Patterns in stage duration and development among marine and freshwater calanoid and cyclopoid copepods: a review of rules, physiological constraints, and evolutionary significance

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Abstract
Studies of development time of marine and freshwater copepods have taken separate tracks. Most studies on marine copepods report development time of each individual development stage, whereas studies on freshwater copepods report only development time, from egg to nauplius and nauplius to adult. This bias allows comparison of total development time but prevents detailed comparisons of patterns in stage-specific developmental schedules. With respect to egg to adult development time, three general relationships are known: developmental rates are dependent upon temperature and food concentration but independent of terminal body size; freshwater calanoids develop significantly slower than marine calanoids; freshwater cyclopoids develop at the same rate as marine calanoids. Two rules describe stage-specific developmental rates: the equiproportional rule and the isochronal rule. The first rule states that the duration of a given life history stage is a constant proportion of the embryonic development time; the second rule states that the time spent in each stage is the same for all stages. This review focuses on the second rule. From the 80+ published studies of copepod stage-specific developmental times, no species follows the isochronal rule strictly: Acartia spp. come closest with isochronal development from third nauplius (N3) to fourth copepodite (C4). The only pattern followed by all species is rapid development of the first and/or second naupliar stages, slow development of the second and/or third nauplius and prolonged development of the final copepodite stage. Once adulthood is reached, males are usually short-lived, but females can live for weeks to months in the laboratory. Adult longevity in the sea is, however, on the order of only a few days. The evolution of developmental patterns is discussed in the context of physiological constraints, along with consideration of possible relationships between stage-specific mortality rates and life history strategies. Physiological constraints may operate at critical bottlenecks in development (e.g. at the first feeding nauplius, N6, and the fifth copepodite stage). High mortality of eggs may explain why broadcast eggs hatch 2–3 times faster than eggs carried by females in a sac; high mortality of adults may explain why adults do not grow rather they maximize their reproductive effort by partitioning all energy for growth into egg production.

Introduction
Studies of copepod development were once aimed primarily at the raising of copepod eggs from a female of a known species, with the purpose of describing naupliar and copepodite stages. Results showed that all copepods have five copepodite (juvenile) stages, but a variable number of naupliar (larval) stages: calanoids have six naupliar stages, cyclopoids five.

Interest in the population dynamics and production of coastal marine copepods led to detailed studies of development times because such data are needed to estimate copepod recruitment rates and to calculate production rates. Seminal works on stage-specific developmental rates published by C. Corkett, M. Landry, I. McLaren, and C. Miller set the stage for a debate which continues today as to the nature of rules that might govern copepod development (McLaren, 1966;

This review was prepared for the symposium on Copepod development: its evolutionary and ecological implications, at the 7th International Conference on Copepoda in Curitiba, Brazil. The purpose of this review is to attempt to summarize the state of our knowledge concerning developmental rates of marine and freshwater calanoid and cyclopoid copepods. My goals were, firstly, to look for common patterns in egg–adult developmental times among marine and freshwater pelagic copepods; and, secondly, to compare stage-specific development times among taxa, with the idea of using such information to deduce life history strategies and to discuss these strategies in the context of physiological and evolutionary constraints. I relied heavily upon two reviews: Hart (1990) and Kiørboe & Sabatini (1995). The Hart review treated development of freshwater and marine calanoids, cyclopoids and harpacticoids. Kiørboe & Sabatini (1995) reviewed fecundity, growth and development of marine calanoids and cyclopoids. Both are excellent, and all serious students of copepodology should become familiar with their contents.

While preparing this review, it became clear that there were severe biases among data sets that prevented some comparisons: first, almost all studies of freshwater copepods report only total time for development of nauplii and copepodites, whereas nearly all studies of marine copepods include estimates of development times of each developmental stage. Second, most marine studies have been on calanoids. Third, virtually all the marine species studied are from estuarine or coastal environments with life cycles that are completed within a month or two. To my knowledge, there are no laboratory data on development of boreal and/or antarctic copepod species that do not complete a life cycle within a given year (e.g. Calanus hyperboreus, Neocalanus spp.).

Results

Common features of copepod development

Hart (1990) and Kiørboe & Sabatini (1995) summarized the features of development that are common among all copepods. These are presented in the list below with little discussion since data and arguments relevant to each finding have already been published in those two papers:

1. Developmental rates are dependent upon temperature and food concentration;
2. When grown under conditions of unlimited food resources, development times from egg to adult are independent of adult body size;
3. Developmental rates are similar for egg-carrying and broadcast-spawning copepods;
4. Males develop to adult more quickly than females;
5. Marine calanoids develop significantly faster than freshwater calanoids but at the same pace as freshwater cyclopoids at all temperatures;
6. Both the nauplii and copepodites of marine calanoids develop faster than nauplii and copepodite stages of freshwater calanoids.

Some of these points are illustrated here. Figure 1 shows that development time is independent of adult body size for marine calanoid copepods (note that this relationship holds only for development: there is evidence that growth rate declines with body size (see Hirst & Lampitt, 1998 and references therein).

Figure 2 shows that at any given temperature, freshwater calanoids develop 1.5–2 times slower than marine calanoids, and that freshwater cyclopoids develop at the same pace as marine calanoids. Figure 3 shows that the development of both nauplii and copepodites of marine calanoid species are faster than for freshwater calanoid species. Data shown in Figures 1–3 include information from Table 2 of Hart (1990) and Table 3 of Kiørboe & Sabatini (1995), as well as other measurements that were either not included in those reviews or were published since 1994. The other measurements are shown in Table 1 of this paper.