rivers often contain more than one species of *Gammarus* (and *Echinogammarus*). For example, *balcanicus*, *berilloni*, *pulex*, *roeseli* and *wautieri* sometimes occur in mixed populations of two or even three species. These intermingle in areas between zones that may contain only one of the species. These tend to occupy either the headwaters, middle reaches or lower reaches of a river system, although this is not universal (e.g. Roux 1969). Where the longitudinal zonation of species is marked it has been related to differences in tolerance to physical and chemical features, e.g. temperature, water velocity, oxygen content, acidity, and amount of organic pollution (Vobis 1973; Karaman & Pinkster 1977a,b, 1987; Kinzelbach & Claus 1977; Roux & Roux 1980; Goedmakers 1981a,b; Goedmakers & Pinkster 1981; Foeckler & Scrimpf 1985; Pockl & Humpesch 1990; Meijering 1991; Pockl 1992).

It would be interesting to see if reproductive effort and life-history strategies alter in response to interspecific competition or coexistence between species in these mixed populations, compared with single-species populations in the same river system. There might be small, subtle changes, such as the time taken to reach sexual maturity, and egg

size in relation to fecundity, when habitat space and food resources are shared between species. Changes in the timing of peak reproductive activity might also occur, as in some populations of coexisting saltwater species (see Fig. 10).

Does *duebeni* have different strategies in fresh and saline waters?

In his study of *duebeni* from fresh and brackish habitats on the Isle of Man, Hynes (1954) found evidence of small population differences in the mean body size (length) of males and females, fecundity, and the mean longest diameter of eggs, speculating that freshwater populations might produce fewer but larger eggs than their counterparts in salt water; this is a well-established phenomenon in decapod crustaceans (e.g. Mashiko 1990). Differences in reproductive effort and strategies of size at sexual maturity etc. could be profitably examined by comparing populations of *duebeni celticus* from inland fresh waters in Ireland (and Brittany) with coastal saltwater populations of *duebeni duebeni* (Sutcliffe 1972; Dennert 1975; Gledhill et al. 1993). The increased cost of osmoregulation in fresh water (Sutcliffe 1984) presumably reduces the total amount of energy available for oogenesis, and reproductive strategies in *duebeni* might reflect this difference in the manner supposed by Hynes (1954). As a corollary, in habitats with similar seasonal temperature regimes, freshwater populations of *duebeni celticus* might produce fewer broods per year than populations of *duebeni duebeni* living in salt water, exemplified by the more recent studies of Sheader (1983) and Nayloretal. (1988).

Is there a latitudinal cline in *lacustris*¹.

The freshwater species *lacustris* has an immense circumpolar distribution throughout much of the holararctic region. In the southerly parts of its range the life-span appears to be 1 or 2 years and there is a distinct spring - summer reproductive season in which females may produce 2-3 broods (Hynes 1955; Hynes & Harper 1972). This reproductive strategy is similar to that of *duebeni* (Hynes 1954; Kinne 1959; Sheader 1983). In more northerly waters, however, *lacustris* has a life-span of up to 3-4 years and it produces only 1 brood in the very short Arctic summer (Bjerknes 1974; DeMarch 1981, 1982), resembling the Arctic marine species *setosus* and *wilkitzkii* referred to earlier in this article. One may therefore predict that mean egg size in northern populations of *lacustris* should be larger than in southern populations and, where only one brood is produced each year, the number of eggs produced may also be relatively large (per standard length female), in order to maximise the female's reproductive effort. Moreover, as in *wilkitzkii*, the reproductive

resting period might occur earlier (in mid summer) than in southern populations, and at intermediate latitudes there may be a long precopulatory mate-carrying period under ice during autumn-winter (Bjerknes 1974; DeMarch 1981), associated with mating and production of a second clutch of eggs in spring. These suppositions are based on rather fragmentary evidence in the literature and point to a need for more detailed studies on natural populations at different latitudes. The same points obviously apply to other malacostracan crustaceans, such as the freshwater isopod *Asellus aquaticus* (Strus & Blejec 1983; Vitagliano Tadini & Migliore 1985; Vitagliano Tadini et al. 1988). It is widely believed that each generation of *A. aquaticus* usually has only one brood, but in fact there are several broods per generation in some populations (see Gledhill et al. 1993).

The energetic cost of reproduction, and strategies in response to stress

The reproductive process has a metabolic cost, including the amount of energy required to produce a batch of eggs and brood them, although egg production is energetically more efficient than the production of somatic mass, i.e. growth of the parent's body tissues (Calow 1983; Sibly & Calow 1986). Another cost of reproduction is the probability that parental survival will be decreased, exemplified by the fact that males generally live longer than females. Steele & Steele (1986a) experimentally examined the effects of continuous breeding in saltwater *lawrencianus* kept at various constant photoperiods, under some of which the females stopped breeding. Their survival rate (at 10°C) is significantly greater than that of continuously-breeding females (Fig. 15A). In a second experiment, individuals reaching sexual maturity at a relatively early age (ca. 30 days at 20°C) have a lower life-expectancy than those taking longer to reach maturity (Fig. 15B).

In stressful circumstances where metabolism of the female is adversely affected, e.g. when exposed to pollutants, or parasites, or when food is scarce, the animal's "scope for growth" is reduced or stops altogether, thereby decreasing the amount of energy available for reproductive effort as well as decreasing the individual's probability of survival (Naylor et al. 1989; Calow & Sibly 1990; Maltby 1992). For example, cadmium is more toxic to mature females of *pulex* than it is to males, recently-moulted females being especially susceptible (McCahon & Pascoe 1988). McCahon et al. (1991) and Pascoe et al (1991) also found that feeding rates of *pulex* are reduced when exposed to pollutants, and adult *pulex* in precopulatory amplexus are more likely to separate and abandon precopula. Reproductive pairing is also greatly reduced in *kischineffensis* exposed to pollutants (Meliyan 1992).

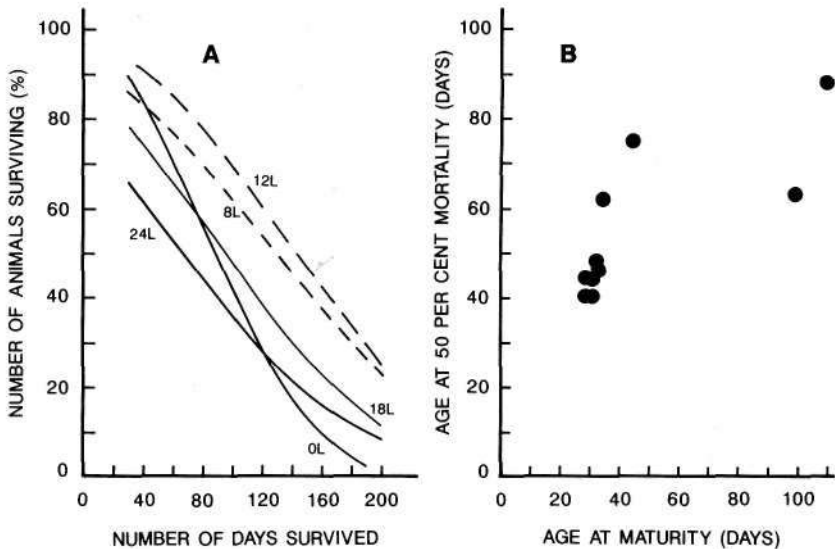


FIG. 15. Saltwater *lawrencianus* were exposed to various photoperiods which either stimulated or stopped reproduction at 10°C in experimental cultures. (A), in continuously-breeding females (solid lines) at photoperiods of 18L:6D (18 hours light and 6 hours dark), 0L:24D and 24L:0D, survival is lower than in non-breeding females (broken lines) where breeding stopped at photoperiods of 12L:12D, 8L:16D and 4L:20D (not shown; very similar to 12L:12D). Lines are survival curves fitted by probit analysis. (B), when newly-hatched young were kept at 20°C, some individuals became sexually mature after 30–35 days; of these 50% survived for another 40–50 days. Other juveniles took longer to reach maturity, after 40 to 110 days; of these 50% survived for a further 60–90 days. Thus early-maturing females had shorter life-spans. (After Steele & Steele 1986a for *lawrencianus* from Witless Bay, Newfoundland).

When stressed by experimental exposure to zinc, *pulex* eats less food (conditioned alder leaves) and therefore absorbs less energy. Fecundity remains unaltered but the offspring are significantly smaller, which suggests that reproductive effort may be reduced by reducing egg size; the percentage of aborted broods also increases (Maltby & Naylor 1990). Reproductive (energetic) investment in fewer, larger offspring (and, presumably, fewer but larger eggs) also occurs in the isopod *Asellus aquaticus* living in polluted water (Tolba & Holdich 1981; Maltby 1991).

Female behaviour

When considering the various reproductive strategies adopted by *Gammarus* males, research so far has concentrated on aspects of the male's behaviour in selecting a potential mate (see Sutcliffe 1993), and it appears that males exercise a strong element of choice in selecting females which are reproductively acceptable, including large body size. In contrast, research on the reproductive strategies of females has been focussed on aspects of egg production and the response to environmental variables, especially temperature and daylength. Little has been done on the female's precopulatory and brooding behaviour, but she is not entirely passive in the matter of mate selection when pairing takes place (Borowsky 1991; Dunham & Hurshman 1991), and various authors mention that females, particularly larger (older) ones, may reject the advances of some males and literally "kick them out"! (e.g. Clemens 1950; Ward 1984a).

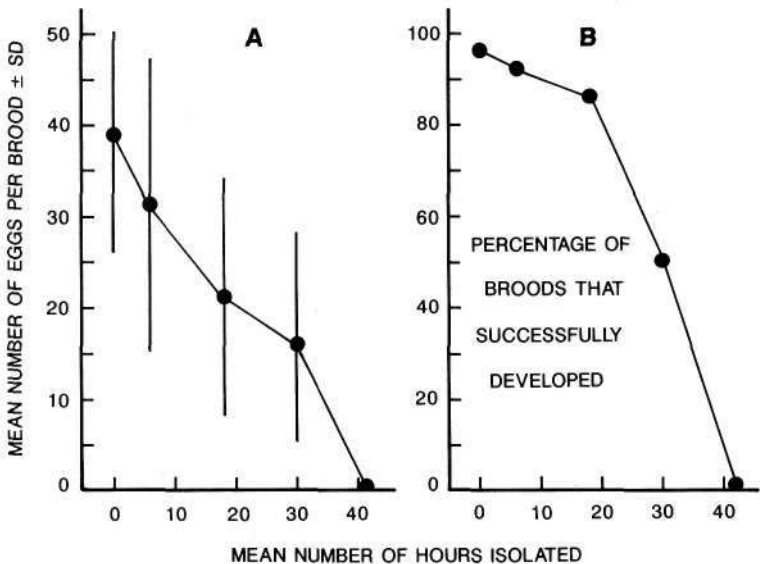


FIG. 16. Fecundity and hatching success are reduced in saltwater *palustris* when copulation is experimentally delayed at ca. 22°C. (A), mean numbers of eggs per brood are reduced when females in precopulatory amplexus are separated from the guarding males, kept with other females until they moult, and then isolated for periods of up to 40 hours after the moult before a male partner is reintroduced to induce ovulation and to fertilise the eggs. Vertical bars shown standard deviations from the means. (B), the hatching success of broods is also reduced when copulation is delayed by isolating the females, as above. (After Borowsky 1988 from *palustris* from Jamaica Bay, Brooklyn, New York).

Females (and males) of *pulex* may postpone their moult in the absence of a mate, and also postpone egg-laying if they moult when no male is present (in experimental situations), although some other species do lay eggs - which are then aborted in the absence of fertilisation (Ward 1984b)

The importance of mating immediately after the female's moult has already been stressed (Sutcliffe 1992, 1993). When copulation in the saltwater species *palustris* was experimentally delayed, by keeping females separate from males for periods of up to 40 hours after the female had moulted, the number of eggs subsequently laid was markedly decreased, being halved after 30 hours and falling to zero after 40 hours (Fig. 16A). This reduction in fecundity may have been partly due to a delay in the female's moult, in the enforced absence of a male, as well as a direct effect of delayed copulation after the moult, i.e. the absence of a stimulus to ovulate. Like *pulex*, *palustris* does not ovulate without prior copulation (Borowsky 1988). In addition to reduced fecundity, the survival of those broods which subsequently developed was also greatly reduced when copulation was prevented for more than a few hours (Fig. 16B). Clearly, reproductive success is dependent on the formation of a close pair bond and an uninterrupted moult by the female, followed immediately by ovulation, deposition of sperms by the male, and early fertilisation of eggs in the broodpouch. Successful development of embryos to hatching is primarily dependent on physical - chemical features in the environment, e.g. water quality (see section above) and temperature (see Sutcliffe 1992), but females of saltwater species display protective behaviour towards their developing embryos and hatchlings (Borowsky 1980; 1983).

Note added in proof

Dr M. Pockl (1993) has a paper in press which reports on egg volumes and reproductive effort in two freshwater species, *fossarum* and *roeseli*, in Austrian streams.

Acknowledgements

My grateful thanks are due to Ian Pettman and his staff in the FBA's library for their help in obtaining references, and Rosalie Sutcliffe for help in preparing the bibliography.

References

- Borowsky, B. (1980). Factors that affect juvenile emergence in *Gammarus palustris* (Bousfield, 1969). *Journal of Experimental Marine Biology and Ecology*, 42, 213-223.

- Borowsky, B. (1983). Placement of eggs in their brood pouches by females of the amphipod Crustacea *Gammarus palustris* and *Gammarus mucronatus*. *Marine Behaviour and Physiology*, 9, 319-325.
- Borowsky, B. (1988). Delaying copulation in the amphipod *Gammarus palustris*: effects on female fecundity and consequences for the frequency of amplexus. *Marine Behaviour and Physiology*, 13, 359-368.
- Borowsky, B. (1991). Patterns of reproduction of some amphipod crustaceans and insights into the nature of their stimuli. In *Crustacean Sexual Biology* (eds R. T. Bauer & J. W. Martin), pp. 33-49. Columbia University Press, New York.
- Bjerknes, V. (1974). Life cycle and reproduction of *Gammarus lacustris* C.O. Sars (Amphipoda) in a lake at Hardangervidda, western Norway. *Norwegian Journal of Zoology*, 22, 39-43.
- Brzezinska-Blaszczyk, E. & Jazdzewski, K. (1980). Reproductive cycle of *Gammarus fossarum* Koch (Crustacea, Amphipoda) in different thermic conditions. *Acta Universitatis Lodziensis, Series 2*, 33, 129-153.
- Calow, P. (1983). Energetics of reproduction and its evolutionary implications. *Biological Journal of the Linnean Society*, 20, 153-165.
- Calow, P. & Sibly, R. M. (1990). A physiological basis of population processes: ecotoxicological implications. *Functional Ecology*, 4, 283-288.
- Chambers, M. R. (1977). The population ecology of *Gammarus tigrinus* (Sexton) in the reed beds of the Tjeukemeer. *Hydrobiologia*, 53, 155-164.
- Clemens, H. P. (1950). Life cycle and ecology of *Gammarus fasciatus* Say. *Franz Theodore Stone Institute of Hydrobiology Series of Contributions*, 12, 1-63. Ohio State University.
- DeMarch, B. G. E. (1981). *Gammarus lacustris lacustris* C.O. Sars. In *Manual for the Culture of Selected Freshwater Invertebrates* (ed. S. G. Lawrence), pp. 79-94. Canadian Special Publication of Fisheries and Aquatic Sciences No. 54. Department of Fisheries and Oceans, Ottawa.
- DeMarch, B. G. E. (1982). Decreased day length and light intensity as factors inducing reproduction in *Gammarus lacustris lacustris* Sars. *Canadian Journal of Zoology*, 60, 2962-2965.
- Dennert, H. G. (1975). The variability of the dimensions of the merus of the fifth pereopod in the amphipod *Gammarus duebeni* Liljeborg, 1895. *Bijdragen Tot de Dierkunde*, 45, 1-19.
- Doyle, R. W. & Hunte, W. (1981). Demography of an estuarine amphipod (*Gammarus lawrencianus*) experimentally selected for high "r": a model of the genetic effects of environmental change. *Canadian Journal of Fisheries and Aquatic Sciences*, 38, 1120-1127.
- Fenchel, T. M. (1987). *Ecology - Potentials and Limitations*. Excellence in Ecology No. 1, Ecology Institute, Oldendorf/Luhe. 206 pp.
- Fenchel, T. M. & Kolding, S. (1979). Habitat selection and distribution

- patterns of five species of the amphipod genus *Gammarus*. *Oikos*, 33, 316-322.
- Foessler, F. & Schrimpf, E. (1985). Gammarids in streams of Northern Bavaria, F.R.G. II. The different hydrochemical habitats of *Gammarus fossarum* Koch, 1835 and *Gammarus roeseli* Gervais, 1835. *Archiv für Hydrobiologie*, 104, 269-286.
- Fredette, T. J. & Diaz, R. J. (1986). Life history of *Gammarus mucronatus* Say (Amphipoda, Gammaridae) in warm temperate estuarine habitats, York River, Virginia. *Journal of Crustacean Biology*, 6, 57-78.
- Gable, M. F. & Croker, R. A. (1977). The salt marsh amphipod, *Gammarus palustris* Bousfield, 1969 at the northern limit of its distribution. I. Ecology and life cycle. *Estuarine and Coastal Marine Science*, 5, 123-134.
- Gledhill, T., Sutcliffe, D. W. & Williams, W. D. (1993). British Freshwater Crustacea Malacostraca: a key with ecological notes. *Scientific Publications of the Freshwater Biological Association*, No. 52.
- Goedmakers, A. (1981a). Population dynamics of three gammarid species (Crustacea, Amphipoda) in a French chalk stream. II. Standing crop. *Bijdrage Tot de Dierkunde*, 51, 31-69.
- Goedmakers, A. (1981b). Population dynamics of three gammarid species (Crustacea, Amphipoda) in a French chalk stream. IV. Review and implications. *Bijdrage Tot de Dierkunde*, 51, 181-190.
- Goedmakers, A. & Pinkster, S. (1981). Population dynamics of three gammarid species (Crustacea, Amphipoda) in a French chalk stream. III. Migration. *Bijdrage Tot de Dierkunde*, 51, 145-180.
- Hynes, H. B. N. (1954). The ecology of *Gammarus duebeni* Lilljeborg and its occurrence in fresh water in western Britain. *Journal of Animal Ecology*, 23, 38-84.
- Hynes, H. B. N. (1955). The reproductive cycle of some British freshwater Gammaridae. *Journal of Animal Ecology*, 24, 352-387.
- Hynes, H. B. N. & Harper, F. (1972). The life histories of *Gammarus lacustris limnaeus* and *G. pseudolimnaeus* in southern Ontario. *Crustaceana Supplement*, 3, 329-341.
- Iversen, T. B. & Jesen, J. (1977). Life-cycle, drift and production of *Gammarus pulex* L. (Amphipoda) in a Danish spring. *Freshwater Biology*, 7, 287-296.
- Jankovic, M. (1983). The contribution to the ecological studies of *Rivulogammarus balcanicus*. *Bulletin Tome LXXXIII de l'Academie Serbe des Sciences et des Arts Classe des Sciences Naturelles et Mathematiques Sciences Naturelles*, 24, 5-15.
- Jazdzewski, K. (1973). Ecology of gammarids in the bay of Puck. *Oikos Supplementum*, 15, 121-126.
- Karaman, G. S. & Pinkster, S. (1987). Freshwater *Gammarus* species from

- Europe, North Africa and adjacent regions of Asia (Crustacea, Amphipoda). Part III. *Gammarus balcanicus*-group and related species. *Bijdragen Tot de Dierkunde*, 47, 165-196.
- Karaman, G. S. & Ruffo, S. (1986). Amphipoda: *Niphargus*-group (Niphargidae sensu Bousfield, 1982). In *Stygofauna Mundi. A Faunistic, Distributional, and Ecological Synthesis of the World Fauna Inhabiting Subterranean Waters (Including the Marine Interstitial)*, (ed. L. Botosaneanu), pp. 514-534. E. J. Brill/Dr W. Backhuys, Leiden.
- Kinne, O. (1959). Ecological data on the amphipod *Gammarus duebeni*. A monograph. *Veroffentlichungen des Instituts fur Meeresforschung in Bremerhaven*, 6, 177-202.
- Kinzelbach, R. & Claus, W. (1977). Die Verbreitung von *Gammarus fossarum* Koch, 1835, *G. pulex* (Linnaeus, 1758) und *G. roeselii* Gervais, 1835, in den linken Nebenflüssen des Rheins zwischen Wieslauter und Nahe. *Crustaceana Supplement*, 4, 164-172.
- Kolding, S. (1981). Habitat selection and life cycle characteristics of five species of the amphipod genus *Gammarus* in the Baltic. *Oikos*, 37, 173-178.
- Kolding, S. (1985). Genetic adaptation to local habitats and speciation processes within the genus *Gammarus* (Amphipoda: Crustacea). *Marine Biology*, 89, 249-255.
- Kolding, S. & Fenchel, T. M. (1981). Patterns of reproduction in different populations of five species of the amphipod genus *Gammarus*. *Oikos*, 37, 167-172.
- Leineweber, P. (1985). The life-cycles of four amphipod species in the Kattegat. *Holarctic Ecology*, 8, 165-174.
- Maltby, L. (1991). Pollution as a probe of life-history adaptation in *Asellus aquaticus* (Isopoda). *Oikos*, 61, 11-18.
- Maltby, L. (1992). The use of the physiological energetics of *Gammarus pulex* to assess toxicity: a study using artificial streams. *Environmental Toxicology and Chemistry*, 11, 79-85.
- Maltby, L. & Naylor, C. (1990). Preliminary observations on the ecological relevance of the *Gammarus* 'scope for growth' assay: effect of zinc on reproduction. *Functional Ecology*, 4, 393-397.
- Marchant, R. (1981). The ecology of *Gammarus* in running water. In *Perspectives in Running Waters Ecology* (eds M. A. Lock & D. D. Williams), pp. 225-249. Plenum Press, New York and London.
- Marchant, R. & Hynes, H. B. N. (1981). The distribution and production of *Gammarus pseudolimnaeus* (Crustacea: Amphipoda) along a reach of the Credit River, Ontario. *Freshwater Biology*, 11, 169-182.
- Mashiko, K. (1990). Diversified egg and clutch sizes among local populations of the fresh-water prawn *Macrobrachium nipponense* (de Haan). *Journal of Crustacean Biology*, 10, 306-314.

- McCahon, C. P. & Pascoe, D. (1988). Increased sensitivity to cadmium of the freshwater amphipod *Gammarus pulex* (L.) during the reproductive period. *Aquatic Toxicology*, **13**, 183-194.
- McCahon, C. P., Poulton, M. J., Thomas, P. C., Xu, Q., Pascoe, D. & Turner, C. (1991). Lethal and sub-lethal toxicity of field simulated farm waste episodes to several freshwater invertebrate species. *Water Research*, **25**, 661-671.
- Meijering, M. P. D. (1991). Lack of oxygen and low pH as limiting factors for *Gammarus* in Hessian brooks and rivers. *Hydrobiologia*, **223**, 159-169.
- Meliyan, R. I. (1992). Effect of pesticides on reproductive function of the freshwater amphipod *Gammarus kischineffensis*. *Hydrobiological Journal*, **27(6)**, 33-36.
- Miller, S. A. (1982). The life history of *Gammarus pseudolimnaeus* Bousfield in a central Wisconsin stream (Amphipoda, Gammaridea). *Crustaceana*, **43**, 89-99.
- Musko, I. (1990). Qualitative and quantitative relationships of Amphipoda (Crustacea) living on macrophytes in Lake Balaton (Hungary). *Hydrobiologia*, **191**, 269-274.
- Naylor, C, Adams, J. & Greenwood, P. (1988). Population dynamics and adaptive sexual strategies in a brackish water crustacean, *Gammarus duebeni*. *Journal of Animal Ecology*, **57**, 493-507.
- Naylor, C, Maltby, L. & Calow, P. (1989). Scope for growth in *Gammarus pulex*, a freshwater benthic detritivore. *Hydrobiologia*, **188/189**, 517-523.
- Nilsson, L. M. (1977). Incubation time, growth and mortality of the amphipod *Gammarus pulex* under laboratory conditions. *Oikos*, **29**, 93-98.
- Pascoe, D., Gower, D. E., McCahon, C. P., Poulton, M. J., Whiles, A. J. & Wulfhorst, J. (1991). Behavioral responses to pollutants - application in freshwater bioassays. In *Bioindicators and Environmental Management* (eds D. W. Jeffrey & B. Madden), pp. 245-254. Academic Press, London.
- Pinkster, S. & Broodbakker, N. W. (1980). The influence of environmental factors on distribution and reproductive success of *Eulimnogammarus obtusatus* (Dahl, 1938) and other estuarine gammarids. *Crustaceana Supplement*, **6**, 225-241.
- Pinkster, S., Smit, H. & Brandse-de Jong, N. (1977). The introduction of the alien amphipod *Gammarus tigrinus* Sexton, 1939, in the Netherlands and its competition with indigenous species. *Crustaceana Supplement*, **4**, 91-105.
- Pockl, M. (1992). Effects of temperature, age and body size on moulting and growth in the freshwater amphipods *Gammarus fossarum* and *G.*

- roeseli*. *Freshwater Biology*, **27**, 211-225.
- Pockl, M. (1993). Reproductive potential and lifetime potential fecundity of the freshwater amphipods *Gammarus fossarum* and *G. roeseli* in Austrian streams and rivers. *Freshwater Biology*, in press.
- Pockl, M. & Humpesch, U. H. (1990). Intra-and inter-specific variations in egg survival and brood development time for Austrian populations of *Gammarus fossarum* and *G. roeseli* (Crustacea: Amphipoda). *Freshwater Biology*, **23**, 441-455.
- Roux, A. L. (1969). L'extension de l'aire de repartition géographique de *Gammarus roeseli* en France nouvelles données. *Annales de Limnologie*, **5**, 123-127.
- Roux, A. L. (1971). Les Gammare du groupe *pulex* essai de systématique biologique. II. Quelques caractéristiques écologiques et physiologiques. *Archives de Zoologie Experimental et Generate*, **112**, 471-503.
- Roux, C. & Roux, A. L. (1980). Repartition écologique et métabolisme respiratoire de *Gammarus roeselii* Gervais, 1835. *Crustaceana Supplement*, **6**, 148-159.
- 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.
- Shedden, M. (1983). The reproductive biology and ecology of *Gammarus duebeni* (Crustacea, Amphipoda) in southern England. *Journal of the Marine Biological Association, United Kingdom*, **63**, 517-540.
- Sibly, R. M. & Calow, P. (1986). *Physiological Ecology of Animals. An Evolutionary Approach*. Blackwell Scientific Publications. 179 pp.
- Skadsheim, A. (1982). The ecology of intertidal amphipods in the Oslofjord. The life cycles of *Chaetogammarus marinus* and *C. stoerensis*. *Pubblicazioni Stazione Zoologica Napoli (Marine Ecology)*, **3**, 213-224.
- Skadsheim, A. (1984a). Coexistence and reproductive adaptations of amphipods: the role of environmental heterogeneity. *Oikos*, **43**, 94-103.
- Skadsheim, A. (1984b). Life cycles of *Gammarus oceanicus* and *G. salinus* (Amphipoda) in the Oslofjord, Norway. *Holarctic Ecology*, **7**, 262-270.
- Skadsheim, A. (1989). Regional variation in amphipod life history: effects of temperature and salinity on breeding. *Journal of Experimental Marine Biology and Ecology*, **127**, 25-42.
- Southwood, T. R. E. (1988). Tactics, strategies and templates. *Oikos*, **52**, 3-18.
- Steele, D. H. & Steele, V. J. (1975a). The biology of *Gammarus* (Crustacea, Amphipoda) in the northwestern Atlantic. IX. *Gammarus wilkitzkii* Birula, *Gammarus stoerensis* Reid and *Gammarus mucronatus* Say. *Canadian Journal of Zoology*, **53**, 1105-1109.
- Steele, D. H. & Steele, V. J. (1975b). The biology of *Gammarus*

- (Crustacea, Amphipoda) in the northwestern Atlantic. XI. Comparison and discussion. *Canadian Journal of Zoology*, 53, 1116-1126.
- Steele, D. H. & Steele, V. J. (1975c). Egg size and duration of embryonic development in Crustacea. *Internationale Revue der Gesamten Hydrobiologie und Hydrographie*, 60, 711-715.
- Steele, D. H. & Steele, V. J. (1986a). The cost of reproduction in the amphipod *Gammarus lawrencianus* Bousfield, 1956. *Crustaceana*, 51, 176-182.
- Steele, V. J. & Steele, D. H. (1986b). The influence of photoperiod on the timing of reproductive cycles in *Gammarus* species (Crustacea, Amphipoda). *American Zoologist*, 26, 469-467.
- Straskraba, M. (1966). On the distribution of the macrofauna and fish in two streams, Lucina and Moravka. *Archiv fur Hydrobiologie*, 61, 515-536.
- Strus, J. & Blejec, A. (1983). Reproductive activity in *Asellus aquaticus* (Crustacea, Isopoda) from Ljubljansko Barje. *Bioloski Vestnik*, 31, 83-92.
- Sutcliffe, D. W. (1972). An examination of subspecific differences in the merus of the fifth walking leg of the amphipod *Gammarus duebeni* Lilljeborg. *Freshwater Biology*, 2, 203-216.
- Sutcliffe, D. W. (1984). Quantitative aspects of oxygen uptake by *Gammarus* (Crustacea, Amphipoda): a critical review. *Freshwater Biology*, 14, 443-489.
- Sutcliffe, D. W. (1991). British freshwater malacostracan "shrimps". *Freshwater Forum*, 1, 225-237.
- Sutcliffe, D. W. (1992). Reproduction in *Gammarus* (Crustacea: Amphipoda): basic reproductive processes. *Freshwater Forum*, 2, 102-128.
- Sutcliffe, D. W. (1993). Reproduction in *Gammarus* (Crustacea: Amphipoda): male strategies. *Freshwater Forum*, 3, in press.
- Sutcliffe, D. W. & Carrick, T. R. (1981). Number of flagellar segments and moulting in the amphipod *Gammarus pulex*. *Freshwater Biology*, 11, 497-509.
- Sutcliffe, D. W., Carrick, T. R. & Willoughby, L. G. (1981). Effects of diet, body size, age and temperature on growth rates in the amphipod *Gammarus pulex*. *Freshwater Biology*, 11, 183-214.
- Teichmann, W. von (1982). Lebenslaufe und Zeitplane von Gammariden unter ökologischen Bedingungen. *Archiv fur Hydrobiologie Supplement*, 64, 240-306.
- Thomas, P. C, Turner, C. & Pascoe, D. (1991). An assessment of field and laboratory methods for evaluating the toxicity of ammonia to *Gammarus pulex* (L.) - effects of water velocity. In *Bioindicators and Environmental Management* (eds D. W. Jeffrey & B. Madden), pp. 353-363. Academic Press, London.
- Tolba, M. R. & Holdich, D. M. (1981). The effect of water quality on the

- size and fecundity of *Asellus aquaticus* (Crustacea: Isopoda). *Aquatic Toxicology*, 1, 101-112.
- VanDolah, R. F. & Bird, E. (1980). A comparison of reproductive patterns in epifaunal and infaunal gammaridean amphipods. *Estuarine and Coastal Marine Science*, 11, 593-604.
- VanDolah, R. F., Shapiro, L. E. & Rees, C. P. (1975). Analysis of an intertidal population of the amphipod *Gammarus palustris* using a modified version of the egg-ratio method. *Marine Biology*, 33, 323-330.
- Vassallo, L. & Steele, D. H. (1980). Survival and growth of young *Gammarus lawrencianus* Bousfield, 1956, on different diets. *Crustaceana Supplement*, 6, 118-125.
- Vitagliano Tadini, C. & Migliore, L. (1985). Regulation of the numerical density in geographical populations of *Asellus aquaticus* (L.). *Atti Della Accademia Nazionale dei Lincei, Memorie Classe di Scienze Fisiche, Matematiche e Naturali, Series 8*, 18, Sezione III, Fascicolo 1, 1-26.
- Vitagliano Tadini, C., Fano, E. A. & Colangelo, M. (1988). The life history evolution of *Asellus aquaticus* (L.) explains its geographical distribution. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, 23, 2099-2106.
- Vobis, H. (1973). Rheotaktisches Verhalten einiger Gammarus-Arten bei verschiedenem Sauerstoffgehalt des Wassers. *Helgolander Wissenschaftliche Meeresuntersuchungen*, 25, 495-508.
- Ward, P. I. (1984a). The effects of size on the mating decisions of *Gammarus pulex* (Crustacea Amphipoda). *Zeitschrift für Tierpsychologie*, 64, 174-184.
- Ward, P. I. (1984b). *Gammarus pulex* control their moult-timing to secure mates. *Animal Behaviour*, 32, 927.
- Ward, P. I. (1986). A comparative field study of the breeding behaviour of a stream and pond population of *Gammarus pulex* (Amphipoda). *Oikos*, 46, 29-36.
- Welton, J. S. (1979). Life-history and production of the amphipod *Gammarus pulex* in a Dorset chalk stream. *Freshwater Biology*, 9, 263-275.
- Welton, J. S. & Clarke, R. T. (1980). Laboratory studies on the reproduction and growth of the amphipod, *Gammarus pulex*, *Journal of Animal Ecology*, 49, 581-592.