

Critique of Some Practices in Life-history Studies, with Special Reference to Harpacticoid Copepods

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Abstract

Published studies on the demography and reproductive strategies of harpacticoid copepods are examined critically. At the technical level, the popular approximation $r \approx \ln R_0/T_c$ is shown to be inappropriate as an estimate of the intrinsic rate of increase of harpacticoids. It leads to a systematic underestimation, by 8-29%, for life histories typical of fast-breeding species. Various *ad hoc* variants of r and R_0 calculations occurring in the literature are also criticized. At the conceptual level, a more discriminating approach to life-history characteristics is necessary; this applies both to the assessment of their 'strategic' significance, and to their diagnostic power with regard to the various 'strategies'. Special attention is given to the non-equivalence of parity and voltinism. Recommendations that should promote the construction of a more rigorous cognitive framework are included.

Introduction

A science comes of age when the purely descriptive approach begins to be complemented with purposeful experimental studies, generated by explicit hypotheses. By this criterion, life-history studies and demography of meiofaunal organisms are at present crossing the boundary (e.g. Lopez 1982). It appears timely, then, to examine critically the existing data base and concepts upon which future developments will have to be founded.

The subject matter is vast. For certain groups, such as harpacticoid copepods, reviews of several topics are already available [e.g. phenology and reproductive seasonality (Coull and Vernberg 1975); reproductive strategies (Hicks 1979); use of demographic parameters in interspecific comparisons (Bergmans 1981); general ecology (Hicks and Coull 1983)]. In the present paper, I address two specific topics of methodological interest, viz technical aspects concerning the computation of demographic parameters, and conceptual aspects relating to life histories. Biased estimates of demographic parameters may be quite harmless for certain purposes (e.g. establishing the existence of particular environmental effects) but will thwart a proper evaluation of population processes, which is what demography is about. The effect of loose and inexplicit concepts, though less readily apparent, may prove an even greater handicap in the long run. It is hoped that the criticisms expressed in this paper may help eradicate a few widespread errors which, being easily remediable, should not be allowed to perpetuate themselves by mere inertia.

Although I have confined myself to the literature on harpacticoid copepods, the conclusions reached below are equally relevant to other invertebrate groups (such as nematodes) with a roughly similar spectrum of life cycles, our knowledge of which is at a similar stage of development, and the literature of which is beset with similar problems (Vranken and Heip, personal communication).

Computation of Reproductive Rates

Fundamental quantities in any demographic analysis include measures of offspring number, temporal pattern of births, and measures incorporating both these elements. All of these may be derived from the age-specific survival (l_x) and fecundity (m_x) schedules; accurate computational methods applicable to such data can be found in textbooks such as Pielou (1977) and in those harpacticoid life-cycle studies that deal in full detail with demographic procedures (Parise and Lazzaretto 1966; Bergmans 1981). For easy reference, the definitions of the parameters most often used are given in Table 1 (adopting the

Table 1. Principal formulae used in descriptive demography

The only information required is that contained in the age-related schedules of female survivorship, l_x (probability to reach age x) and fecundity, m_x (number of female offspring produced by a surviving female during the interval $[x, x+dx]$)

Equation No.	Equation	What equation defines
1	$\int l_x m_x e^{-rx} dx = 1$	Exponential rate of increase, r , in terms of the age-specific mortality and fecundity schedules
2	$T_c = \int x l_x m_x dx / \int l_x m_x dx$	Cohort generation time, T_c , in terms of the age-specific mortality and fecundity schedules
3	$R_0 = \int l_x m_x dx$	Net reproductive rate, R_0 , in terms of the age-specific mortality and fecundity schedules
4	$r = \ln R_0 / T$	Generation time (in the narrow sense), T , in terms of r and R_0
5	$r_c = \ln R_0 / T_c$	Capacity for increase, r_c , in terms of T_c and R_0

continuous-time model). Fig. 1 depicts the logical relationships among them and, in particular, highlights the contrast between r and T_c on the one hand, and r_c and T on the other. The former have a clear biological meaning: r is the exponential growth rate to which a population with fixed l_x, m_x schedules converges as its age structure stabilizes; T_c is the mean age of a mother at childbirth. T and r_c , though easily defined by symmetry, lack such clear interpretation.

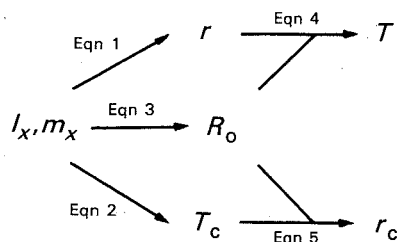


Fig. 1. 'Flow chart' of the logical relationships between the equations and concepts of Table 1.

The formulae in Table 1 are applicable to any given l_x, m_x schedule. Different schedules will correspond to different population densities, feeding conditions, etc. In particular, equation 1 for the exponential rate of increase may be applied to life-cycle data obtained in a predator- and competitor-free environment with resources unlimited, to yield what is then usually designated r_m . This is the *innate* or *intrinsic* rate of increase (Andrewartha and Birch 1982); it is still a function of temperature, salinity, etc. The other symbols, R_0 , T , ..., are commonly used both in the general sense and in tacit reference to the ideal situation of the ecological vacuum. In the following, I shall adopt the general

notation (r for the rate of increase) even though, of the studies to be considered, all but one concern single-species low-density laboratory cultures in which r_m may virtually have been realized.

Exponential Rate of Increase

There is no doubt that confusion exists between the meaning of r (eqn 1) and r_c (eqn 5) in harpacticoid papers. It shows up in Lazzaretto and Parise (1967), Volkmann-Rocco and Fava (1969), Heip and Smol (1976)—in spite of the lucid remarks in their Material and Methods section—, Gaudy and Guérin (1977, 1978), D'Apolito and Stancyk (1979). In some instances, confusion stems simply from the misleading similarity between equations 4 and 5, often in conjunction with ambiguity about the meaning of 'generation time' and/or the illegitimate assumption that T_c will always give a reasonable approximation of T . Sometimes the belief that r and r_c can be interchanged at will crops up unexpectedly when the context suggests otherwise: D'Apolito and Stancyk (1979) profess to apply the Lotka formula (eqn 1) but proceed quite unnecessarily to lump all reproductive activity into a single age class (the first reproductive one). This effectively reduces equation 1 to ' $r = \ln R_0/T_{\min}$ ', yet another of the various approximations to r , which, admittedly, involves a smaller absolute bias than does equation 5.

As can easily be checked, $r_c \approx r$ if, and only if, either (1) $R_0 \approx 1$, or (2) the organism under study is semelparous, all offspring being produced in a single simultaneous batch. Equation 1 is the only one yielding the correct value (exact within limits imposed by grouping over time intervals) in *all* cases, and, therefore, also in the case of iteroparous organisms. In the latter, generation time T is defined in terms of r , not vice versa (eqn 4 and Fig. 1), and, as is known at least since Parise (1966), r_c will seriously and systematically underestimate r . [Even if one chooses to call the bias 'slight', as do Gaudy *et al.* (1982), it would seem preferable to call r_c by its own name.] May (1976) gives formulae to estimate or, in the case of simple idealized life-tables, compute the relative systematic error $(r - r_c)/r_c$. In several species of *Tisbe* for which values of both parameters are available (Bergmans 1981, table 4), the bias introduced by equation 5 ranges from 8 to 29%. Another example is provided by *Tachidiulus discipes*, using Heip and Smol's (1976) values at 20°C (six egg-sacs per female produced on the eighteenth day and every third day subsequently, 41 eggs per egg-sac, a sex-ratio of 67% females and no embryonic or juvenile mortality). The bias involved in applying equation 5 is estimated at 11%. In fact, Heip and Smol (1976) did *not* apply $r \approx \ln R_0/T_c$, as claimed later (Heip *et al.* 1978) but used $r \approx \ln N/T_{\min}$, where N is the number of female eggs in the first egg-sac; this results in an underestimate by 21%. (Of course, this does not affect the authors' perfectly valid conclusion regarding the considerable effect of temperature on r .)

Finally, a comment is due on a somewhat idiosyncratic procedure. Starting from the correct observation that the calculation of r_c should take into account (larval) mortality, Heip (1972) corrected his preliminary estimate of r_c (based on egg numbers per adult female) by subtracting adult mortality as observed in the field. Whether this is an acceptable substitute for the procedure that should have been followed (*viz* incorporating egg-to-adult survival into the value of R_0) is a matter of faith.

To put things squarely, the computation of r from observed $l_x m_x$ by equation 1 is so straightforward that use of r_c as an approximation must be discouraged altogether: equation 5 introduces an unnecessary bias while not even fully exploiting high-resolution observations of l_x and m_x .

Net Reproductive Rate

Lack of insight into the meaning of R_0 may be another problem, as exemplified by D'Apolito and Stancyk's (1979) paper. The fundamental life-table parameter l_x , i.e. the probability of survival to age x , is sometimes scaled to 1000 initial individuals and

sometimes to 1 (Pielou 1977, p. 66). Obviously only the latter scaling is appropriate in computing R_0 , the number of daughters expected to be born to each newborn female. Choice of the wrong l_x values led D'Apolito and Stancyk to compute R_0 and r values for a field population of *Euterpina acutifrons* that by chance happen to be of a plausible order of magnitude for harpacticoids, but that nevertheless bear no justifiable relationship to their own data. (The latter, in fact, are indicative of a declining population.)

Another point in the same paper concerns R_0 as the factor by which the population size is multiplied from one generation to the next. Its value remains unaffected by the stage that one chooses to use as zero age class, as long as x , l_x and m_x adopted encompass one complete life cycle. [The equivalent 'life-history graph method' (Hubbell and Werner 1979) may be helpful in providing insight into this.] So it makes no sense to have m_x values in terms of nauplii 'corrected' for embryonic mortality (D'Apolito and Stancyk 1979, table 4): by thus increasing m_x by a factor M^{-1} , where M is embryonic mortality, without concurrently decreasing l_x by M , fecundity in terms of eggs is being combined with n_1 -to-adult survival. Clearly, correct transitions to m_x and l_x values based on a 'new' zero age class always cancel each other out to yield the unique R_0 value associated with a given fecundity and mortality schedule.

Loose Ways with Published Information

Biased estimates of r and R_0 are by far the most common, but not the only, blemish on the harpacticoid demographic literature. Faulty data on the number of ontogenetic stages abound (Walker 1979; many references in Bergmans 1981). On this matter one could be inclined to take a lenient view, as there is something of an historical tradition here. Misuse of correct information is less excusable. Reviewers commonly fail to distinguish 'larval period', 'generation time' (to be defined) and 'minimum generation time' (Gaudy and Guérin 1977, table 3; D'Apolito and Stancyk 1979, table 5). Gaudy and Guérin (1977) wondered at Hoppenheit's (1975) observation of realized rates of increase of up to 2.33 for *Tisbe holothuriae*, apparently without realizing that this value was expressed on a weekly instead of a daily basis. The same authors approvingly quote Heip's (1972) $r_c = 0.237$ for *Tachidius discipes* in the laboratory, though Heip himself clearly stated that this value becomes 0.193 when the sex ratio is taken into account. All these instances illustrate the general principle that the accuracy with which information is interpreted can only decrease in the course of transmission.

Reproductive Strategies

The classical unidimensional r - K -concept has, for some time, ceased to be the unchallenged paradigm of reproductive strategies [see in particular Stearns (1977) for criticism, Grime (1977) and Whittaker and Goodman (1979) for one possible alternative]. For harpacticoids, a thought-provoking alternative view—at the very general level of the order as a whole—has in fact already been proposed by Hicks (1979). He suggests that dimensions relevant to such strategies include trophic resource abundance, specificity of dietary requirements and substrate persistence. This approach also leads to a roughly dichotomous pattern, viz *phytal species* (food supposedly never limiting; short life cycles and production of many small eggs) v. *sediment dwellers* (resources limiting with one seasonally predictable optimum; annual life cycles and 'parsimonious' production of few large eggs). Within each category, however, much residual variation remains which may be related to (within-habitat) variation in diet breadth and substrate persistence. Hicks' categories appear to correspond to Grime's *ruderal* and *stress-tolerant* species, respectively. If phytal harpacticoids do not in general behave like typical *competitive* species, it must be that some environmental factor (predation or local 'catastrophes') prevents their populations from saturating their otherwise favourable environments.

It would be beyond the scope of this paper to enter the debate on the utility of the r - K -dichotomy as a description—or perhaps as a null hypothesis—of reproductive patterns. Instead, I propose to examine whether authors professing to apply the classical concept—whatever its intrinsic merits—have done so in a correct and internally consistent manner. Unfortunately, this is not always the case.

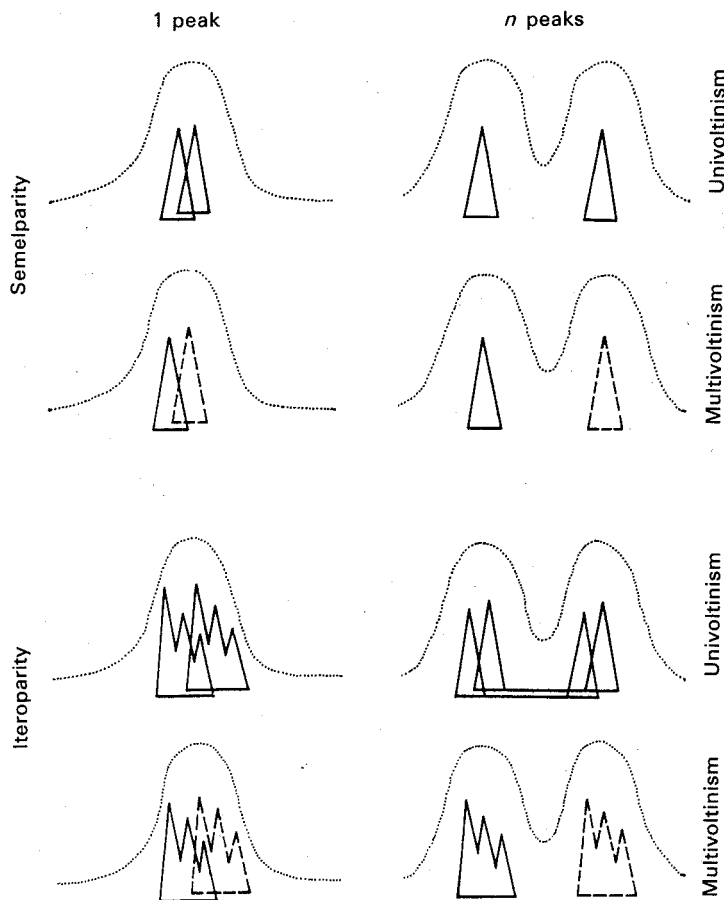


Fig. 2. Various possible combinations of voltinism, parity and number of discernible population peaks. Population density over the course of one reproductive season. — Fecundity schedule m_x of one or two females of the first generation. --- Fecundity schedule m_x of one female of the second generation where relevant. Life cycles extending over more than 1 year, as have been reported in freshwater species (Rouch 1968; Sarvala 1984), require a different time scale for their interpretation.

Diagnosing Strategies

Valid correlates of particular strategies have sometimes been wrongly ascribed to presumed representatives of those strategies, as when Hicks (1979, p. 145) took *univoltinism* (the existence of a single generation annually) to indicate *semelparity* (the concentration of a female's entire reproductive activity into a single age class). Similarly, the existence

of more than one generation annually is hardly evidence for iteroparity. The error stems, at least in part, from the ambiguity of the word 'brood', which sometimes seems to refer to a single egg batch, sometimes to total F_1 (as in Jewett and Feder 1977). A shift of meaning explains why what was interpreted as three generations of *Porcellidium dilatatum* in Hicks (1977), is interpreted as three broods in Hicks (1979) and is there taken to indicate iteroparity. As Fig. 2 shows, however, parity, voltinism and number of population maxima bear no necessary relationship to each other and all combinations are logically possible. [See also Hutchinson (1967), p. 241.] The distinction between some cases (e.g. whether a given bloom is due to an asynchronous multivoltine population of semelparous individuals or to a univoltine population of iteroparous ones) may be exceedingly difficult on the basis of *in situ* observations only, yet this distinction is crucial for a correct assessment of hypotheses on reproductive strategies. Without information on generation turnover, current indices such as percentage number of ovigerous females or percentage number of juveniles are difficult to interpret if not altogether misleading. Long-term presence of nauplii, for example, may indicate slow development rather than prolonged recruitment (Feller 1980).

It is only fair to point out that at least one ubiquitous misconception has been avoided by copepodologists, namely, the belief that a large absolute value of r_m and small absolute size are in themselves evidence for *r*-strategy. This belief, and the corollary that entire high-ranking taxa can be classified as either *r*- or *K*-strategists, goes back straight to Pianka (1970). It continues to influence current thinking, as when Kozłowski (1980), in an otherwise appropriate criticism of the logistic equation, suggests that '*r*-strategist' would merely be a synonym of 'small animal'. In fact, the interesting patterns are those remaining when the physiological imperatives of size (Fenchel 1974) have been removed! In more general terms, once 'forced correlations' of the 'Bauplan' (*sensu* Gould and Lewontin 1979) are being taken into account, high-ranking taxa or lineages are always seen to contain relative '*r*-' and relative '*K*-strategists'. Deviations of particular species from established intralinear trends thus provide a more meaningful diagnosis of strategies than do interlineage comparisons (*pace* Stearns 1980). Hicks (1979) and Heip (1980) have adopted a sound viewpoint on this matter.

Search for Evolutionary Meaning

It has been suggested (Heip 1974) that the short life cycles of some harpacticoids may have evolved in response to predation pressure. This may well be correct, provided one interprets 'life span' as 'minimum generation time' throughout, lest one should end with the suggestion that these animals kill themselves to avoid being killed and eaten. The evidence advanced in support of Heip's view does not, however, bear on his thesis. The statement that a catastrophic population crash ensues whenever a female's expected time to fatal encounter with a predator grows less than T_{min} , is tautological—it holds just as well for even the most extreme *K*-strategist.

Desire to make evolutionary sense out of every observed reproductive phenomenon led Hoppenheit (1978) to the incongruous suggestion that individuals that find themselves in relatively dense populations may adopt the 'strategy' of being unsuccessful breeders (i.e. of producing egg-sacs from which no adult offspring result). Apart from attributing adaptive value to an obviously undesirable waste of resources, this interpretation ignores more parsimonious alternative explanations (such as allelopathy, shortage of essential micronutrients, etc.). The distinction between the latter kind of unavoidable proximal effects (the *direct* action of temperature, food limitation, interference competition and the like) and actual adaptations is, however, fundamental. This may be illustrated by a trivial example: increasing the temperature will in general raise a poikilotherm's r_m , but this does not automatically turn it into an *r*-strategist at the higher temperature. Every 'strategy', in order to deserve that name, should contribute to some evolutionarily desirable property

(fitness) of the individual in a specified ecological context; moreover, the phenomena cited as evidence for it must not be the mere expression of environmental influences on the organism.

Some Recommendations

Experience and knowledge in the culturing of harpacticoid copepod species (and other meiobenthic organisms), representing a broad spectrum of life histories, have steadily increased in recent years. Thus, these species have become excellent material for quantitative studies, especially with regard to the temporal aspects of reproduction. That is why demographic research on them holds promises of new insights, perhaps even of broad ecological significance. It will be clear from the above that greater strictness in the handling of demographic concepts can only be beneficial to such developments. Practitioners of invertebrate demography should pursue rigour in two areas in particular.

(1) All calculations and interpretations must duly respect demographic theory and logic. This applies with even greater force when new techniques are brought to bear on demographic problems. In this connection, it is my feeling that superficial and occasionally misguided analogies borrowed from thermodynamics and cybernetics might profitably be omitted, especially in papers with an interesting empirical content that hardly needs such dressing-up [see, for example, Walker (1979) for a fanciful account of selection under density limitation].

(2) The term 'strategy' should not be used unless some stringent conditions are met. This comment does not refer to the fashionable, if somewhat sterile, discussion on its semantic appropriateness (Louw 1979): many initial 'misnomers' eventually became consecrated by usage without ill effects (cf. *prudent* predation, reproductive *investment*, *trade-off*). The real danger does not lie in the unlikely suggestion of deliberating capacities in lower organisms; rather, it lies in the erosion of a concept turned into a blanket for phenomena, the adaptive nature of which is sometimes far from obvious. To demonstrate the adaptive, or 'strategic', nature of a particular character state, one ought to address the following two issues: (i) the character state should make a positive contribution to fitness; it should be superior, in this respect, to other physiologically attainable character states (cf. Bergmans 1984); (ii) a parsimonious explanation of the character state in terms of the direct action of external agents should be inadequate (cf. Stearns 1980, section 2.2). An animal's response to particular conditions can be part of a strategy only when this response demonstrably transcends physiological necessity, and a *different* response (entailing lower fitness) is at least theoretically possible.

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