

A review of the reproductive bionomics of aquatic gammaridean amphipods: variation of life history traits with latitude, depth, salinity and superfamily

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Abstract

Life history traits (mean and maximum body length of females, number of embryos per brood = brood size, embryo diameter, number of broods per female, lifespan of females) for 302 populations of aquatic gammaridean amphipods, representing 214 species in 16 superfamilies, were reviewed. The variation of these traits, of lifetime potential fecundity (i.e. the number of embryos produced per female lifespan) and of reproductive potential (i.e. the number of embryos produced per female per year), with temperature (latitude), depth, salinity and superfamily, was investigated by various univariate and multivariate methods. Gammaridean amphipods comprise semelparous and iteroparous populations and species, with semiannual, annual, biannual or perennial life cycles. However, most gammarideans studied so far are iteroparous annuals. Body length explains most of the variation in brood size and embryo diameter. The reproductive potential may be increased by increasing body size for a constant breeding frequency, by increasing brood size at the expense of smaller embryos, by increasing breeding frequency for a constant lifespan at the expense of smaller individual broods and/or embryos, and by increasing longevity for a constant breeding frequency and brood size. Combinations of these different options constitute the life history patterns of gammarideans, which vary across superfamilies, latitude and depth, and cannot simply be explained by variations in body length. High latitude species were generally characterized by biannual or perennial life histories, large body size, delayed maturity, and single or few broods with many, relatively large embryos; converse sets of traits characterized low latitude species. Deep-living species had relatively smaller broods and embryos than their shallow-living relatives, yet did not produce more broods. However, different superfamilies dominated in different habitats. The importance of natural selection relative to phylogenetic (historical) and physiological constraints in the forging of these patterns is discussed.

Introduction

Gammaridean amphipods constitute a diverse and ubiquitous suborder of Crustacea (Bousfield, 1983). They are generally dioecious, with external fertilization, and the embryos are carried by females in a ventral brood pouch, called marsupium (Schram, 1986). Detailed accounts of the reproductive and brooding behaviour of a few

gammarideans have been produced (Kinne, 1954; Borowsky, 1983, 1984, 1986; Borowsky & Borowsky, 1987; Shillaker & Moore, 1987). There exists a very large body of literature on the life history traits of gammaridean amphipods, which several workers have attempted to synthesize: reviews have either been broad (Morino, 1978; Nelson, 1980; Van Dolah & Bird, 1980; Wildish, 1982) or narrow in taxonomic scope, the

latter concentrating on the superfamily Talitroidea (Wildish, 1988), the family Gammaridae (Steele & Steele, 1975c), and on the genera *Orchestia* (Wildish, 1979) and *Ampelisca* (Bellan-Santini & Dauvin, 1988).

Morino (1978) proposed a simple classification of gammaridean life histories based on breeding rhythms (seasonal or year-round breeding) and longevity, and suggested that life history types were distributed according to latitudinal (temperature) gradients. He predicted semiannual populations for tropical regions, annual populations for temperate regions, and biannual or perennial populations for polar regions. Wildish (1982) recognized six basic life histories within the Gammaridea: multivoltine (more than one generation per year) semiannual, univoltine (one generation per year) or multivoltine annual, semelparous (single-brooded) biannual, and semelparous or iteroparous (multiple-brooded) perennial. Females of semiannual species or populations grow rapidly, mature early and are very fecund; this set of traits is presumably associated with warm and tropical habitats (for confirmation in talitroids, see Wildish, 1988) or with populations subjected to high rates of predation. In contrast, females of biannual or perennial species or populations tend to grow more slowly, mature later, and are less fecund; this set of traits is presumably characteristic of populations in habitats where mortality is influenced by unpredictable physical factors. Both Morino's and Wildish's classifications of gammaridean life histories were derived from relatively few observations and thus need to be tested against larger data sets.

Nelson (1980) compared average body length of reproductive females and number of embryos per brood (called brood size hereafter) for several species of aquatic gammaridean amphipods. He concluded that females were larger and embryos more numerous per brood in 'epibenthic' versus 'endobenthic' gammarideans, in brackish- versus fresh- and saltwater gammarideans, and in the family Gammaridae versus the Ampeliscidae and Haustoriidae. Furthermore, semelparous species produced more embryos per brood than iteroparous species. Although his conclusions relating

to fecundity have been widely accepted, they are questionably based on comparisons of brood size alone or of the ratio of brood size to body size; the former does not take into account the known positive relation between brood size and body size (e.g. Van Dolah & Bird, 1980) and the latter is a statistically incorrect way to account for this relation.

Van Dolah & Bird (1980) reported that 'epibenthic' species of aquatic gammarideans had more, smaller embryos per brood than 'endobenthic' species, for a constant female body size, and found positive correlations between latitude and embryo size for populations of a given species. They hypothesized that 'adult mortality risk is correlated positively with egg number and inversely with egg size'. Nelson (1980) gave this adaptive hypothesis strong support, but it was challenged by Fenwick (1984) who argued that Nelson and Van Dolah & Bird had misclassified species into the epi- and endobenthic categories and that their reviews were too narrow in taxonomic scope for meaningful comparisons.

There exists compelling evidence of habitat effects on the life history traits of individual species of gammaridean amphipods. Body size at maturity, brood size, size of embryos, number of broods per female, age at maturity, and breeding season have been reported to vary intraspecifically with temperature, latitude, depth, salinity or exposure to predators (e.g. Hynes, 1954; Segerstråle, 1967, 1970; Fish & Preece, 1970; Strong, 1972; Wiederholm, 1973; Morino, 1978; Pinkster & Broodbakker, 1980; Kolding & Fenchel, 1981; Sainte-Marie & Brunel, 1983; Sheader, 1983; Skadsheim, 1984, 1989; Clarke *et al.*, 1985; Leineweber, 1985; Siegfried, 1985; Fredette & Diaz, 1986; Bellan-Santini & Dauvin, 1988; Naylor *et al.*, 1988). In particular, for individual boreal gammaridean species, a northerly (or decreasing temperature) trend of bigger bodies and smaller broods relative to body size appears to be the rule (D.H. Steele, 1967; Steele & Steele, 1975c; Van Dolah & Bird, 1980). If such trends are common to most Gammaridea, they should be obvious at the interspecific level as well. Attributing such variation to environmental or genetic

effects has in practice rarely been possible (Wildish, 1970; Strong, 1972; Skadsheim, 1989).

Considering the apparent limitations of previous general reviews and the relatively large number of recent contributions to the study of the reproduction of aquatic gammaridean amphipods, it seemed timely to undertake a new review. Herein, six life history traits (mean and maximum body length of females and males, brood size, embryo diameter, number of broods per female, life expectancy of females), lifetime potential fecundity (i.e. the number of embryos produced per female lifespan) and reproductive potential (i.e. the number of embryos produced per female per year), were considered in relation to habitat and superfamily. A total of 302 aquatic gammaridean populations, representing 214 species in 16 superfamilies, were reviewed. Relationships among life history traits were explored by simple and partial correlations, and by simple and multiple regressions. Univariate statistics, canonical discriminant analysis, and analysis of covariance were used to quantify variation of reproductive traits across habitats and superfamilies.

The general objectives of this review were two-fold. The first was to determine the extent and nature of correlations among selected life history traits for aquatic gammarideans. Collectively, these traits constitute the life history pattern (I shun the words strategy and tactic), which may be characteristic of populations in specific habitats and superfamilies. The second objective was to contrast life history traits, lifetime potential fecundity and reproductive potential, across habitats and superfamilies, the former being defined following rough temperature, depth and salinity gradients. Life history patterns were then discussed in light of some recent developments in life history theory (habitat templets and r-K-A selection).

Materials and methods

Derivation of data

Published literature on the reproduction of aquatic gammaridean amphipods was reviewed.

My aim was to make the population and species list as exhaustive as possible, but inevitably some publications must have been overlooked, with no prejudice intended. Other publications could not be secured through interlibrary loans or by other means. The sole criterion for inclusion in this study was that reports provide information at least on the mean body length of reproductive females and on the mean number of embryos per brood. Additionally, where available, I gathered information on maximum body length of females and males, on the longevity of reproductive females, on the frequency of brooding during female lifespan (semelparous or iteroparous, and maximum number of broods produced per female), on the diameter of embryos, and on the habitat (temperature, salinity, depth) occupied by individual populations or species. The following remarks pertain to the derivation and presentation of raw data in Appendix 1.

Taxonomic affiliation. The status of each species was verified, especially those appearing in older publications, to ascertain that they had not been synonymized or attributed to a new genus or superfamily. Species were grouped according to superfamily, following Bousfield's (1983) classification of the gammaridean Amphipoda. All species belonging to the '*Gammarus*' complex were referred to the genus *Gammarus*, because attempts to divide the latter have not generated consensus. Of course, the value of predictive regressions and conclusions derived for superfamilies depends closely on the timeliness of the adopted taxonomic groupings.

Some species were studied in more than one site, by the same or different authors. Data from different authors were always included in my review, while those from the same author, based on populations in different areas or seasons, were included only if life history traits or habitats differed markedly. Appendix 1 also presents incidental information for species which were not studied with the purpose of elucidating reproductive bionomics (taxonomy, ecology, genetics or physiology motivated the work). This body of literature was not scrutinized systematically, and

was not the preferred source of data, but was included when species belonged to poorly represented superfamilies or habitats.

Body length of reproductive females. Body length of gammaridean amphipods is generally measured from the anterior end of the cephalon to the distal end of the telson. However, amphipods have occasionally been measured from the anterior end of the cephalon to the base of the telson. Since the telson generally contributes only marginally to total body length, the difference between both measures of body length was presumed to be negligible. When not provided directly in the original study, mean body length was, in decreasing order of preference, derived from raw data, calculated as the average of minimum and maximum body length, or inferred from graphs. In all cases, maximum body length was also noted.

A few workers used relative indices of female body length based on measures of the cephalon (e.g. Goedmakers, 1981; Fenwick, 1985), of an article of the second antennae (Gaylor, 1922), of the basal segment of a pereopod (Moore, 1981), or on a partial measure of body length (e.g. Dexter, 1971; Fish, 1975). While these measures are easier to obtain and less prone to error than total body length, they are obviously less suitable for interspecific comparisons of length-fecundity relationships. Still fewer workers have used female weight as a standard by which to compare number of embryos per brood (e.g. Cheng, 1942; Sameoto, 1969b; Duncan, 1969 for a terrestrial example) or age determined by counts of articles on the antennular flagella of a terrestrial gammaridean (Tamura & Koseki, 1974). Some of the workers who used non-conventional measures of body size provided equations to estimate total body length from the length index or body weight, and their results were incorporated into this review. Ultimately, body volume may prove to be the best measure of amphipod size for comparative purposes (Wildish & Frost, 1991).

Half-range of mature female body length. A statistic was developed to characterize variability in body length of females at maturity. The half-range of

mature female body length, called *HMFBL* for sake of brevity, was determined by the equation

$$HMFBL = BL_{max} - BL_{mean},$$

where *BL* is body length of mature females. This index, corrected for body length, became the *HMFBL* ratio (*HMFBLr*), given by the equation:

$$HMFBLr = (BL_{max} - BL_{mean})/BL_{mean}.$$

The *HMFBL* ratio was intended to serve as an index of the number of broods produced by females, when that information was lacking in the original study. Gammaridean amphipods must moult to oviposit (Charniaux-Cotton, 1985). In iteroparous populations and species, successive brooding instars may be interspaced by resting (V.J. Steele, 1967) or preparatory stages (Ingram & Hessler, 1987). There may be no growth when females moult from preparatory to brooding stages, but moulting from brooding to preparatory stages is apparently always accompanied by an increment in body size (e.g. Bone, 1972; Ingram & Hessler, 1987). When no preparatory or resting stage exists, i.e. broods are carried by each sequential mature instar, females apparently grow at each moult (e.g. Sexton, 1928). Hence, whatever the case may be, there should exist a positive relationship between the *HMFBL* ratio and the number of broods.

Brood size, i.e. number of embryos per brood. Since brood mortality occurs in several gammaridean species, ranging over the full incubation period from 0 to 58.5% of initial oviposited eggs (see review by Moore, 1981), a standard embryo developmental stage should be used to compare brood size. Stage V embryos (*sensu* Thurston, 1968) represent effective recruits, but data for this developmental stage are rarely available and are unreliable because Stage V embryos may temporarily exit the marsupium (e.g. Embury, 1911; Nayar, 1956; Sheader & Chia, 1970; Borowsky, 1980b; Moore, 1981; Shillaker & Moore, 1987). My alternative was to consider numbers of Stage I embryos, for which most authors have

provided data. However, a small number of studies have been included in which authors did not specify the embryo developmental stage or counted only Stage II or III embryos. Still fewer studies, mainly of deep-sea populations, provided only counts of oocytes in gonads. Brood size may be overestimated for some of these populations because oocyte maturation may be accompanied by a decrease in oocyte numbers (Hessler *et al.*, 1978). Where mean brood size was not given directly in the original study, it was, in order of decreasing preference, calculated from raw data, predicted from regression lines of brood size on body length, estimated as the mean of minimum and maximum values, or inferred from graphs.

Embryo diameter was the mean of measurements of the long and short axes of Stage I embryos. Several authors gave only the measure of the long axis of embryos, so it was necessary to convert these data for comparisons. For this purpose, measurements of the small axis (*SA*, in mm), of the long axis (*LA*, in mm) and of embryo diameter (*ED*, in mm) of Stage I embryos of 19 species (from Ivanov, 1961; Kannevorf, 1965; Bregazzi, 1972; Thurston, 1974; Morino, 1978) were regressed and the following predictive regression equations determined:

$$SA = 0.7556 LA + 0.0263, r^2 = 0.984$$

$$ED = 0.8778 LA + 0.0131, r^2 = 0.996$$

$$ED = 1.1510 SA - 0.0113, r^2 = 0.995$$

$$\text{range: } SA = 0.35\text{--}1.15 \text{ mm, } LA = 0.43\text{--}1.53 \text{ mm}$$

The size of Stage I embryos in deep-sea species was estimated by authors or myself with growth curves of ova (in Hessler *et al.*, 1978; Ingram & Hessler, 1987).

Semelparity, iteroparity and maximum number of broods. In most of the reviewed literature, the semelparous or iteroparous condition of females was determined by examination of the ovaries. Alternatively, the maximum number of broods produced per female was determined from size-frequency (polymodal) analyses, growth factors

and inferred moult instars, or laboratory cultures. The maximum number of broods may vary in different generations of multivoltine populations: in these cases, upper values were used herein.

Lifespan of females was recorded where available from the literature. Investigators mainly used cohort analysis or laboratory cultures to determine age. Several authors presented a range of lifespans, corresponding to life expectancies of females in different generations (summer or winter) of multivoltine populations, so upper values were retained for analyses.

Alternative indices of fecundity. *Lifetime potential fecundity* (*LF*, in number of embryos per female) is given by the equation:

$$LF = BS * NB,$$

where *BS* is the mean number of embryos in a brood and *NB* is the maximum number of broods produced by a female during her lifespan. Wildish (1982) proposed and discussed another index of fecundity, standardized for a 12-mo lifespan, called the reproductive potential (*R*, in number of embryos female⁻¹ yr⁻¹):

$$R = b * n * p,$$

where *b* is brood size, *n* is the number of broods per year per female, and *p* is the proportion of adult females in relation to the total number of adult females and males present in the population. Maternally-biased sex ratios may increase the number of female descendants and, consequently, of offspring calculated over several generations (Wildish, 1971, 1982). Skewed adult sex ratios are frequent in the Gammaridea (Moore, 1981; Wildish, 1982; Costello & Myers, 1989). However, they may often be unrelated to direct maternal effects: apparent or real biases may result from parasitism (Bulnheim, 1978), from differential longevity (Heller, 1968; Shearer, 1978) or maturation rates (Gable & Croker, 1977) of sexes, from spatial segregation of sexes in the horizontal or vertical planes (e.g. Bregazzi, 1972; Bosworth,

1976; Smith & Baldwin, 1984), or from differential mortality of sexes in the juvenile and subadult stages (Heller, 1968; Moore, 1981). For most gammaridean populations, it may be difficult to ascribe biased sex ratios either to maternal or ecological effects, so I have elected to disregard this variable in my calculations of *reproductive potential* (*RP*, in number of embryos per female per year), which is thus simply:

$$RP = BS * NB * 12/LS,$$

where *BS* is brood size, *NB* is the number of broods per female, and *LS* is the female's lifespan in months.

Temperature. Populations were classified according to habitat temperature either as warm- or cold-living. Warm designated shallow tropical or warm temperate habitats; cold designated polar or cold-temperate habitats, as well as bathyal or abyssal environments. The northern limit of warm areas was set by a line running from the most easterly point of Cape Cod (United States) to the middle of the westerly mouth of the English Channel, to Calais (France), to the southern extremity of the Kyū Shū Island (Japan), and across to the northern border of California (United States). The Mediterranean Sea and inland seas of Europe and eastern Asia were included in the warm habitats. The southern limit of warm areas was set by a line running from the northern border of Argentina, across the Atlantic and Pacific well to the south of the African continent and Australia, through the Strait of Cook (New Zealand), and to Santiago (Chile). Thus, excepting the few deep-living gammarideans, the classifications of populations following temperature in fact reflects a latitudinal separation.

Salinity. Populations were described as inhabiting freshwater, brackish ($\leq 20\%$ average over a tidal cycle) or marine ($> 20\%$ average over a tidal cycle) habitats. Supralittoral and salt-marsh talitroids were classified as marine forms.

Depth. Deep-living populations of gammarideans were those inhabiting waters deeper than 200 m. Shelf-living populations of gammarideans were those encountered in depths less than 200 m, including supralittoral and salt-marsh talitroids.

Treatment of data

Canonical discriminant analysis was used to compare variation of life history traits of populations and species across superfamilies, and across temperature, salinity and depth gradients. In this analysis, linear combinations of independent variables, here the life history traits, are constructed to produce discriminant functions (Legendre & Legendre, 1984). The relative importance of each discriminant function in separating the groups (defined as populations in different habitats or superfamilies) is shown by the percentage of the total eigenvalue and by the strength of the canonical correlation. Group means give the average position of groups in reduced multi-dimensional space when there is more than one discriminant function, or along a simple axis when there is only one discriminant function (i.e. two groups). The standardized canonical coefficients indicate what independent variables contribute most to the discrimination of groups along each of the axes (discriminant functions). Only four life history traits, body length, brood size, embryo diameter and the *HMFBL* ratio, were used in canonical discriminant analyses: this was done to maximize the number of superfamilies under comparison, because data on lifespan were too often lacking. The minimum number of observations necessary for inclusion of a group in analyses was arbitrarily fixed at five. All data were \log_{10} -transformed prior to analyses so they met or approached a normal distribution.

Frequencies were tested for independence of classification criteria by means of the G-test with William's correction (Sokal & Rohlf, 1981). The mean and standard deviation were calculated for life history traits, lifetime potential fecundity and reproductive potential. Group means were compared with the non-parametric Kruskal-Wallis

test, a single-factor analysis of variance by ranks (Sokal & Rohlf, 1981).

Relationships between life history traits were explored through the use of simple (Pearson) and partial correlations. Simple correlations measure the relation between two independent variables; partial correlations measure the relation between two independent variables while holding the effects of other variables constant (Sokal & Rohlf, 1981). Correlation matrices were derived from listwise comparisons of variables, i.e. only populations with complete sets of observations for all life history traits were used.

Predictive (Model I) simple or multiple regressions were calculated for selected relationships. When necessary, slopes (regression coefficients) and elevation of significant regressions were compared by analysis of variance (ANOVA) and covariance (ANCOVA). Note that elevation may be compared only among lines with homogeneous slopes (Sokal & Rohlf, 1981). Prior to all correlation and regression analyses, data were \log_{10} -transformed to satisfy conditions of normality and/or because mean and variance were positively correlated. The interpretation of coefficients for regressions of log-transformed dependent and independent variables has been discussed at length by White & Gould (1965).

Results

General observations

Information on the life history traits of aquatic gammaridean amphipods was available for a total

of 302 populations, representing 214 species in 16 superfamilies (Appendix 1). The vast majority of these populations were from the northern hemisphere. Eight superfamilies were well represented: the Gammaroidea (20.2% of reviewed populations), the Pontoporeioidea (13.9%), the Corophioidea (12.6%), the Lysianassoidea (11.6%), the Eusiroidea (9.3%), the Talitroidea (8.6%) and the Ampeliscoidea (8.0%). Cold and warm water populations accounted for 71.2% and 28.8% of investigated populations, respectively. Populations were predominantly marine (75.8%), and the remaining were from brackish (15.2%) or fresh (9.0%) waters. Finally, 96.4% of reviewed populations were from waters < 200 m deep and 3.6% were from deeper waters.

Extreme values for life history traits reviewed in the literature were the following. The lilljeborgiid *Seborgia minima* (Bousfield, 1970) had the smallest females (0.9 mm mean body length) and broods (1 embryo). The greatest mean body length (≥ 23 cm) and largest mean embryo diameter (~ 9.11 mm) were found in the lysianassoid *Alicella gigantea* (Barnard & Ingram, 1986), while the lysianassoid *Anonyx nugax* produced the largest mean broods (630 embryos), with one ~ 47 -mm female carrying in excess of 950 embryos (Kuznetsov, 1964). The smallest embryos (0.23 mm diameter) were found in the commensal corophiid *Gammaropsis inaequistylis* (Steele *et al.*, 1986). Several gammaridean females live only a few weeks or months (Appendix 1), in contrast to the ~ 13 -yr lifespan of the lysianassoid *Eurythenes gryllus* (Ingram & Hessler, 1987). The lifespan of the abyssal giant

Table 1. Sex-related differences in maximum adult body length (BL), expressed as the relative frequency of total observations (N), for populations from superfamilies of gammaridean amphipods with > 10 observations. Females and males were considered equal in size when the difference in body length between both sexes was < 2.5% of the larger value.

Superfamily	♀ BL > ♂ BL	♀ BL = ♂ BL	♀ BL < ♂ BL	N
Gammaroidea	2.5%	0.0%	97.5%	40
Talitroidea	25.0%	33.3%	41.7%	12
Ampeliscoidea	31.3%	62.5%	6.2%	16
Corophioidea	47.1%	35.3%	17.6%	17
Lysianassoidea	88.2%	5.9%	5.9%	17
Pontoporeioidea	94.4%	5.6%	0.0%	18

Alicella gigantea is likely greater, but no estimate of longevity exists at present. Finally, the maximum number of broods produced per female varies from one, in a flurry of gammarideans (Appendix 1), to 26 in the gammaroid *Gammarus chevreuxi* (Sexton, 1928).

In gammaridean amphipods, maximum female body length may be greater, equal or less than maximum male body length (Table 1); the occurrence of such cases is apparently closely dependent on superfamily affiliation ($G = 61.20$, $df = 10$, $P < 0.001$). Female gammaroids were virtually always smaller than males (97.5% of cases), with the sole possible exception of *Gammarellus angulosus* (see Fig. 2 in D.H. Steele & Steele, 1972b). In contrast, body length of females was equal to or greater than that of males in pontoporeioids (100% of cases), lysianassoids (> 94%), ampelisoids (> 93%) and corophioids (> 82%). Finally, talitroids formed a mixed group with populations or species where female maximum body length exceeded, equalled or was less than that of males (Table 1).

The stegocephaloid *Stegocephalus inflatus* (D.H. Steele, 1967), some leucothoids (Schram, 1986) and the lysianassoid genus *Acantiostoma* (Lowry & Stoddart, 1986) may have small males because they are protandrous hermaphrodites. The corophioid *Corophium bonnellii* apparently represents another departure from dioecism, since it is probably parthenogenetic (Moore, 1981; Costello & Myers, 1989).

Number of broods, HMFBL ratio and classification of life histories

The simple correlation between the maximum number of broods produced per female and the *HMFBL* ratio was highly significant ($r = 0.64$, $N = 93$, $P < 0.001$). In cold waters, the *HMFBL* ratio ranged from 0.0110 to 0.3478 in semelparous populations and from 0.1304 to 0.7846 in iteroparous populations. The *HMFBL* ratio can hence be used to separate semelparous from iteroparous populations: this separation was carried out only for the cold-water habitat, because only there

were semelparous populations adequately represented. All unclassified cold-water populations with a *HMFBL* ratio < 0.1304 were considered to be semelparous, while populations with a *HMFBL* ratio > 0.3478 were considered to be iteroparous (Appendix 1).

Iteroparity was apparently more frequent than semelparity within the suborder Gammaridea (Appendix 1 and Fig. 1A). Semelparous populations were significantly more frequent in cold

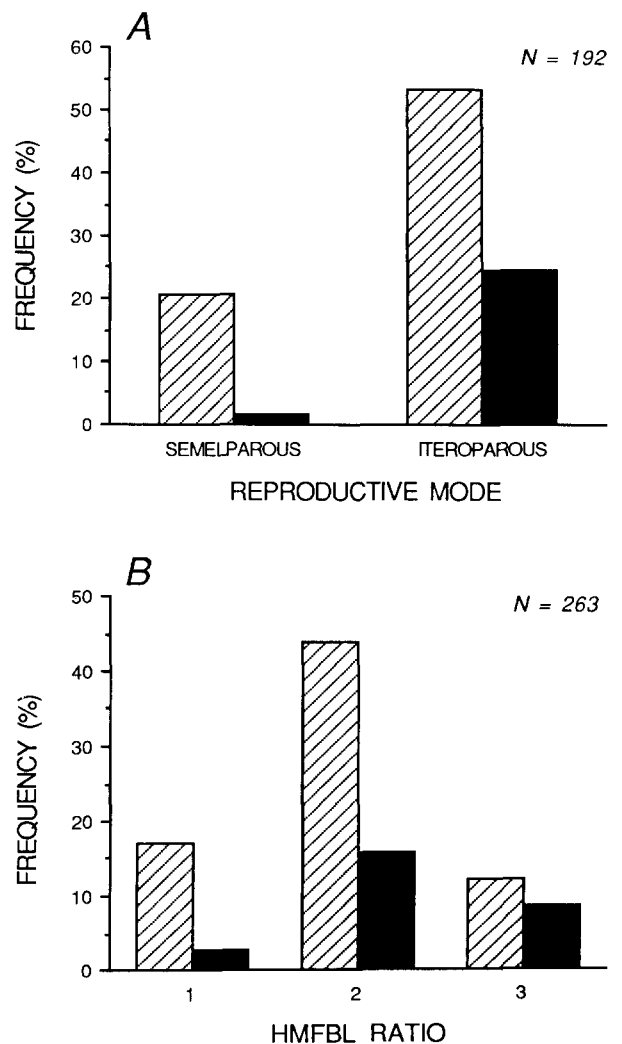


Fig. 1. Frequency distributions of (A) semelparous and iteroparous populations and of (B) *HMFBL* ratios for aquatic gammaridean amphipods in cold (hatched bars) and warm (black bars) habitats. *HMFBL* ratios: 1 is < 0.1304 , 2 is ≥ 0.1304 and ≤ 0.3478 , 3 is > 0.3478 .

than in warm waters (Fig. 1A; $G = 12.45$, $df = 1$, $P < 0.001$). This conclusion was supported by a broader-based analysis using the *HMFBL* ratio in lieu of the number of broods per female (Fig. 1B), which indicated that distribution of *HMFBL* ratios was dependent on temperature ($G = 11.05$, $df = 2$, $P < 0.01$).

In cold waters, frequency distributions of mean female body length relative to the semelparous/iteroparous condition or the *HMFBL* ratio suggested that small females tended to be more iteroparous than large ones (Fig. 2), but testing of this hypothesis yielded conflicting conclusions. The occurrence of semelparity and iteroparity was independent of mean female body length (Fig. 2A; $G = 2.64$, $df = 2$, $P > 0.1$), while the *HMFBL* ratio was highly dependent on mean female body length (Fig. 2B; $G = 16.18$, $df = 4$, $P < 0.01$). In warm waters, the range of body lengths was too small and females of the semelparous habit or with small *HMFBL* ratios were too few for meaningful conclusions.

All corophioids and gammaroids reviewed herein were iteroparous (Appendix 1). Nelson (1980) erroneously listed four semelparous Gammaroidea: *Gammaracanthus loricatus*, *Gammarellus angulosus*, *Gammarus setosus* and *G. wilkitzkii*. This misinterpretation may have arisen from the ambiguous wording in a review paper by Steele & Steele (1975c), which refers to these species as single-brooded arctic gammaroids. However, careful reading of papers by V.J. Steele (1967), V.J. Steele & Steele (1970) and D.H. Steele & Steele (1972b, 1975a, 1976) indicates that these species are in fact iteroparous (confirmed herein by their large *HMFBL* ratios), but that they produce only one brood per year.

Semelparity was represented to some extent in most other superfamilies with populations in cold waters (Appendix 1). The Ampeliscoidea and Phoxocephaloidea were reported to be mostly iteroparous, even in cold waters. However, females of the potentially double-brooded, cold-living ampeliscoids and phoxocephaloids, may only rarely produce a second brood (Carrasco & Arcos, 1984; Slattery, 1985; Bellan-Santini & Dauvin, 1988).

To suit all amphipod life histories reviewed herein, Wildish's (1982) proposed classification must be expanded and modified slightly to include eight categories: the (multivoltine) semelparous and iteroparous semiannuals (lifespan < 12 mo.), the semelparous annual ($12 \leq LS < 24$ mo.) and (multivoltine) iteroparous annuals, the semel-

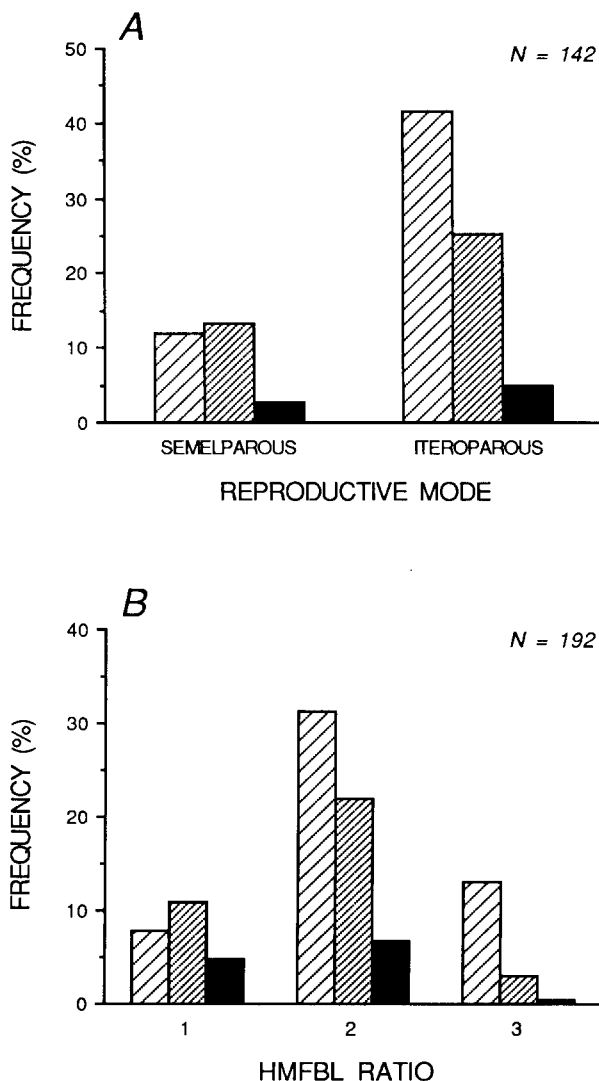


Fig. 2. Frequency distributions of (A) semelparous and iteroparous populations and of (B) *HMFBL* ratios (see legend of Fig. 1) as a function of body length (mm) for gammaridean amphipods in cold habitats. Lightly hatched bars represent small females (< 10 mm body length), heavily hatched bars represent medium females (10 to < 20 mm), dark bars represent large females (≥ 20 mm).

parous and iteroparous biannuals ($24 \leq LS$ 36 mo.), and the semelparous and iteroparous perennials ($LS \geq 36$ mo.). The distinction between semelparous and iteroparous semiannual populations is necessary, since females in each of the alternating 4- and 8-mo. generations of the ampelisoids *Ampelisca abdita* and *A. vadorum* only breed once at the northern extremity of their distributional range (Mills, 1967; Nelson, 1978; Van Dolah & Bird, 1980). Furthermore, addition of an iteroparous biannual category is required to accommodate the ampelisoid *A. armoricana*, the corophioid *Leptocheirus pinguis*, the gammaroids *Gammarus lacustris* and *Pallasea quadrispinosa*, and the lysianassoids *Hippomedon propinquus*, *Psammonyx nobilis* and *P. terranova*, all of which may produce ≥ 2 broods in a 2-yr lifespan (Appendix 1).

Annual populations were by far the most common, representing 54.2% of all cases ($N = 107$); followed by semiannual (19.6%), biannual (14.0%) and perennial (12.2%). Iteroparity prevailed in semiannual (90.5%) and annual (82.8%) populations, but was significantly less frequent ($G = 6.94$, $df = 2$, $P < 0.05$) in biannual and perennial populations (60.7%).

Correlations among life history traits

Simple (Pearson) correlations showed that mean female body length, brood size, embryo diameter and female lifespan were all positively and significantly intercorrelated; the number of broods per female was negatively and significantly correlated

with other life history traits (Table 2). The positive partial correlations between brood size and body length, and between embryo diameter and body length, were significant but of rather limited interest since they were obvious or have been repeatedly demonstrated. However, other partial correlations were of particular interest. The positive and significant partial correlation between body size and number of broods indicates that large females have more broods than small females when investment into individual broods is comparable (same number and size of embryos). The significant negative partial correlations between brood size and embryo diameter, between the number of broods and embryo diameter, and between the number of broods and brood size, show what comprises are possible among these life history traits for a constant body size. The positive partial correlation between lifespan and body length was marginally not significant ($r = 0.22$, $P < 0.1$). Using *HMFBL* in place of the number of broods substantially increased sample size ($N = 65$) and yielded the same significant partial correlations as above, except for the partial correlation between lifespan and body length which was significant ($r = 0.29$, $P < 0.05$).

Canonical discriminant analyses and univariate statistics for life history traits

Canonical discriminant analysis was unable to separate gammaridean populations according to salinity (Table 3). Of the four life history traits considered in discriminant analyses, only the

Table 2. Pearson (below diagonal) and partial (above diagonal) correlations between selected life history traits of gammaridean amphipods: *BL* = body length of females, *BS* = brood size, *ED* = embryo diameter, *NB* = number of broods per female, *LS* = lifespan. All correlations based on listwise comparisons of log-transformed data, $N = 51$. *** = $P < 0.001$, * = $P < 0.05$, *ns* = not significant.

	<i>BL</i>	<i>BS</i>	<i>ED</i>	<i>NB</i>	<i>LS</i>
<i>BL</i>	–	0.71***	0.58***	0.34*	0.22 <i>ns</i>
<i>BS</i>	0.81***	–	–0.32*	–0.48***	0.13 <i>ns</i>
<i>ED</i>	0.73***	0.52***	–	–0.29*	0.19 <i>ns</i>
<i>NB</i>	–0.34*	–0.53***	–0.38**	–	–0.11 <i>ns</i>
<i>LS</i>	0.69***	0.63***	0.60***	–0.39**	–

Table 3. Statistics for canonical discriminant analyses across habitats and superfamilies.

Discriminant function	% total eigenvalues	Canonical correlation	F	P
Temperature				
1	100.0	0.439	7.21	<0.001
Bathymetry				
1	100.0	0.533	12.00	<0.001
Salinity				
1	59.0	0.200	1.06	0.394
2	41.0	0.168	1.17	0.326
Superfamily				
1	64.7	0.648	3.70	<0.001
2	21.1	0.437	2.17	0.004
3	12.6	0.352	1.60	0.110
4	1.6	0.135	0.48	0.752

HMFBL ratio differed significantly with salinity, being greater in brackish than in marine populations (Table 5). Accordingly, the mean number of broods per female differed significantly with salinity and was also greatest in brackish populations.

Gammaridean populations separated neatly following temperature (Table 3). Judging from the values of the standardized canonical coefficients and group means in Table 4, cold water populations had larger embryos but smaller *HMFBL* ratios (i.e. fewer broods). However, the Kruskal-Wallis test (Table 5) indicated that all life history traits used in discriminant analysis dif-

fered significantly with temperature. On average, females, broods, and embryos were larger, while *HMFBL* ratios were smaller (i.e. fewer broods), in cold- than in warm-water gammaridean populations. The difference between the mean number of broods in cold and warm waters was marginally not significant.

The sharpest abiotic contrast between gammaridean populations was obtained in comparing deep- and shallow-living populations, as seen by the higher canonical correlation (0.533) in Table 3. Standardized canonical coefficients and group means indicated that females of deep-living populations had larger bodies and smaller *HMFBL* ratios (i.e. fewer broods) than females of shallow-living populations (Table 4). However, the Kruskal-Wallis test pointed to significant differences between mean body length, embryo diameter and *HMFBL* ratios (Table 5).

Superfamilies were neatly segregated by canonical discriminant analysis (Table 3), with embryo diameter and *HMFBL* ratio contributing most to separation along the first discriminant function, and body length and brood size contributing most to separation along the second discriminant function (Table 4 and Fig. 3). Superfamilies most separated by their group means were the lysianasoids, characterized by large embryos and large body size; the gammaroids, characterized by large *HMFBL* ratios (i.e. numerous broods) and rather large body size; the corophioids, charac-

Table 4. Standardized canonical coefficients and group means derived for significant discriminant functions presented in Table 3. Gammaridean populations are described as living in cold (C), warm (W), shallow (S) or deep (D) habitats. *BL* = body length of females, *BS* = brood size, *ED* = embryo diameter, *HMFBLr* = *HMFBL* ratio.

Discriminant function	<i>BL</i>	<i>BS</i>	<i>ED</i>	<i>HMFBLr</i>	Group means
Temperature					
1	-0.32	0.31	0.96	-0.46	C = 0.23 W = -0.99
Bathymetry					
1	-1.66	1.25	-0.16	0.17	S = 0.14 D = -2.79
Superfamily					
1	0.48	0.18	-1.02	0.94	See
2	1.46	-0.88	0.09	0.56	Fig. 3

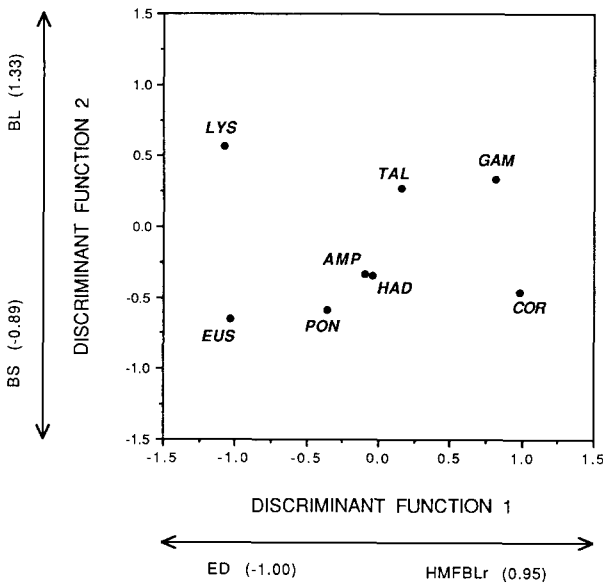


Fig. 3. Plot of group means derived from canonical discriminant analysis of the gammaridean superfamilies Ampeliscoidea (AMP), Corophioidea (COR), Eusiroidea (EUS), Gammaroidea (GAM), Hadzioidea (HAD), Lysianassoidea (LYS), Pontoporeioidea (PON) and Talitroidea (TAL). ED = embryo diameter, HMFBLr = HMFBL ratio, BL = body length, BS = brood size.

terized by large *HMFBL* ratios (i.e. numerous broods) and large brood size; and the eusiroids, characterized by large embryos and large brood size. Mean values and the Kruskal-Wallis test (Table 5), corroborated the marginal positions of these four superfamilies within the suborder Gammaridea. Lysianassoids had the largest mean embryo diameter (1.18 mm), gammaroids had the second largest mean *HMFBL* ratio (0.32), corophioids had the largest mean *HMFBL* ratio (0.34), and eusiroids had the second largest mean embryo diameter (0.70 mm) and largest mean brood size (66.9 embryos).

Although lifespan could not be used in canonical discriminant analyses, because data were lacking for too many gammaridean populations, mean values and the Kruskal-Wallis test pointed to some interesting variations across habitats and superfamilies (Table 6). Mean lifespan was significantly greater in cold- than in warm-living populations, but did not vary with salinity. Data

were lacking for all but one deep-living species (the lysianassoid *Eurythenes gryllus*), but one can expect the mean lifespan of all large deep-living gammarideans to be quite high because of the positive correlations between body length and lifespan (Table 2 and in text above) and of the not greater than average growth rates of deep- compared to shallow-living crustaceans (Mauchline, 1988a). Mean lifespan varied significantly across superfamilies, and was by far greatest in the Eusiroidea (31 mo.) and Lysianassoidea (30 mo.).

Embryo size, brood size, lifetime potential fecundity, and reproductive potential

Most of the variation in brood size was accounted for by body size (Table 7). However, prediction of brood size was improved significantly through the combined use of body size, embryo diameter, and *HMFBLr* or the number of broods per female, as independent variables in a multiple regression (Table 7).

Comparisons of regressions of brood size or of

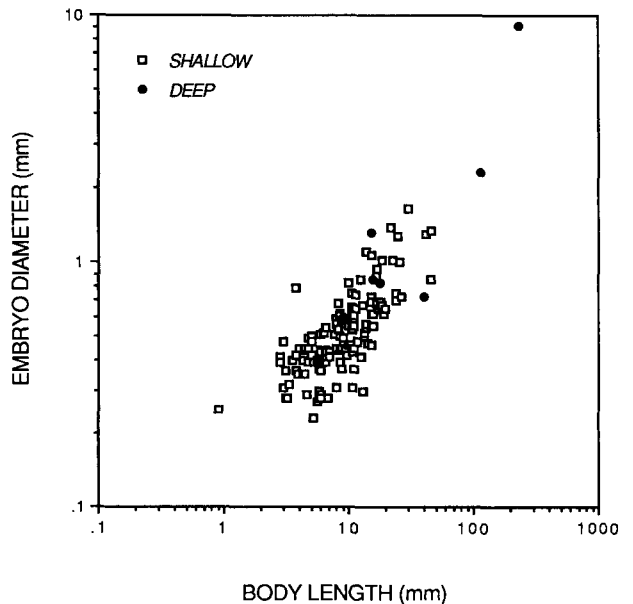


Fig. 4. Scattergram of embryo diameter as a function of body length of gammaridean amphipods.

Table 5. Mean and standard deviation of life history traits of gammaridean populations in different habitats and superfamilies. Means are presented only for groups with ≥ 5 observations for body length, brood size, embryo diameter and *HMFBL* ratio. A Kruskal-Wallis test was used to compare class levels with ≥ 5 observations; sample size is given in parentheses. AMP = Ampeliscoidea, COR = Corophioidea, EUS = Eusiroidea, GAM = Gammaroidea, HAD = Hadzioidea, LYS = Lysianassoidea, PON = Pontoporeioidea, TAL = Talitroidea, KW = Kruskal-Wallis statistic, *** = $P < 0.001$, ** = $P < 0.01$, * = $P < 0.05$, *ns* = not significant.

Groups	Body length (mm)	Brood size	Embryo diameter (mm)	<i>HMFBL</i> ratio	Number of broods
Temperature					
Cold	13.0 \pm 18.3 (215)	42.0 \pm 72.2 (215)	0.69 \pm 0.84 (118)	0.23 \pm 0.13 (190)	3.5 \pm 3.8 (98)
Warm	7.0 \pm 2.9 (87)	19.2 \pm 14.4 (87)	0.38 \pm 0.07 (34)	0.29 \pm 0.15 (73)	6.5 \pm 6.8 (14)
KW	25.63***	9.60**	39.22***	7.90**	3.42 (P = 0.06)
Bathymetry					
Deep	45.9 \pm 68.4 (11)	50.6 \pm 57.7 (11)	2.02 \pm 2.93 (8)	0.15 \pm 0.07 (9)	1.5 \pm 0.7 (2)
Shallow	9.9 \pm 7.0 (291)	34.9 \pm 62.4 (291)	0.55 \pm 0.24 (144)	0.25 \pm 0.14 (254)	3.9 \pm 4.4 (110)
KW	9.29**	1.35 <i>ns</i>	9.48**	5.98*	–
Salinity					
Freshwater	8.8 \pm 2.8 (27)	24.7 \pm 12.7 (27)	0.44 \pm 0.14 (9)	0.28 \pm 0.15 (24)	4.9 \pm 4.6 (15)
Brackish	9.4 \pm 4.0 (46)	23.2 \pm 14.8 (46)	0.54 \pm 0.17 (19)	0.30 \pm 0.17 (40)	6.2 \pm 6.2 (21)
Marine	11.9 \pm 17.9 (229)	39.1 \pm 70.6 (229)	0.65 \pm 0.82 (124)	0.24 \pm 0.13 (199)	3.0 \pm 3.5 (76)
KW	0.68 <i>ns</i>	0.62 <i>ns</i>	2.28 <i>ns</i>	6.40*	15.71***
Superfamily					
AMP	9.6 \pm 3.4 (24)	27.8 \pm 14.8 (24)	0.51 \pm 0.12 (12)	0.19 \pm 0.08 (21)	1.3 \pm 0.5 (12)
COR	6.6 \pm 3.7 (38)	28.7 \pm 37.8 (38)	0.38 \pm 0.08 (19)	0.34 \pm 0.15 (27)	5.0 \pm 3.2 (9)
EUS	17.0 \pm 9.5 (28)	66.9 \pm 54.6 (28)	0.70 \pm 0.30 (12)	0.16 \pm 0.13 (28)	1.0 \pm 0.0 (6)
GAM	12.2 \pm 7.3 (61)	48.5 \pm 86.2 (61)	0.53 \pm 0.16 (33)	0.32 \pm 0.12 (59)	6.6 \pm 5.8 (25)
HAD	9.0 \pm 6.9 (12)	21.4 \pm 18.3 (12)	0.47 \pm 0.14 (9)	0.31 \pm 0.30 (8)	8.0 \pm 12.1 (3)
LYS	23.1 \pm 40.9 (35)	59.7 \pm 113.5 (35)	1.18 \pm 1.78 (23)	0.19 \pm 0.10 (33)	2.6 \pm 1.9 (20)
PON	6.0 \pm 2.5 (42)	14.0 \pm 16.5 (42)	0.52 \pm 0.16 (12)	0.22 \pm 0.10 (39)	1.9 \pm 3.0 (16)
TAL	8.6 \pm 3.9 (26)	16.8 \pm 9.3 (26)	0.52 \pm 0.18 (13)	0.28 \pm 0.12 (19)	5.1 \pm 2.7 (10)
KW	89.01***	63.57***	37.78***	58.37***	55.94***

embryo diameter on body length, across habitats, appear in Table 8. Slopes and elevations of regressions of brood size on body length did not differ with temperature or salinity, but the slope of the regression was significantly less in deep- than in shallow-living populations. The regression of embryo diameter on body length was significantly steeper in cold- than in warm-water populations, in marine- compared to brackish populations, and in deep- compared to shallow-living populations. However, few data points were available to characterize the deep-living populations (Fig. 4). All slopes of regressions of embryo diameter on body length were much less than unity, indicating that relative embryo size

decreased with increasing body length of females, as noted in other crustaceans (Mauchline, 1988b).

Differences between slopes and regressions of brood size on body length of females in different superfamilies were marginally not significant (Table 9). Note the very small slope for the Eusiroidea. The coefficient of determination for the Talitroidea regression was extremely small ($r^2 = 0.04$) and the slope did not differ significantly from zero, despite the fairly large number of observations. Elevation of regression lines differed significantly among superfamilies (Table 9): adjusted mean brood size, presented in Table 10, was greatest in corophioids ($\log_{ABS} = 1.49$) and least in stegocephaloids ($\log_{ABS} = 1.02$). For a

Table 6. Lifespan (in mo.), lifetime potential fecundity (in embryos) and reproductive potential (in embryos female⁻¹ yr⁻¹) of gammaridean amphipods in different habitats and superfamilies. A Kruskal-Wallis test was used to compare groups with ≥ 5 observations; sample size is given in parentheses. See Table 5 for abbreviations.

Groups	Lifespan	Lifetime fecundity	Reproductive potential
Temperature			
Cold	19.6 ± 17.4 (102)	87.7 ± 114.0 (98)	66.9 ± 122.4 (75)
Warm	11.8 ± 6.3 (30)	119.3 ± 144.2 (14)	355.1 ± 342.5 (7)
KW	6.47*	0.03 _{ns}	10.10**
Bathymetry			
Deep	156.0 (1)	83.6 ± 19.2 (2)	–
Shallow	16.8 ± 10.3 (131)	91.8 ± 119.0 (110)	91.5 ± 170.1 (78)
KW	–	–	–
Salinity			
Freshwater	16.5 ± 6.8 (15)	119.1 ± 118.5 (15)	121.1 ± 253.2 (12)
Brackish	12.6 ± 4.9 (25)	145.8 ± 166.4 (21)	161.0 ± 231.3 (15)
Marine	19.5 ± 18.4 (92)	71.2 ± 95.9 (76)	66.0 ± 119.5 (55)
KW	2.93 _{ns}	12.97**	10.79**
Superfamily			
AMP	17.6 ± 9.9 (18)	33.6 ± 30.7 (12)	27.1 ± 12.0 (9)
COR	10.3 ± 6.8 (16)	71.6 ± 65.7 (9)	162.6 ± 222.4 (8)
EUS	31.0 ± 18.0 (6)	107.6 ± 54.7 (6)	42.3 ± 13.1 (4)
GAM	15.4 ± 9.7 (31)	167.7 ± 171.0 (25)	157.0 ± 226.1 (21)
HAD	17.5 ± 17.7 (2)	151.1 ± 183.6 (3)	445.6 ± 601.8 (2)
LYS	30.1 ± 32.6 (19)	81.8 ± 132.6 (20)	43.3 ± 48.9 (15)
PON	18.8 ± 5.9 (20)	34.2 ± 35.5 (16)	14.1 ± 14.5 (10)
TAL	11.0 ± 4.0 (10)	95.4 ± 63.0 (10)	61.2 ± 44.5 (4)
KW	32.15***	37.35***	32.81***

given body size, corophioids produced more embryos per brood than all other gammaridean superfamilies, with the exception of the Eusiroidea. The Ampeliscoidea, Eusiroidea and Gammaroidea, tended to have larger adjusted mean brood sizes than the Pontoporeioidea, Lysianassoidea and Stegocephaloidea.

Regressions of log₁₀ embryo diameter and log₁₀ body length were significant for the Ampeliscoidea (slope = 0.37, $N = 12$, $P < 0.05$), Corophioidea (slope = 0.25, $N = 19$, $P < 0.01$), Eusiroidea (slope = 0.57, $N = 12$, $P < 0.001$), Gammaroidea (slope = 0.47, $N = 33$, $P < 0.001$), Hadzioidea (slope = 0.30, $N = 9$, $P < 0.01$) and

Table 7. Predictive simple and multiple regressions of brood size on body length (BL , in mm), embryo diameter (ED , in mm), $HMFBL$ ratio ($HMFBLr$), number of broods per female (NB) and lifespan (LS , in mo.) for all gammaridean populations. All coefficients in the multiple regressions are significant at the 1% level or less. *** = $P < 0.001$.

Equation of regression	N	r^2	F
$\log BS = -0.328 \log HMFBLr + 1.087$	261	0.04	12.02***
$\log BS = -0.343 \log NB + 1.462$	112	0.10	12.85***
$\log BS = 1.162 \log ED + 1.625$	151	0.25	48.54***
$\log BS = 1.221 \log BL + 0.152$	302	0.59	433.02***
$\log BS = 1.686 \log BL - 0.944 \log ED - 0.585$	152	0.67	152.05***
$\log BS = 1.714 \log BL - 1.087 \log ED - 0.200 \log HMFBLr - 0.772$	126	0.70	94.34***
$\log BS = 1.480 \log BL - 0.546 \log ED - 0.411 \log NB - 0.138$	71	0.71	55.03***

Table 8. Predictive regressions of brood size (*BS*) and of embryo diameter (*ED*, in mm) on body length (*BL*, in mm) for gammaridean populations in different habitats. Significant regression lines are compared by analysis of variance and of covariance. *** = $P < 0.001$, ** = $P < 0.01$, * = $P < 0.05$, *ns* = not significant.

Groups	Brood size	Embryo diameter
Temperature		
Warm	$\log BS = 1.326 \log BL + 0.086$ $N = 87, r^2 = 0.49, F = 82.91^{***}$	$\log ED = 0.157 \log BL - 0.547$ $N = 34, r^2 = 0.17, F = 6.72^*$
Cold	$\log BS = 1.218 \log BL + 0.147$ $N = 215, r^2 = 0.60, F = 313.66^{***}$	$\log ED = 0.539 \log BL - 0.785$ $N = 118, r^2 = 0.67, F = 232.86^{***}$
Slopes	$F = 0.38ns$	$F = 17.08^{***}$
Elevation	$F = 0.50ns$	-
Bathymetry		
Shallow	$\log BS = 1.348 \log BL + 0.050$ $N = 291, r^2 = 0.62, F = 464.89^{***}$	$\log ED = 0.449 \log BL - 0.717$ $N = 144, r^2 = 0.57, F = 184.47^{***}$
Deep	$\log BS = 0.937 \log BL + 0.171$ $N = 11, r^2 = 0.73, F = 24.54^{***}$	$\log ED = 0.695 \log BL - 0.919$ $N = 8, r^2 = 0.81, F = 25.33^{**}$
Slopes	$F = 5.15^*$	$F = 8.51^{**}$
Salinity		
Freshwater	$\log BS = 0.832 \log BL + 0.562$ $N = 27, r^2 = 0.21, F = 6.54^*$	$\log ED = 0.433 \log BL - 0.783$ $N = 9, r^2 = 0.26, F = 2.52ns$
Brackish	$\log BS = 0.973 \log BL + 0.364$ $N = 46, r^2 = 0.44, F = 34.91^{***}$	$\log ED = 0.326 \log BL - 0.591$ $N = 19, r^2 = 0.52, F = 18.47^{***}$
Marine	$\log BS = 1.261 \log BL + 0.112$ $N = 229, r^2 = 0.62, F = 377.40^{***}$	$\log ED = 0.550 \log BL - 0.802$ $N = 124, r^2 = 0.69, F = 277.56^{***}$
Slopes	$F = 1.63ns$	$F = 5.80^*$
Elevator	$F = 0.53ns$	-

Lysianassoidea (slope = 0.65, $N = 23$, $P < 0.001$). Slopes differed significantly ($F = 4.91$, $P < 0.001$).

Mean values of the lifetime potential fecundity and reproductive potential for gammaridean populations in different habitats and superfami-

Table 9. Predictive regressions of brood size (*BS*) on body length (*BL*, in mm) for superfamilies with significant relations comprising ≥ 5 observations. The predictive regression for the Talitroidea was not significant despite the large sample size.

	Equation of regression	<i>N</i>	r^2	<i>F</i>
Ampeliscoidea	$\log BS = 1.335 \log BL + 0.089$	24	0.49	21.30 ^{***}
Corophioidea	$\log BS = 1.465 \log BL + 0.141$	38	0.61	55.83 ^{***}
Eusiroidea	$\log BS = 0.866 \log BL + 0.668$	28	0.28	9.97 ^{**}
Gammaroidea	$\log BS = 1.490 \log BL + 0.084$	61	0.59	83.81 ^{***}
Hadzioidea	$\log BS = 1.263 \log BL + 0.073$	12	0.74	29.18 ^{***}
Leucothoidea	$\log BS = 1.439 \log BL - 0.118$	6	0.70	9.30 [*]
Lysianassoidea	$\log BS = 1.062 \log BL + 0.204$	35	0.55	40.54 ^{***}
Oedicerotoidea	$\log BS = 1.978 \log BL - 0.446$	8	0.69	13.67 [*]
Pontoporeioidea	$\log BS = 1.806 \log BL - 0.375$	42	0.72	103.79 ^{***}
Stegocephaloidea	$\log BS = 1.010 \log BL + 0.132$	5	0.88	21.61 [*]
Slopes	$F = 1.83$ ($P = 0.06$)			
Elevation	$F = 4.58^{***}$			
Talitroidea	$\log BS = 0.288 \log BL + 0.904$	26	0.04	1.08 ^{ns}

Table 10. Probability levels for multiple comparisons of logarithmic estimates of brood size adjusted for body length of females (*ABS*) in gammaridean superfamilies with significant predictive regressions and ≥ 5 observations (see Table 9). The boxed area encloses pairs which differ or tend to differ significantly. AMP = Ampeliscoidea, COR = Corophioidea, EUS = Eusiroidea, GAM = Gammaroidea, HAD = Hadzioidea, LEU = Leucothoidea, LYS = Lysianassoidea, OED = Oedicerotoidea, PON = Pontoporeioidea, STE = Stegocephaloidea.

	log <i>ABS</i>	COR	EUS	AMP	GAM	OED	HAD	PON	LEU	LYS	STE
COR	1.49	–									
EUS	1.40	0.19	–								
AMP	1.35	0.05	0.58	–							
GAM	1.35	0.02	0.44	0.93	–						
OED	1.32	0.09	0.47	0.72	0.75	–					
HAD	1.27	0.01	0.19	0.38	0.37	0.72	–				
PON	1.23	0.00	0.02	0.07	0.04	0.40	0.63	–			
LEU	1.19	0.01	0.12	0.21	0.20	0.42	0.59	0.79	–		
LYS	1.17	0.00	0.00	0.01	0.00	0.20	0.30	0.43	0.86	–	
STE	1.02	0.00	0.00	0.01	0.01	0.06	0.09	0.12	0.31	0.25	–

lies are shown in Table 6. Univariate analyses indicated that reproductive potential, but not lifetime potential fecundity, was significantly greater in warm than in cold waters. Regardless of the index used, gammaridean populations were significantly more fecund in brackish and fresh waters than in marine environments. Nothing can be said about the reproductive potential of deep-living populations, because data on the lifespan and number of broods for the calculation of reproductive potential were too few. Lifetime potential fecundity and reproductive potential varied significantly with superfamily affiliation: pontoporeioids and ampeliscoids were the least fecund of gammaridean amphipods according to either index, gammaroids and eusiroids had the highest lifetime potential fecundity, and corophioids and gammaroids had the greatest reproductive potential.

Discussion

Correlations among life history traits

Simple correlations indicated that all life history traits were intercorrelated for populations of aquatic gammarideans (Table 2). A novel, although intuitively obvious finding, was the significant positive correlation between the maximum number of broods produced per female and the *HMFBL* ratio. This occurs in iteroparous females because each oviposition is preceded by one or more moults (Charniaux-Cotton, 1985), which are generally accompanied by an increment in body length. The coefficient of the correlation between the number of broods per female and the *HMFBL* ratio was rather small ($r = 0.64$), indicating scatter about the mean trend. The unexplained variance may result from several factors, other than obvious imprecisions on measurements of body length. Alternating generations of females in

multivoltine populations may mature at different body lengths (e.g. Mills, 1967; Nelson, 1980; Van Dolah & Bird, 1980), yielding excessively large *HMFBL* ratios when mean and maximum body length are considered irrespectively of specific generations. Also, in a given population, semelparous or iteroparous females belonging to a same generation may mature asynchronously and in different moult instars (Nair & Anger, 1979a; Sagar, 1980; Sainte-Marie & Brunel, 1983; see Caine, 1979 for a caprellid example), iteroparous females may oviposit irregularly in the instars following the initial moult to maturity (e.g. Legueux, 1926; Sexton, 1928; Nair & Anger, 1979a), or their breeding life may be punctuated by obligate resting stages, accompanied by growth (e.g. Kinne, 1953a; V.J. Steele, 1967; Morino, 1978).

Partial correlations (Table 2) offer a different perspective into relationships between life history traits, because they consider relations between two variables while removing the effects of other variables. Brood size and embryo diameter were positively and strongly correlated with body length; this has long been known for malacostracan crustaceans (e.g. Cheng, 1942; Jensen, 1958; Steele & Steele, 1975c; Mauchline, 1988b). Brood size and embryo diameter were negatively correlated with each other: for a given female body size and number of broods, production of large broods thus entails smaller embryos, and *vice versa*. The negative relation between brood and embryo size, given a fixed body size, had previously been reported for gammarideans (e.g. Steele & Steele, 1975c; Van Dolah & Bird, 1980) and for a variety of other crustaceans (Kerfoot, 1977; Clarke, 1979; Corey, 1981; Mauchline, 1988b).

Partial correlations pointed to other important compromises which may occur between reproductive traits. *HMFBL* and the number of broods produced per female were negatively correlated with embryo diameter (Table 2) and with brood size. This means that for a given body size, females breeding more frequently produce fewer and/or smaller embryos than females breeding less frequently. Hence, considerable variation of the reproductive output (measured as the ratio of brood volume or weight to female body length or

volume) may be expected between gammaridean populations and species, as demonstrated for a few species (Wildish, 1982; Clarke *et al.*, 1985). Nelson (1980) reported that semelparous females produced more embryos per brood than iteroparous females, but the former were also larger, and the effect of body length was not accounted for by ANCOVA. Implications of repeat-breeding for embryo size were hitherto unrecognized. The strong negative partial correlations among several gammaridean life history traits imply that there are limits on directional selection for any given trait (Doyle & Hunte, 1981; Skadsheim, 1990).

The reduction in brood and/or embryo size with increasing frequency of reproduction may be due to physical and/or physiological constraints. In iteroparous species, ova of the maturing brood 'compete' for limited body cavity space and nutritional reserves with underlying germinal tissues, containing subsequent broods in a more or less developed state, and with the gut which generally remains functional (Sainte-Marie *et al.*, 1990). In contrast, the body cavity of some semelparous species may be invaded by the ovaries (Bregazzi, 1972), completely constricting the gut and causing the ventral sternites to bulge outwards (Sainte-Marie *et al.*, 1990). Additional constraints on brood and embryo size are marsupium capacity, which is somewhat expandable (Sainte-Marie *et al.*, 1990), and the probable existence of a minimum viable embryo size (Mauchline, 1988b). Ultimately, brood and embryo size are limited by the amount of energy devoted by the female to reproduction, which depends on growth and maintenance costs (Clarke, 1987).

Based on an unspecified number of observations, Ingram & Hessler (1987) proposed a general predictive equation for brood size of gammaridean amphipods, which used body length as an independent variable. Their equation diverges sharply from mine (Table 7), notably because their data were not log-transformed prior to regression analysis. At any rate, such general predictive equations are of rather limited value, considering the significant variations of regressions of brood size on body length across some habitats and superfamilies (Tables 8, 9 and 10).

Among the superfamilies which were represented by a large number of observations, only the Talitroidea yielded a non significant regression size on body length. The extreme diversity of habitats occupied by this superfamily – terrestrial, supralittoral, fully aquatic; cold and warm; fresh water, brackish and marine (see Friend & Richardson, 1986; Wildish, 1988) – may result in species having very different life history patterns.

The strong partial correlations among life history traits observed herein imply that more than body size is necessary for good predictions of brood size of gammaridean amphipods. The best general predictive regression was a multiple regression, with body length, embryo diameter and the *HMFBL* ratio or number of broods per female, as independent variables (Table 7) which, in that order, explained decreasing proportions of variation in brood size.

Comparisons of gammaridean life history patterns

Most previous reviews of peracaridan life history patterns have focused only on brood size, body length and, to a lesser extent, embryo diameter (Steele & Steele, 1975c; Nelson, 1980; Van Dolah & Bird, 1980; Corey, 1981; Luxmoore, 1982). However, these variables were not the only, and certainly not always the most important, traits characterizing life history patterns of aquatic gammaridean amphipods. For example, the *HMFBL* ratio (i.e. number of broods) contributed more than brood size to the separatory power of the first discriminant function, in two out of three canonical discriminant analyses (Table 4).

Different life history patterns are often interpreted as ‘strategies’ or ‘tactics’, resulting from natural selection on covarying life history traits, to adjust fecundity so that some measure of individual fitness is maximized (Williams, 1966). Adaptationists therefore commonly infer mortality rates from fecundity. Nelson (1980) and Van Dolah & Bird (1980) measured gammaridean fecundity as brood size, standardized or not for body length, and hypothesized that adult mortality is greater in species with larger broods.

However, as argued above, and in light of the observed differences between number of broods produced by females in different habitats or superfamilies, brood size alone is a very poor index of total offspring production and hence, in the adaptationist scheme, of mortality rates. The most desirable index of fecundity will depend on the purpose of the study (Wildish, 1982): lifetime potential fecundity is a good overall indicator, but reproductive potential, which actually is a fecundity rate, seems most suitable for the inference of mortality rates. Indices of fecundity are not interchangeable: one is led to strikingly different conclusions depending on which index is used. For instance, mean brood size was significantly greater in gammaridean females of cold- than of warm-water habitats, but the reverse was true of reproductive potential (Table 6), while regressions of brood size on body length (Table 8) and lifetime potential fecundity (Table 6) did not differ significantly.

In this review, gammaridean superfamilies were represented inconsistently across habitats. Hence, there may be confounding or interactive effects within and between habitats and superfamilies (e.g. Brown, 1983); for example, most deep-living species reviewed herein were lysianasoids. This observation is important for the discussion of habitat and superfamily effects on life history traits.

Habitat harshness and life history patterns

Patterns of geographical and ecological variation of life history traits (mostly ‘clutch’ size) have been recorded for a great variety of animal taxa, either at the intra- or interspecific level (e.g. Bagenal, 1966; Steele & Steele, 1975c; Clarke, 1979; Kaplan & Salthe, 1979; Ricklefs, 1980; Van Dolah & Bird, 1980; Berven, 1982; Koenig, 1984; Healey & Heard, 1984; Belk *et al.*, 1990). Various hypotheses have been put forth to account for these trends in life history patterns; some of the most recent and most widely considered hypotheses link them to some index of habitat harshness: for instance, seasonality of

food resources ('Ashmole's hypothesis': Ashmole, 1963; Ricklefs, 1980), stability ('bet-hedging': Schaffer, 1974), or predictability ('r-K selection': MacArthur & Wilson, 1967; Pianka, 1970; redefined, re-interpreted and expanded as 'r-K-adversity selection': Greenslade, 1972; 1983). The habitat would thus provide 'the templet on which evolution forges characteristic life-history strategies' (Southwood, 1977; 1988). There is some agreement about the habitat characteristics which are of evolutionary significance to the organism's life history: the first is the frequency of disturbance and the second is productivity or environmental adversity (e.g. Southwood, 1977; 1988; Hildrew & Townsend, 1987; Greenslade, 1983).

The r-K-A selection hypothesis predicts that animals will tend to be K-selected in highly productive (favourable) and rarely disturbed (predictable) habitats, A-selected in poorly productive (adverse) and rarely disturbed habitats, and r-selected in frequently disturbed (unpredictable) habitats (Greenslade, 1983). Following the Greenslade (1983) and Southwood (1988) habitat templates, and with respect to criteria used to distinguish habitats of gammaridean amphipods in my review, the following generalizations seem possible. High latitudes and the deep sea are adverse but predictable habitats, thus A-selected (see Greenslade's 1983 re-interpretation of Clarke's 1979 data); brackish habitats are very unpredictable (Southwood, 1988), thus r-selected. The predicted species attributes are: for K-selection, intermediate longevity, intermediate maturity and intermediate fecundity; for A-selection, great longevity, late maturity and low fecundity; for r-selection, short longevity, early maturity and high fecundity (Greenslade, 1983).

Latitude

High-latitude (cold-water) gammaridean amphipods were characterized in general by univoltinism, large body size, delayed maturity, great longevity, large embryos, and few broods in a lifetime. The opposite set of traits tended to typify

low-latitude (warm-water) populations. Reproductive potential was much greater in the latter only because of the greater number of broods and shorter lifespan of females (i.e. increased reproductive tempo). These general observations support and extend previous observations and predictions on the latitudinal distribution of gammaridean life history patterns (Morino, 1978; Wildish, 1982, 1988; Bellan-Santini & Dauvin, 1988).

There was no significant difference between regressions of brood size on body length for high- and low-latitude gammarideans. However, the slope of the regression of embryo diameter on body length was significantly greater in cold- than in warm-living populations (Table 6). These conclusions are robust, since restricting analyses to consider only shallow-living, marine populations gives the same results (Sainte-Marie, pers. observ.). They imply that brood volume was greater in high-latitude than in low-latitude gammarideans, for any given body size. Steele & Steele (1975c) noted that the ratio between brood volume and parent volume tended to be greater in polar than in boreal or temperate populations of the Gammaridae and of the eusiroid *Calliopius laeviusculus*. In light of my findings, the proximate reason for this trend seems to be the greater number of broods produced by females of warm- versus cold-water species, which entails a reduction of relative embryo size and, ultimately, of brood volume. A reduction in the number of broods carried per female with increasing latitude occurs also at the intraspecific level, in at least one lysianassoid species (Sainte-Marie, unpubl. observ.), in the ampeliscooids *Ampelisca abdita* and *A. brevicornis*, and possibly in the pontoporeioid *Amphiporeia lawrenciana* (Appendix 1). Such latitudinal trends may be related to the poorly understood interactions between investments into maintenance, growth and reproduction (Clarke, 1987).

The greater longevity, later maturity and smaller reproductive potential of high- compared to low-latitude gammaridean species is consistent with A-selection. However, fecundity, measured as brood size, brood size adjusted for body length

or lifetime potential fecundity, was significantly greater or no less in high- than in low-latitude gammarideans. These latter observations, essentially based on northern hemisphere gammarideans, contrast with reports of reduced 'clutches' of antarctic relative to temperate benthos (reviewed by Clarke, 1979). It is possible that life history patterns of the antarctic fauna differ from those of the arctic fauna. However, Thurston (1974) was unable to detect any difference between embryo size of antarctic and arctic or boreal gammarideans. Moreover, there is no significant difference between regressions of embryo diameter or brood size on body length for antarctic and arctic gammaridean populations reviewed herein (Sainte-Marie, pers. obser.), which were mostly eusiroids and lysianassoids at both poles (raw data in Schellenberg, 1926; Stephensen, 1923, 1944; MacGinitie, 1955; Kuznetsov, 1964; Bregazzi, 1972; Rakusa-Suszczewski, 1972, 1982; Thurston, 1974; Sagar, 1980).

For a given body size, the constant brood size with increasing latitude (herein) also contrasts with many reported intraspecific trends of decreasing peracarid brood size with increasing latitude (D.H. Steele, 1967; Van Dolah & Bird, 1980; Wägele, 1987) or decreasing ambient temperature (summer versus winter populations, see for example Hynes, 1955; Heller, 1968; Vlasblom, 1969; Chambers, 1977; Van Dolah & Bird, 1980; Kolding & Fenchel, 1981; Moore, 1981; Shearer, 1983; Skadsheim, 1984; Naylor *et al.*, 1988). There are however exceptions to this rule, where brood size increases with temperature (Dexter, 1971; Fish, 1975). The reason for this and the above discrepancies may be rooted in the extreme diversity of gammaridean species, superfamilies and/or ecological types (see below), and of their unequal representation with latitude. Larger broods, for a given body size, are expected of the mainly semelparous eusiroids and lysianassoids which dominate high-latitude populations in my database. Phylogenetic constraints may therefore override latitudinal variation in life history traits, as demonstrated by Stebbins (1989) for a northern hemisphere isopod genus which shows a smaller-north trend in female body size, in contrast to the

bigger-north trend apparent in other isopod genera.

Many benthic animals apparently synchronize brood release with optimum conditions for survival (e.g. Thorson, 1950; Todd & Doyle, 1981). Semelparity or reduced frequency of breeding, decreased voltinism or univoltinism, and possibly increased longevity of gammarideans at high latitudes, are almost certainly related to the extreme seasonality of resources. The slow development of large embryos (McLaren, 1966; Steele & Steele, 1973b; Wear, 1974; Todd & Doyle, 1981), particularly at cold temperatures (Wittmann, 1984), along with obligate resting stages (V.J. Steele, 1967; Bone, 1972), increase the time required to produce a brood and thus contribute to synchronize offspring release with the yearly pulse in productivity. It has also been argued that reduced growth rates, longer inter-brood periods or delayed sexual maturity may be due to severe (seasonal) food limitation (e.g. Clarke, 1980, 1983, 1987; Siegfried, 1985). Physiological constraints and/or food limitation may thus play a key rôle in the evolution of life history traits of high-latitude animals (e.g. Thorson, 1950; Vance, 1973; Luxmoore, 1982; Wildish, 1982).

Depth

Apparently, deep-living gammaridean populations were characterized mainly by their large body size (Table 4). But this conclusion hinges on data for a few extremely big deep-sea lysianassoids (*Alicella gigantea*, *Eurythenes gryllus*, *Hirondellea gigas*), which have been the focus of research because of their peculiar ecology and presumed importance in the deep sea (e.g. Hessler *et al.*, 1978; Smith & Baldwin, 1984; Ingram & Hessler, 1987). One may hence argue that they are not representative of deep-sea gammarideans in general. Comparisons of body size of all gammarideans (Barnard, 1962) and of lysianassoids in particular (Steele, 1983), across depth and latitudinal gradients, indeed suggest that deep-sea assemblages differ from shallow, cold-water

assemblages only in the presence of a few extremely large members.

Although females of deep-sea gammarideans were on average 4.5 times larger than their shallow-living counterparts, brood size was not significantly greater (Table 5). Sainte-Marie *et al.* (1990) compared regressions of brood size and embryo diameter on body length and concluded that the rate of increase of brood size relative to body length was greater in shallow- than in deep-living lysianassoids, while the rate of increase of embryo size was similar for both groups. A broader analysis of all shallow- and deep-living gammarideans indicated that the regression between brood size and body length was identical in both groups, but that the rate of increase of embryo size relative to body length was greater in deep-living gammarideans (Table 8). It is unlikely that the smaller relative size of broods of deep-living gammarideans results from a greater frequency of breeding, given the significantly smaller mean *HMFBL* ratio of deep- compared to shallow-living Gammaridea or Lysianassoidea (Table 5).

One can only speculate about the reproductive potential of deep-living lysianassoids, because information on the number of broods and/or lifespan were lacking. Reproductive potential may be small, because the *HMFBL* ratio is less in deep- than in shallow-living populations of gammarideans (and of lysianassoids in particular). However, for the abyssal lysianassoid *Eurythenes gryllus*, Ingram & Hessler (1987) inferred a lifespan of 156 mo. and 5 potential brooding instars (XV, XVII, XIX, XXI and XXIII), which would yield a maximum reproductive potential of 74.6 embryos female⁻¹ yr⁻¹. This value is similar to the mean value of 91.5 embryos female⁻¹ yr⁻¹ for shallow-living gammarideans (Table 6) and greater than the mean value of 43.3 embryos female⁻¹ yr⁻¹ for cold-living lysianassoids.

Deep-sea lysianassoids seem to be A-selected. Nutrient limitation is regarded as an important factor structuring deep-sea communities (e.g. Stockton & DeLaca, 1982) and life history traits of deep-living invertebrates (Thorson, 1950; Mileikovsky, 1971; Vance, 1973). The large body

size of deep-sea lysianassoids may be an adaptation to efficiently forage on unpredictable and ephemeral carrion over large areas of bottom (Sainte-Marie, 1986). At the same time, nutrient limitation may be selecting for small body size in suspension and detritus feeders (Thiel, 1979; Carney *et al.*, 1983), with yet unknown effects on the life history traits of detritivorous gammarideans.

Salinity

Univariate comparisons of life history traits, of lifetime potential fecundity and of reproductive potential across salinity gradients pointed only to differences in *HMFBL* ratios, number of broods, lifetime potential fecundity and reproductive potential, with greater values of these variables occurring in brackish water (Tables 5 and 6). Regression analysis indicated that the rate of size increase of embryos relative to body length was greater in marine than in brackish gammarideans (Table 8); this is no doubt related to the greater breeding frequency observed in the latter. These results differ markedly from those of Nelson (1980), who reported that female body and brood size were greater in brackish than in marine gammaridean species in general. The significantly greater lifetime potential fecundity and reproductive potential (but not brood size) of gammaridean populations in brackish waters, and their tendency to be shorter-lived, is consistent with r-selection.

The present comparisons may have been biased because gammaroids represented $\geq 42\%$ of observations for any given trait in fresh-water populations, $\geq 33\%$ of observations in brackish waters, but $\leq 18\%$ of observations in marine waters. Considering only the Gammaroidea, there was no significant difference between any of the life history traits, lifetime potential fecundity or reproductive potential (Sainte-Marie, pers. observ.), but the number of observations was small. At the intraspecific level, there exists empirical or experimental evidence for the effect of salinity on life history traits of the Gammaroi-

dea (Hynes, 1954; Pinkster & Broodbakker, 1980; Skadsheim, 1989) and Talitroidea (Wildish, 1970, 1982).

Superfamily and ecological habit

Life history patterns differed sharply among gammaridean superfamilies. Lysianassoids and eusiroids had fewer broods, larger embryos and a lower reproductive potential than gammaroids and corophioids (Fig. 3, Tables 5 and 6). These two latter superfamilies were unique in retaining iteroparity even at high latitudes, a trait which enhances reproductive potential and lifetime potential fecundity. These same life history patterns may also be evidenced by a restricted analysis of only cold water, shallow-living species (Sainte-Marie, pers. obser.).

The relatively clear separation of gammaridean superfamilies should not be interpreted as a sign of extreme uniformity of life history traits for species of a given superfamily. Ecological habits are quite similar among species of the Gammaroidea or Pontoporeioidea, but other superfamilies are remarkably heterogeneous. For instance, the Lysianassoidea comprise predators, carrion-feeders, omnivorous scavengers, detritivores, herbivores, associated species (commensals and parasites), as well as typically endobenthic, epibenthic and suprabenthic forms (Besner, 1976; Bousfield, 1983; Sainte-Marie & Brunel, 1985). These different lifestyles may be correlated with very different life history traits. The below-average body size of some corophioids (e.g. *Gammaropsis inaequistylis*) and lysianassoids (e.g. *Opisa tridentata* and *Euonyx chelatus*), and of many leucothoids, coincides with their known commensal or symbiotic associations with macrofauna (Vader, 1983; Steele *et al.*, 1986; Bousfield, 1987; Comely & Ansell, 1988). Compared to free-living isopods, commensal isopods are smaller in order to fit on their host, shorter- or longer-lived depending on their host's life expectancy, and less fecund, presumably reflecting the reduced risks associated with a commensal lifestyle (Marsden, 1982; Stebbins, 1989). The small body size of

most pontoporeioids, and of some lysianassoids and lilljeborgioids, may result from their endobenthic lifestyle (Nelson, 1980) and microphagous feeding habits; the large body size of some eusiroids, lysianassoids and oedicerotoids may relate to their long-range, suprabenthic foraging capabilities and to their predaceous or necrophagous feeding habits (Sainte-Marie & Brunel, 1985).

Nelson (1980) and Van Dolah & Bird (1980) compared some life history traits of so-called endo- and epibenthic gammarideans, irrespective of superfamily affiliation. Their conclusions were the following: on average, 'epibenthic' females were larger than 'endobenthic' females (Nelson, 1980); mean brood size as well as the ratio of brood size to body length (Nelson, 1980), and brood size adjusted for body length (Van Dolah & Bird, 1980), were greater in 'epi-' than in 'endobenthic' females; mean size of embryos was greater in 'endo-' than in 'epibenthic' species (Van Dolah & Bird, 1980). It was hypothesized that the numerous embryos in broods of 'epibenthic' females reflected a greater mortality risk to adults, due to predation (see also Wildish, 1982) and an inclement environment, and that the large embryos of 'endobenthic' females represented an adaptation to maximize survivorship of juveniles facing severe predation or competition for resources (see also Smith & Fretwell, 1974; Stearns, 1976; Kerfoot, 1977; Todd & Doyle, 1981).

Both Nelson's and Van Dolah & Bird's reviews contained several common flaws, some of which were pointed out by Fenwick (1984). Firstly, brood size was used as an index of fecundity. This approach skirts the problem of iteroparity and longevity, both of which must be taken into account if one attempts to relate fecundity to risks of adult mortality (Wildish, 1982). Secondly, the majority of species and populations belonged to the 'epibenthic' Gammaroidea and to the 'endobenthic' Pontoporeioidea (72% of reviewed populations in Nelson, 1980; 80% in Van Dolah & Bird, 1980); thus comparisons of 'epi-' and 'endobenthic' species were in essence comparisons between two superfamilies. But the Gammaroi-

dea, whose classification as epibenthic was criticized by Fenwick (1984), differ from the Pontoporeioidea in more than just their supposed 'epibenthic' habit. Gammaroids are essentially littoral amphipods which live in a high-risk environment: exposure at low tide, osmotic stress and temperature shocks are common threats. Moreover, the Gammaroidea may be unique among the Gammaridea in having a lengthy precopula during which the male carries the female (Kinne, 1954; Borowsky, 1984; Borowsky & Borowsky, 1987); this requires the males to be large (robust) relative to females, a characteristic which is shared fully by no other superfamily reviewed herein (Table 1), and may entail greater vulnerability to predators. The greater fecundity of Gammaroidea may thus be simply related to phylogenetic constraints (see Wanntorp *et al.*, 1990) or, if it is indeed adaptive, to their high-risk littoral habitat and/or precopulatory behaviour rather than to their purported 'epibenthic' habit. Finally, the classification scheme in both reviews was clearly deficient: eusiroids were grouped with corophioids and hadzioids into the 'epibenthic' category, but the former are powerful free-swimming forms (Besner, 1976; Bousfield, 1973; Sainte-Marie & Brunel, 1985), while corophioids and hadzioids are generally poor swimmers which live cryptically on hosts, in burrows or in epibenthic tubes (e.g. Enequist, 1949; Kühne & Becker, 1964; Bousfield, 1973; Frith, 1977; Atkinson *et al.*, 1982; Sainte-Marie & Brunel, 1985; Steele *et al.*, 1986). Lysianassoids and oedicerotoids, which were classified into the 'endobenthic' category, include some of the most natant species of gammarideans (e.g. Ingram & Hessler, 1983; Sainte-Marie & Brunel, 1985), as well as truly endobenthic species, but also some poorly mobile or cryptic associated species (Besner, 1976; Bousfield, 1987; Vader, 1983). Considering the diversity of ecological habits within some superfamilies, and the generally deficient state of our knowledge of the autoecology of gammarideans, superfamily or family are dubious criteria for classification of ecological habits.

There is little direct evidence to support the contention that adult mortality risks are greater in

epibenthic than in endobenthic species: Nelson (1978, 1979a, 1979b) presented experimental evidence, based on caging experiments with a few species, that so-called epibenthic forms suffered greater mortality than so-called endobenthic forms. Other evidence also suggests that demersal predators, such as fish, may target epibenthic and suprabenthic species or developmental stages (e.g. Richards, 1963; Fincham, 1974; Stoner, 1979; Wakabara *et al.*, 1982; Sainte-Marie & Brunel, 1985; Sudo *et al.*, 1987). However, the differences between several epi- and endobenthic species in terms of exposure to predators are by no means clearcut and may vary during life. The swimming activities of several members of the 'endobenthic' Ampeliscoidea, Lysianassoidea and Oedicerotoidea are only seasonal in nature, as seen for instance in the ephemeral reproductive swarming of the lysianassoid *Paratryphosites abyssi* (Sainte-Marie & Brunel, 1985), but predators may at that time exact heavy tolls on adult populations before they breed (e.g. > 80% mortality for an ampeliscoid, Klein *et al.*, 1975).

Life history traits and size-specific or cohort mortality patterns obtained by Fenwick (1984) for some crustaceans were inconsistent with Van Dolah & Bird's (1980) predicted larger clutches/smaller embryos and inferred greater adult mortality for 'epi-' compared to 'endobenthic' gammarideans. The data reviewed herein also show that the very epi- or suprabenthic Eusiroidea produced among the largest embryos relative to body size (in text above and see Fig. 3), in sharp contrast to predictions. All endo- and epibenthic species in Fenwick (1984) suffered moderate to high juvenile mortality and generally high adult mortality. A similar pattern has been shown for three *Gammarus* species (Doyle & Hunte, 1981; Steele & Steele, 1986; Skadsheim, 1990).

Interpretation of life history patterns

Habitat-specific and superfamily-specific life history patterns apparently exist within the aquatic Gammaridea. Across habitats, life history patterns were fairly consistent with r-K-A selection. Most of the variation in life history traits – and of

brood size in particular – of gammaridean amphipods may be explained by body size (Tables 7 and 8), as has been demonstrated for other taxonomic groups (e.g. Stearns, 1983, 1984). Variations in the body size of gammarideans have been interpreted as adaptations to directly cope with differential, age-specific mortality rates (e.g. Nelson, 1980). However, other non-adaptive or adaptive interpretations of variations of body size across superfamilies or habitats may be more straightforward and at least as plausible (e.g. reduced body size of parasitic, commensal or deep-living detritivorous forms; gigantism of deep-living predaceous and necrophageous forms; body size constrained by temperature or food limitations). In the absence of proper life tables for the Gammaridea, interpretation of variations in body size, as of body size-independent variations of other life history traits, are thus highly conjectural; these variations may represent a ‘strategy’ resulting from selection or, more simply, a phylogenetic (historical) constraint (e.g. Brown, 1983; Stearns, 1983, 1984; Fenwick, 1984; Wanntorp *et al.*, 1990) or a phenotypic expression of environmental stress (e.g. Bailey & Mackie, 1986; Clarke *et al.*, 1985; Järvinen, 1986). Clearly, more information on age-specific mortality rates, and on their causes, is needed to reconcile ecological observation with life history theory for gammaridean amphipods.

Conclusions

Life histories of aquatic gammaridean amphipods fall into either of eight categories: semelparous or iteroparous semiannual (both multivoltine), semelparous (univoltine) or iteroparous (multivoltine) annual, semelparous or iteroparous (some multivoltine) biannual, and semelparous or iteroparous perennial (both univoltine). Most gammarideans described so far are of the iteroparous annual type. Semiannual and annual populations, with high reproductive potentials, are more characteristic of low latitude habitats, while annual and perennial gammarideans, with low reproductive potentials, are more frequent at high latitudes and in the deep sea. Exceptions

exist, and they probably may be explained in terms of phylogenetic constraints or selection for particular ecological habits.

All life history traits covary, but body size explains most of the variation in brood size and embryo diameter of gammaridean amphipods. There exists four options to increase reproductive potential or lifetime fecundity of gammaridean amphipods: increase body size for a constant breeding frequency, increase brood size by reducing embryo size, increase frequency of breeding for a constant lifespan, or increase longevity for a constant breeding rate. Brood size may be predicted with simple (using body size) or preferably multiple regression equations (using body size, embryo diameter and number of broods), and these predictive functions are very specific to superfamilies and habitats.

Previous reviews of gammaridean life history patterns – excepting those of Wildish (1982, 1988) – have focused singularly on brood size, which is thought to be adaptive and directly proportional to adult mortality. However, brood size alone may be a very poor indicator of total reproductive output, because longevity and the frequency of breeding are not taken into account. The reproductive potential (from Wildish, 1982), which is actually a fecundity rate, may be a more appropriate index from which to infer mortality rates. The reproductive potential varied significantly across superfamilies and habitats, but interpretations remain highly conjectural because information on mortality rates of gammarideans was virtually lacking. Phylogenetic or physiological constraints, and not only selection, may be useful for the interpretation of gammaridean life history patterns.

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Appendix 1. Reproductive and habitat parameters of aquatic gammaridean amphipods. Body length of females (in mm), brood size (*BS*), lifespan of females (*LS*, in mo), maximum number of broods per female (*NB*), mean embryo diameter (*ED*, in mm); information on temperature (C = cold, W = warm), salinity (B = brackish, F = freshwater, M = marine) and depth (D = deep, S = shallow) are grouped under the heading habitat. Numbers of broods in parentheses were inferred from HMFBL ratios (see text).

Species	Female length						Habitat	Authority
	Mean	Max.	<i>NE</i>	<i>LS</i>	<i>NB</i>	<i>ED</i>		
Ampeliscoidea								
<i>Ampelisca abdita</i>	6.6	7.7	26.0	10	1	0.43	CMS	Mills 1967
<i>Ampelisca abdita</i>	5.3	–	13.7	–	1	0.39	WMS	Nelson 1978
<i>Ampelisca abdita</i>	4.9	6.5	22.0	3	>1	–	WMS	Thoemke 1979
<i>Ampelisca armoricana</i>	10.8	12.4	42.4	24	>1	–	WMS	Dauvin 1988d
<i>Ampelisca araucana</i>	4.8	6.3	4.7	8	2	0.45	CMS	Carrasco & Arcos 1984
<i>Ampelisca brevicornis</i>	11.6	15.3	29.5	6	>1	0.48	WMS	Kaim-Malka 1969
<i>Ampelisca brevicornis</i>	13.7	15.4	23.0	15	1	–	CMS	Klein <i>et al.</i> 1975
<i>Ampelisca brevicornis</i>	12.8	14.7	37.1	12	1	–	CMS	Hastings 1981
<i>Ampelisca brevicornis</i>	11.5	14.0	32.6	18	>1	–	WMS	Dauvin 1988b
<i>Ampelisca brevicornis</i>	13.6	15.1	45.9	18	>1	–	WMS	Dauvin 1988b
<i>Ampelisca diadema</i>	9.0	11.0	12.3	–	–	0.49	WMS	Ivanov 1961
<i>Ampelisca macrocephala</i>	16.8	19.2	60.0	36	2	0.68	CMS	Kanneworf 1965
<i>Ampelisca sarsi</i>	6.7	7.8	15.6	21	>1	–	WMS	Dauvin 1989
<i>Ampelisca spinipes</i>	16.5	18.0	52.5	–	–	–	WMS	Bellan-Santini & Dauvin 1988
<i>Ampelisca tenuicornis</i>	8.8	10.5	23.6	15	2	0.37	CMS	Sheader 1977
<i>Ampelisca tenuicornis</i>	7.8	9.5	26.1	16	>1	–	WMS	Dauvin 1988a
<i>Ampelisca tenuicornis</i>	8.7	10.5	37.8	16	>1	–	WMS	Dauvin 1988a
<i>Ampelisca typica</i>	8.6	9.6	20.4	16	>1	–	WMS	Dauvin 1988c
<i>Ampelisca vadorum</i>	9.5	11.2	32.1	10	1	0.56	CMS	Mills 1967
<i>Ampelisca vadorum</i>	6.0	7.5	9.1	–	1	0.51	WMS	Van Dolah & Bird 1980
<i>Ampelisca verrilli</i>	10.6	13.7	14.6	–	>1	–	WMS	Thoemke 1979
<i>Haploops fundiensis</i>	7.0	–	5.0	–	1	0.43	CMS	Wildish 1982
<i>Haploops tenuis</i>	8.0	–	35.0	36	1	0.59	CMS	Kanneworf 1966
<i>Haploops tubicola</i>	10.5	11.0	45.0	36	1	0.75	CMS	Kanneworf 1966
Corophioidea								
<i>Ampithoe lacertosa</i>	15.1	25.5	64.0	–	>1	0.46	CMS	Heller 1968
<i>Ampithoe longimana</i>	5.8	–	9.4	–	>1	0.38	WMS	Nelson 1978
<i>Ampithoe ramondi</i>	8.0	11.0	21.0	14	–	0.31	WMS	Gilat 1962
<i>Ampithoe rubricata</i>	16.2	20.0	62.0	–	–	–	CMS	Skutch 1926
<i>Ampithoe rubricata</i>	15.3	20.0	57.5	–	–	–	CMS	Kuznetsov 1964
<i>Ampithoe valida</i>	9.7	13.1	22.0	–	>1	0.42	WMS	Barrett 1966
<i>Chelura terebrans</i>	4.0	6.0	3.7	–	8	0.45	WMS	Kühne & Becker 1964
<i>Corophium acherusicum</i>	4.1	6.0	18.8	–	>1	–	CMS	Onbé 1966
<i>Corophium acherusicum</i>	3.0	–	7.9	–	>1	0.31	WMS	Nelson 1980
<i>Corophium arenarium</i>	5.1	–	14.3	13	>1	–	CBS	Fish & Mills 1979
<i>Corophium bonnellii</i>	3.1	4.8	6.0	10	3	0.36	CMS	Moore 1978 1981
<i>Corophium insidiosum</i>	3.2	3.7	3.9	–	6	0.28	CMS	Sheader 1978
<i>Corophium insidiosum</i>	3.1	4.4	5.7	12	6	0.28	CMS	Sheader 1978
<i>Corophium insidiosum</i>	3.8	5.6	10.8	5	7	0.36	CMS	Nair & Anger 1979a
<i>Coropium sextonae</i>	4.3	5.8	16.3	12	>1	–	WMS	Hughes 1978
<i>Corophium volutator</i>	7.2	–	30.5	13	>1	–	CBS	Fish & Mills 1979
<i>Corophium volutator</i>	7.8	–	46.8	–	>1	–	CMS	Peer <i>et al.</i> 1986
<i>Corophium volutator</i>	6.4	–	23.8	–	>1	–	CMS	Peer <i>et al.</i> 1986
<i>Cymadusa compta</i>	5.8	–	13.5	–	>1	0.37	WMS	Nelson 1978

Appendix 1. (Continued)

Species	Female length						Habitat	Authority
	Mean	Max.	NE	LS	NB	ED		
<i>Cymadusa filosa</i>	8.5	13.0	29.5	15	–	0.39	WMS	Gilat 1962
<i>Dulichia spinosissima</i>	13.5	15.0	227.0	–	–	0.52	CMS	MacGinitie 1955
<i>Erichthonius brasiliensis</i>	5.0	6.5	9.4	12	>1	–	WMS	Hughes 1978
<i>Gammaropsis inaequistylis</i>	5.2	6.6	27.5	–	–	0.23	CMS	Steele <i>et al.</i> 1986
<i>Gammaropsis longicornis</i>	3.3	4.0	7.5	–	–	–	CMS	Thurston 1974
<i>Gammaropsis megalops</i>	8.8	14.0	10.5	–	–	0.45	CMS	MacGinitie 1955
<i>Grandidierella bonnieroides</i>	5.4	7.5	28.9	3	>1	–	WMS	Thoemke 1979
<i>Ischyrocerus anguipes</i>	6.8	9.0	75.0	–	–	–	CMS	Kuznetsov 1964
<i>Ischyrocerus anguipes</i>	4.9	6.2	34.5	–	–	–	CMS	Kuznetsov 1964
<i>Jassa falcata</i>	6.7	8.2	9.4	8	4	–	CMS	Nair & Anger 1979b
<i>Jassa falcata</i>	4.6	–	25.6	–	>1	0.29	WMS	McGovern in Nelson 1980
<i>Jassa marmorata</i>	4.9	–	19.2	3	–	–	WMS	Franz 1989
<i>Jassa marmorata</i>	6.2	–	40.3	8	–	–	WMS	Franz 1989
<i>Lembos websteri</i>	4.7	–	8.0	–	>1	0.39	WMS	Nelson 1978
<i>Leptocheirus pilosus</i>	3.5	4.0	11.0	–	–	–	CBS	Goodhart 1939
<i>Leptocheirus pinguis</i>	14.1	17.0	49.8	30	2	0.47	CMS	Wildish 1980
<i>Microdeutopus gryllotalpa</i>	6.3	8.0	21.0	4	11	–	WMS	Myers 1971
<i>Photis reinhardi</i>	5.0	5.5	14.0	–	–	0.50	CMS	MacGinitie 1955
<i>Rudilemboides naglei</i>	3.2	4.3	5.8	3	>1	–	WMS	Thoemke 1979
Crangonyctoidea								
<i>Crangonyx gracilis</i>	8.1	11.0	45.7	–	–	–	CFS	Emboly 1911
<i>Crangonyx gracilis</i>	7.8	10.0	33.3	19	5	–	CFS	Hynes 1955
<i>Crangonyx richmondensis</i>	13.0	14.0	23.3	12	1	0.30	CFS	Judd 1963
<i>Crangonyx richmondensis</i>	13.8	18.6	43.0	13	1	0.54	CFS	Sprules 1967
<i>Crangonyx rivularis</i>	6.0	7.0	19.3	–	–	–	CFS	Judd 1963
<i>Niphargus aquilex</i>	4.9	6.5	2.9	8	–	–	CFS	Gledhill & Ladle 1969
Dexaminoidea								
<i>Atylus guttatus</i>	5.5	7.0	26.0	–	–	0.40	WMS	Ivanov 1961
<i>Dexamine spinosa</i>	6.0	–	25.0	–	–	–	WMS	Greze 1963
Eusiroidea								
<i>Atyloella magellanica</i>	18.8	19.0	114.3	–	–	0.67	CMS	Thurston 1974
<i>Bovallia gigantea</i>	45.2	49.0	108.0	54	1	1.34	CMS	Thurston 1968 1970 1974
<i>Calliopius laeviusculus</i>	9.8	13.8	85.0	–	–	–	CMS	Kuznetsov 1964
<i>Calliopius laeviusculus</i>	8.0	12.0	48.5	12	>1	0.45	CMS	Steele DH & Steele 1973a
<i>Calliopius laeviusculus</i>	10.5	12.0	65.2	12	>1	0.58	CMS	Steele DH & Steele 1973a
<i>Calliopius laeviusculus</i>	12.0	12.4	83.3	–	–	–	CMS	Sainte-Marie unpubl.
<i>Djerboa furcipes</i>	18.0	20.0	59.0	–	–	–	CMS	Thurston 1974
<i>Epimeria loricata</i>	25.0	30.0	20.5	–	–	–	CMS	Kuznetsov 1964
<i>Epimeria loricata</i>	26.3	31.0	16.0	–	–	–	CMS	Kuznetsov 1964
<i>Epimeria monodon</i>	24.5	25.0	55.5	–	–	1.27	CMS	Thurston 1974
<i>Eurymera monticulosa</i>	24.3	26.0	96.7	–	–	0.75	CMS	Thurston 1974
<i>Liouvillea oculata</i>	15.5	17.0	39.0	–	–	–	CMS	Thurston 1974
<i>Metaleptamphopus pectinatus</i>	6.0	6.5	9.3	–	–	0.43	CMS	Thurston 1974
<i>Paramoera hurleyi</i>	6.8	7.0	11.0	–	–	–	CMS	Thurston 1974
<i>Paramoera walkeri</i>	13.8	17.0	106.5	24	1	0.55	CMS	Rakusa-Suszczewski 1972
<i>Paramoera walkeri</i>	14.6	15.7	126.0	36	1	–	CMS	Sagar 1980
<i>Paramoera walkeri</i>	16.8	20.2	200.0	48	1	–	CMS	Sagar 1980

Appendix 1. (Continued)

Species	Female length						Habitat	Authority
	Mean	Max.	NE	LS	NB	ED		
<i>Paramphithoe cuspidata</i>	20.7	25.2	38.0	-	-	-	CMS	Kuznetsov 1964
<i>Pontogeneia antarctica</i>	17.5	19.0	49.0	-	(1)	0.65	CMS	Thurston 1974
<i>Pontogeneia inermis</i>	9.1	9.2	56.3	-	(1)	0.57	CMS	Sainte-Marie unpubl.
<i>Pontogeneia simplex</i>	15.0	16.0	23.0	-	-	-	CMS	Schellenberg 1926
<i>Pontogeniella brevicornis</i>	18.1	21.0	65.8	-	-	0.67	CMS	Thurston 1974
<i>Prostebbingia gracilis</i>	7.9	11.0	24.9	-	-	0.44	CMS	Thurston 1974
<i>Pseudomoera gabrieli</i>	9.5	12.0	41.0	-	-	-	WFS	Smith & Williams 1983
<i>Rhachotropis aculeata</i>	27.7	33.0	62.5	-	-	-	CMS	Kuznetsov 1964
<i>Rhachotropis aculeata</i>	38.0	43.5	236.5	-	-	-	CMS	Kuznetsov 1964
<i>Rhachotropis oculata</i>	12.1	15.0	24.0	-	>1	-	CMS	Desroches 1985
<i>Stenopleura atlantica</i>	5.8	7.5	7.0	-	-	-	CMD	Schellenberg 1926
Gammaroidea								
<i>Gammaracanthus loricatus</i>	40.0	-	327.0	-	-	-	CMS	Barnard 1959
<i>Gammaracanthus loricatus</i>	46.0	60.0	599.2	-	>1	0.85	CMS	Steele DH & Steele 1976
<i>Gammarellus angulosus</i>	11.5	15.0	21.5	12	>1	0.65	CMS	Steele DH & Steele 1972b
<i>Gammarellus homari</i>	25.7	35.4	127.0	-	>1	1.00	CMS	Kuznetsov 1964, Steele 1972
<i>Gammarus chevreuxi</i>	7.0	9.0	30.0	18	26	-	CBS	Sexton 1928
<i>Gammarus crinicornis</i>	9.5	14.0	33.2	-	-	0.44	WMS	Dumay 1972
<i>Gammarus duebeni</i>	14.5	18.0	36.5	13	6	-	CBS	Kinne 1953a 1953b
<i>Gammarus duebeni</i>	10.5	13.0	17.9	15	-	-	CBS	Hynes 1954
<i>Gammarus duebeni</i>	11.2	15.0	24.0	15	6	0.61	CBS	Hynes 1954, 1955
<i>Gammarus duebeni</i>	10.9	14.0	19.8	15	5	0.65	CFS	Hynes 1954, 1955
<i>Gammarus duebeni</i>	14.0	18.0	25.4	12	>1	0.56	CBS	Steele DH & Steele 1969
<i>Gammarus duebeni</i>	13.5	15.0	40.5	-	>1	-	WBS	Jażdżewski 1973
<i>Gammarus fasciatus</i>	8.7	12.0	22.3	-	12	-	CFS	Emboly 1911
<i>Gammarus fasciatus</i>	10.3	15.0	16.6	-	>1	0.46	WFS	Clemens 1950
<i>Gammarus fasciatus</i>	9.5	13.0	29.3	15	4	-	CFS	Hynes 1955
<i>Gammarus finmarchicus</i>	13.5	19.0	21.5	12	>1	0.50	CMS	Steele DH & Steele 1975b
<i>Gammarus inaequicauda</i>	9.5	13.0	36.0	-	-	-	WBS	Jażdżewski 1973
<i>Gammarus lacustris</i>	13.4	16.0	24.3	-	4	-	CFS	Emboly 1911
<i>Gammarus lacustris</i>	11.5	14.0	21.8	15	4	-	CFS	Hynes 1955
<i>Gammarus lacustris</i>	10.0	13.0	17.5	24	4	-	CFS	Hynes & Harper 1972
<i>Gammarus lawrencianus</i>	7.0	9.0	19.2	12	>1	0.41	CMS	Steele DH & Steele 1970b
<i>Gammarus lawrencianus</i>	7.0	10.0	21.8	12	>1	0.41	CMS	Steele DH & Steele 1970b
<i>Gammarus locusta</i>	10.8	16.0	62.1	-	-	0.43	CMS	Spooner 1947
<i>Gammarus locusta</i>	19.6	26.0	104.5	-	-	-	CMS	Kuznetsov 1964
<i>Gammarus locusta</i>	23.9	29.5	130.0	-	-	-	CMS	Kuznetsov 1964
<i>Gammarus locusta</i>	10.0	14.0	49.0	-	-	-	WBS	Jażdżewski 1973
<i>Gammarus marinus</i>	14.0	18.0	16.4	11	4	-	CBS	Vlasblom 1969
<i>Gammarus marinus</i>	14.2	17.4	23.3	14	3	-	CBS	Skadsheim 1982
<i>Gammarus mucronatus</i>	6.0	8.0	14.0	-	>1	0.36	CMS	Steele DH & Steele 1975a
<i>Gammarus mucronatus</i>	8.1	10.0	27.4	-	-	-	WMS	Borowsky 1980a
<i>Gammarus mucronatus</i>	5.8	7.0	21.4	-	-	0.28	WMS	Van Dolah & Bird 1980
<i>Gammarus mucronatus</i>	5.5	7.5	16.8	2	>1	0.43	CBS	LaFrance & Ruber 1985
<i>Gammarus mucronatus</i>	8.0	11.5	35.7	8	>1	0.43	CBS	LaFrance & Ruber 1985
<i>Gammarus mucronatus</i>	9.6	15.5	34.6	5	>1	0.42	WBS	Fredette & Diaz 1986
<i>Gammarus obtusatus</i>	11.0	14.0	9.0	-	6	0.55	CMS	Shedder & Chia 1970
<i>Gammarus obtusatus</i>	10.5	14.0	7.0	-	4	0.61	CMS	Steele DH & Steele 1970a
<i>Gammarus obtusatus</i>	11.5	15.0	13.5	12	4	0.65	CMS	Steele DH & Steele 1970a

Appendix 1. (Continued)

Species	Female length						Habitat	Authority
	Mean	Max.	NE	LS	NB	ED		
<i>Gammarus oceanicus</i>	15.3	20.0	77.2	48	3	0.55	CMS	Steele VJ & Steele 1972
<i>Gammarus oceanicus</i>	15.5	20.0	37.4	48	3	0.55	CMS	Steele VJ & Steele 1972
<i>Gammarus olivii</i>	6.5	10.0	23.0	10	20	–	WMS	Greze 1972
<i>Gammarus palustris</i>	6.5	9.0	9.2	12	5	0.41	WMS	Van Dolah <i>et al.</i> 1975
<i>Gammarus palustris</i>	7.2	10.9	30.5	16	3	–	CBS	Gable & Croker 1977
<i>Gammarus palustris</i>	7.5	8.6	12.0	–	–	–	WBS	Borowsky 1980a
<i>Gammarus pseudolimnaeus</i>	11.5	15.0	39.0	15	3	–	CBS	Hynes & Harper 1972
<i>Gammarus pulex</i>	8.9	12.0	16.0	15	6	–	CFS	Hynes 1955
<i>Gammarus salinus</i>	12.0	14.0	76.5	–	–	–	WFS	Jażdżewski 1973
<i>Gammarus salinus</i>	10.5	14.5	33.0	–	7	0.31	WBS	Kolding & Fenchel 1981
<i>Gammarus setosus</i>	15.0	20.0	24.8	–	>1	0.69	CMS	Steele VJ & Steele 1970
<i>Gammarus setosus</i>	18.0	23.0	36.6	–	>1	0.69	CMS	Steele VJ & Steele 1970
<i>Gammarus stoerensis</i>	6.0	7.0	12.0	–	>1	0.44	CBS	Steele DH & Steele 1975a
<i>Gammarus stoerensis</i>	6.7	7.6	26.9	14	3	–	CBS	Skadsheim 1982
<i>Gammarus subtypicus</i>	11.0	13.8	21.8	–	–	0.37	WMS	Dumay 1972
<i>Gammarus tigrinus</i>	10.0	14.0	30.7	15	>1	0.46	CBS	Steele DH & Steele 1972a
<i>Gammarus tigrinus</i>	6.5	11.6	28.7	6	16	–	CFS	Chambers 1977
<i>Gammarus troglophilus</i>	12.8	14.6	12.0	12	>1	–	WFS	Jenio 1980
<i>Gammarus wilkitzkii</i>	26.5	33.0	159.1	–	>1	0.73	CMS	Barnard 1959, Steele DH & Steele 1975a
<i>Gammarus zaddachi</i>	10.6	13.0	27.8	–	–	0.53	CMS	Spooner 1947
<i>Gammarus zaddachi</i>	9.5	13.0	47.5	–	–	–	WBS	Jażdżewski 1973
<i>Pallasea quadrispinosa</i>	12.0	15.0	57.5	–	–	–	CFS	Samter & Weltner 1904
<i>Pallasea quadrispinosa</i>	11.0	14.4	28.6	24	4	0.58	CFS	Mathisen 1953
<i>Quadrivisio lutzi</i>	4.5	–	3.0	–	–	0.35	WMS	Stephensen 1933
Hadzioidea								
<i>Allomelita pellucida</i>	3.0	6.0	4.0	–	>1	0.48	WBS	Legueux 1926, Stock 1984
<i>Casco bigelowi</i>	15.0	–	40.0	–	1	0.62	CMS	Wildish 1982
<i>Casco bigelowi</i>	19.2	20.7	50.2	30	1	0.62	CMS	Wildish 1980
<i>Elasmopus levis</i>	7.1	9.5	22.3	–	>1	–	WMS	Borowsky 1986
<i>Elasmopus levis</i>	4.3	–	4.7	–	>1	0.40	WMS	Nelson 1978
<i>Melita appendiculata</i>	3.8	–	5.1	–	>1	0.36	WMS	Nelson 1978
<i>Melita celericula</i>	3.3	4.0	3.4	–	–	0.32	WMS	Croker 1971
<i>Melita formosa</i>	24.2	25.4	54.0	–	–	0.70	CMS	MacGinitie 1955
<i>Melita nitida</i>	6.9	8.7	30.0	–	>1	–	WMS	Borowsky 1980a
<i>Melita nitida</i>	5.8	7.0	17.7	–	–	0.30	WMS	Van Dolah & Bird 1980
<i>Melita palmata</i>	10.5	–	8.8	–	–	0.45	WMS	Ivanov 1961
<i>Melita zeylanica</i>	5.0	6.6	16.5	5	22	–	WBS	Krishnan & John 1974
Leucothoidea								
<i>Gitanopsis squamosa</i>	3.6	4.3	5.9	–	–	0.40	CMS	Thurston 1974
<i>Leucothoe spinicarpa</i>	10.7	11.0	20.7	–	–	0.66	CMS	Thurston 1974
<i>Metopa groenlandica</i>	5.0	–	5.0	–	–	–	CMS	Stephensen 1936
<i>Metopa tuberculata</i>	2.9	3.0	2.0	–	–	–	CMS	Schellenberg 1926
<i>Metopelloides micropalpa</i>	4.8	5.2	14.2	–	–	0.49	CMS	Sainte-Marie unpubl.
<i>Probolisca ovata</i>	2.9	3.8	4.5	–	–	–	CMS	Thurston 1974
Lilljeborgoidea								
<i>Seba dubia</i>	3.5	3.8	2.5	–	–	–	CMS	Schellenberg 1926
<i>Seborgia minima</i>	0.9	1.0	1.0	–	>1	0.25	WBS	Bousfield 1970

Appendix 1. (Continued)

Species	Female length						Habitat	Authority
	Mean	Max.	NE	LS	NB	ED		
Lysianassoidea								
<i>Alicella gigantea</i>	230.0	–	98.0	–	>1	9.11	CMD	Barnard & Ingram 1986
<i>Anonyx nugax</i>	42.0	46.0	630.0	40	(1)	1.30	CMS	Kuznetsov 1964, MacGinitie 1955
<i>Anonyx sarsi</i>	22.4	23.8	105.8	26	1	1.02	CMS	Sainte-Marie <i>et al.</i> 1990
<i>Anonyx sarsi</i>	18.6	19.1	84.0	26	1	1.01	CMS	Sainte-Marie unpubl.
<i>Anonyx</i> sp.	30.0	32.0	259.0	–	–	–	CMS	Kuznetsov 1964
<i>Anonyx</i> spp.	17.6	24.0	68.0	–	–	–	CMS	Kuznetsov 1964
<i>Cheirimedon femoratus</i>	13.0	15.0	68.9	48	1	0.67	CMS	Bregazzi 1972 1973
<i>Euonyx chelatus</i>	8.3	9.6	9.0	–	(1)	0.68	CMS	Comely & Ansell 1988
<i>Eurythenes gryllus</i>	112.8	–	194.0	156	>1	2.30	CMD	Ingram & Hessler 1987
<i>Hippomedon kergueleni</i>	11.5	14.5	8.8	48	4	0.74	CMS	Bregazzi 1972 1973
<i>Hippomedon propinquus</i>	10.0	–	10.0	–	>1	0.55	CMS	Stephensen 1923
<i>Hippomedon propinquus</i>	9.7	13.1	8.8	24	5	0.58	CMS	Lamarche & Brunel 1987
<i>Hippomedon propinquus</i>	8.8	10.9	6.5	24	5	0.58	CMS	Lamarche & Brunel 1987
<i>Hippomedon whero</i>	5.3	6.7	3.4	12	8	0.39	CMS	Fenwick 1985
<i>Hirondellea gigas</i>	40.0	43.0	97.2	–	1	0.72	CMD	Hessler <i>et al.</i> 1978
<i>Lepidepcreum cingulatum</i>	6.6	7.0	10.8	–	(1)	0.44	CMS	Thurston 1974
<i>Metambasia faeroensis</i>	5.5	6.0	2.0	–	–	0.40	CMD	Stephensen 1923
<i>Onisimus litoralis</i>	16.9	17.8	44.2	24	1	0.88	CBS	Sainte-Marie <i>et al.</i> 1990
<i>Opisa tridentata</i>	7.0	9.0	6.6	–	–	–	CMS	Bousfield 1987
<i>Orchomene gerulicorbis</i>	11.6	12.9	35.0	–	2	–	CMD	Thurston 1979
<i>Orchomene plebs</i>	17.8	21.0	28.9	–	–	0.83	CMD	Rakusa-Suszczewski 1982
<i>Orchomene rossi</i>	41.0	47.0	37.1	–	>1	–	CMD	Stockton 1982
<i>Orchomene rotundifrons</i>	11.0	–	15.0	–	–	–	CMS	Thurston 1974
<i>Orchomenella minuta</i>	5.3	7.0	9.0	–	–	–	CMS	Kuznetsov 1964
<i>Orchomenella minuta</i>	6.2	7.0	22.0	–	–	–	CMS	Kuznetsov 1964
<i>Orchomenella minuta</i>	6.4	8.8	14.7	12	3	0.52	CMS	Sainte-Marie <i>et al.</i> 1990
<i>Orchomenella minuta</i>	5.1	5.9	16.5	12	2	0.48	CMS	Sainte-Marie unpubl.
<i>Orchomenella pinguis</i>	5.3	7.0	11.0	12	–	–	CMS	Kuznetsov 1964
<i>Orchomenella pinguis</i>	7.8	10.0	41.5	12	3	0.51	CMS	Sainte-Marie <i>et al.</i> 1990
<i>Parawaldeckia stephenseni</i>	4.6	5.5	12.0	–	5	–	WMS	Fincham 1974
<i>Psammonyx nobilis</i>	12.5	17.0	21.5	24	2	–	CMS	Scott & Croker 1976
<i>Psammonyx terranova</i>	15.2	18.0	17.7	24	2	1.07	CMS	Sainte-Marie <i>et al.</i> 1990
<i>Psammonyx terranova</i>	13.8	15.6	18.6	24	2	1.10	CMS	Sainte-Marie unpubl.
<i>Pseudorchomene coatsi</i>	14.0	16.0	62.0	–	–	–	CMS	Schellenberg 1926
<i>Tmetonyx</i> sp.	15.1	18.0	12.3	–	>1	1.32	CMD	Sainte-Marie unpubl.
Oedicerotoidea								
<i>Exoediceros fossor</i>	5.7	8.3	9.6	–	–	–	WMS	Dexter 1985
<i>Exoediceroides maculosus</i>	5.1	6.6	9.4	–	–	–	WMS	Dexter 1985
<i>Monoculodes edwardsi</i>	6.0	6.9	28.4	–	–	0.28	WMS	Van Dolah & Bird 1980
<i>Oediceros saginatus</i>	16.8	17.9	148.8	–	1	0.94	CMS	Sainte-Marie unpubl.
<i>Patuki roperi</i>	9.0	11.8	6.7	9	11	0.48	CMS	Fenwick 1985
<i>Pontocrates altamarinus</i>	4.0	5.0	4.8	–	–	–	CMS	Fincham 1971
<i>Pontocrates arenarius</i>	3.1	4.2	3.1	–	–	–	CMS	Fincham 1971
<i>Westwoodilla caecula</i>	6.0	–	20.0	–	–	–	CMS	Stephensen 1923
Phoxocephaloidea								
<i>Diogidias littoralis</i>	3.9	4.9	2.7	6	7	0.35	CMS	Fenwick 1985
<i>Paraharpinia rotundifrons</i>	6.5	7.5	14.3	–	(1)	0.54	CMS	Thurston 1974

Appendix 1. (Continued)

Species	Female length						Habitat	Authority
	Mean	Max.	NE	LS	NB	ED		
<i>Protophoxus australis</i>	8.6	11.0	19.3	14	13	0.45	CMS	Fenwick 1985
<i>Rhepoxynius abronius</i>	3.8	–	9.1	12	2	0.42	CMS	Slattery 1985
<i>Rhepoxynius abronius</i>	3.6	4.6	9.3	12	2	–	CMS	Kemp <i>et al.</i> 1985
<i>Rhepoxynius fatigans</i>	2.8	–	4.0	12	2	0.41	CMS	Slattery 1985
Pontoporeioidea								
<i>Acanthohaustorius</i> sp.	3.9	4.8	5.2	18	–	–	WMS	Croker 1967
<i>Acanthohaustorius millsi</i>	3.8	4.6	4.8	17	1	0.78	CMS	Sameoto 1969b, Van Dolah & Bird 1980
<i>Acanthohaustorius millsi</i>	5.1	6.2	7.8	17	1	–	CMS	Sameoto 1969b
<i>Amphiporeia lawrenciana</i>	10.0	14.0	14.6	–	>1	0.83	CMS	Downer & Steele 1979
<i>Amphiporeia lawrenciana</i>	8.5	9.2	25.6	–	(1)	0.61	CMS	Sainte-Marie unpubl.
<i>Amphiporeia virginiana</i>	5.1	6.2	8.9	12	1	–	CMS	Hager & Croker 1979
<i>Amphiporeia virginiana</i>	5.5	7.0	6.0	–	–	0.27	WMS	Van Dolah & Bird 1980
<i>Bathyporeia elegans</i>	3.5	4.5	3.5	–	–	–	CMS	Fincham 1971
<i>Bathyporeia guilliamsoniana</i>	7.2	–	22.0	–	–	–	WMS	Salvat 1967
<i>Bathyporeia nana</i>	2.4	2.9	2.4	–	–	–	CMS	Fincham 1971
<i>Bathyporeia pelagica</i>	5.6	6.3	7.5	–	>1	–	WMS	Salvat 1967
<i>Bathyporeia pelagica</i>	4.1	4.7	3.7	–	–	–	CMS	Fincham 1971
<i>Bathyporeia pelagica</i>	5.1	–	6.4	–	>1	0.42	CMS	Fish 1975
<i>Bathyporeia pilosa</i>	5.1	6.0	5.0	–	>1	–	WMS	Salvat 1967
<i>Bathyporeia pilosa</i>	4.4	–	6.9	–	>1	0.44	CMS	Fish 1975
<i>Bathyporeia sarsi</i>	5.5	6.4	9.0	–	>1	–	WMS	Salvat 1967
<i>Bumeralius buchalius</i>	5.0	6.0	4.8	–	–	–	WMS	Dexter 1985
<i>Eohaustorius brevicuspus</i>	3.9	5.0	6.9	–	13	–	CMS	Bosworth 1976
<i>Eohaustorius estuarius</i>	3.7	5.0	6.5	–	–	–	CBS	Bosworth 1976
<i>Eohaustorius sencillus</i>	2.8	3.0	6.3	12	1	0.39	CMS	Slattery 1985
<i>Eohaustorius washingtonius</i>	4.6	6.0	11.9	–	–	–	CMS	Bosworth 1976
<i>Haustorius</i> sp.	6.4	7.5	5.6	18	–	–	WMS	Croker 1967
<i>Haustorius arenarius</i>	9.5	13.0	11.8	–	2	–	WMS	Salvat 1967
<i>Haustorius canadensis</i>	6.8	9.2	7.9	–	–	–	CMS	Donn & Croker 1986
<i>Haustorius dytiscus</i>	4.0	4.7	4.0	18	–	–	WMS	Croker 1967
<i>Neohaustorius biarticulatus</i>	5.0	6.5	7.0	16	>1	–	CMS	Sameoto 1969a
<i>Neohaustorius schmitzi</i>	3.2	4.0	3.5	12	–	–	WMS	Croker 1967
<i>Neohaustorius schmitzi</i>	4.5	6.0	4.8	–	–	0.45	WMS	Van Dolah & Bird 1980
<i>Parahaustorius longimerus</i>	6.3	7.5	7.8	18	–	–	WMS	Croker 1967
<i>Parahaustorius longimerus</i>	6.6	8.4	5.3	17	1	–	CMS	Sameoto 1969b
<i>Pontoporeia affinis</i>	8.1	10.0	16.5	27	1	0.53	CFS	Mathisen 1953
<i>Pontoporeia affinis</i>	7.5	9.0	24.0	24	–	–	CFS	Moore 1979
<i>Pontoporeia femorata</i>	11.5	13.0	71.5	–	1	–	CMS	Marguilis 1970
<i>Pontoporeia femorata</i>	11.0	13.0	63.5	36	2	0.45	CMS	Steele DH & Steele 1978
<i>Pontoporeia femorata</i>	12.5	13.7	57.6	18	1	0.41	CMS	Wildish & Peer 1981
<i>Pontoporeia hoyi</i>	6.5	7.0	17.8	12	1	–	CMS	Siegfried 1985
<i>Pontoporeia hoyi</i>	7.0	–	14.2	24	1	–	CMS	Siegfried 1985
<i>Pontoporeia</i> sp.	11.0	12.1	48.3	–	(1)	0.61	CMS	Sainte-Marie unpubl.
<i>Protohaustorius deichmannae</i>	3.8	4.6	3.2	18	>1	–	CMS	Sameoto 1969b
<i>Protohaustorius deichmannae</i>	4.7	6.2	5.7	18	>1	–	CMS	Sameoto 1969b
<i>Urohaustorius metungi</i>	3.9	5.5	10.1	–	–	–	WMS	Dexter 1985
<i>Urothoe brevicornis</i>	6.4	7.9	23.0	–	1	–	WMS	Salvat 1967

Appendix 1. (Continued)

Species	Female length						Habitat	Authority
	Mean	Max.	NE	LS	NB	ED		
Stegocephaloidea								
<i>Lafystius morhuanus</i>	5.7	6.8	7.3	-	-	-	CMS	Bousfield 1987
<i>Stegocephalina ingolfi</i>	9.0	-	15.0	-	-	0.60	CMD	Stephensen 1944
<i>Stegocephalus inflatus</i>	31.3	40.4	65.5	-	-	-	CMS	Kuznetsov 1964
<i>Stegocephalus inflatus</i>	21.5	26.0	23.5	-	>1	1.37	CMS	Steele DH 1967
<i>Stegocephalus inflatus</i>	30.0	37.0	32.3	-	>1	1.66	CMS	Steele DH 1967
Synopioidea								
<i>Bruzelia tuberculata</i>	16.0	-	30.0	-	-	0.85	CMD	Stephensen 1923
Talitroidea								
<i>Austrochiltonia australis</i>	6.0	7.9	46.5	9	-	-	CFS	Smith & Williams 1983
<i>Austrochiltonia subtenuis</i>	4.0	6.0	22.1	-	>1	-	WBS	Lim & Williams 1971
<i>Hyale barbicornis</i>	7.5	11.5	13.5	9	-	-	CMS	Hiwatari & Kajihara 1984
<i>Hyale nilssoni</i>	6.2	-	20.7	12	-	-	CBS	McBane & Croker 1984
<i>Hyale nilssoni</i>	7.5	8.2	23.8	12	-	-	CMS	McBane & Croker 1984
<i>Hyale prevosti</i>	6.9	9.0	16.0	-	-	-	CMS	Kuznetsov 1964
<i>Hyale schmidtii</i>	4.0	5.0	5.7	-	-	-	WMS	Gilat 1962
<i>Hyalella azteca</i>	4.3	-	8.0	-	>1	0.35	CFS	Strong 1972
<i>Hyalella azteca</i>	5.9	-	18.0	-	>1	0.29	CFS	Strong 1972
<i>Hyalella azteca</i>	6.7	-	17.0	-	>1	0.28	CFS	Strong 1972
<i>Hyalella knickerbockeri</i>	5.5	7.4	17.6	-	11	-	CFS	Emboly 1911
<i>Orchestia cavimana</i>	13.5	15.5	14.6	-	4	-	CBS	Dorsman 1935
<i>Orchestia cavimana</i>	16.0	-	18.0	-	6	0.62	CBS	Wildish 1979
<i>Orchestia gammarellus</i>	15.0	18.0	19.0	-	8	0.73	CBS	Wildish 1979
<i>Orchestia mediterranea</i>	20.0	-	36.0	-	5	0.65	CBS	Wildish 1979
<i>Orchestia platensis</i>	8.4	10.7	13.5	-	>1	0.62	CBS	Nagata 1966
<i>Orchestia platensis</i>	9.5	12.0	18.0	12	4	-	CBS	Behbahani & Croker 1982
<i>Orchestia platensis</i>	9.5	12.0	24.0	10	4	0.58	CBS	Morino 1978
<i>Orchestia roffensis</i>	8.0	-	5.0	-	4	0.56	CBS	Wildish 1979
<i>Parhyalella basrensis</i>	6.3	8.5	15.3	15	4	0.39	WBS	Ali & Salman 1986
<i>Parhyalella pietschmanni</i>	6.5	9.0	12.9	-	>1	0.39	WMS	Steele 1973
<i>Probosciniotus loquax</i>	8.4	10.8	20.0	10	>1	0.50	CMS	Hughes 1982
<i>Talitrus saltator</i>	12.6	14.8	13.0	18	1	0.85	CBS	Williams 1978
<i>Talorchestia margaritae</i>	8.8	12.0	7.2	3	-	-	WBS	Venables 1981
<i>Uhlorchestia sparinophila</i>	7.8	9.0	5.5	-	-	-	WBS	Bousfield & Heard 1986
<i>Uhlorchestia uhleri</i>	9.0	10.0	6.0	-	-	-	WBS	Bousfield & Heard 1986

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