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LARVAL GROWTH PATTERNS IN THE AESOP SHRIMP *PANDALUS MONTAGUI*

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ABSTRACT

Larvae of the Aesop shrimp *Pandalus montagui* Leach (Decapoda: Caridea: Pandalidae), were reared in the laboratory at 5 different temperatures (6, 9, 12, 15, and 18°C), and their growth patterns were analyzed in terms of molting frequency, size increments (total length, *TL*, carapace length, *CL*), and increase in larval dry weight (*W*). *Pandalus montagui* passed through 6 zoeal and 2–5 decapodid stages. While 2 of the latter occurred consistently (obligatory stages), up to 3 additional (facultative) decapodid stages were passed before metamorphosis to the first juvenile. Molting occurred at regular intervals, with little interstage variation, so that the instar number could be described as a linear function of the time of development, with an increasing molting frequency at increasing temperatures. A nonlinear relationship (power function) was found between average intermolt duration and temperature; this regression was linked with data for water temperatures measured during the spring near Helgoland (southern North Sea), in order to predict the approximate duration of larval development and peak settlement in the field. From instar I–VIII, larval size increased as a linear function of the number of molting cycles, but no significant growth and no further morphological changes were observed in later (facultative) larval stages. The morphometric relationship between *TL* and *CL* remained linear throughout larval development, with an increasing trend in the *TL*:*CL* quotient. *W* increased exponentially with the number of instars, and as a power function of larval size. The overall patterns of larval development and growth in *P. montagui* are compared with those known from other pandalid species and in other caridean shrimps.

The caridean shrimp family Pandalidae is distributed world-wide, including a number of ecologically important and commercially exploited species, predominantly in boreal and subarctic regions of the Atlantic and Pacific Oceans (Scrivner and Butler, 1971; Ippolito *et al.*, 1980; Hannah and Jones, 1991). In the North Atlantic, the northern shrimp (*P. borealis* Krøyer) is the largest species and, hence, has been the object of extensive coastal and offshore fisheries in North America and Europe. With the exception of *P. jordani* Rathbun in the Pacific, it is probably the best known pandalid species in terms of life cycle data (Shumway *et al.*, 1985). The Aesop shrimp (FAO name; in the literature also frequently referred to as "pink shrimp") *P. montagui* Leach is another commercially important species in the North Atlantic, but it is smaller and has a lower commercial value than *P. borealis* (see Mistakidis, 1957; Balsiger, 1981). Consequently, its biology has been investigated to a much lesser extent (review: Simpson *et al.*, 1970). Available data are primarily related to aspects of the adult phase of its life cycle, namely fisheries, depth distribution, substrate and food requirements, growth, and reproduction (e.g., Mistakidis, 1957; Allen, 1963; Stevenson and Pierce, 1985). Other information exists also on feeding behavior and migratory patterns (Warren and Sheldon, 1967; Stevenson and Pierce, 1985; Hudon *et al.*, 1992), parasitic infestations (Warren, 1974), and biochemical composition of the eggs and the energy content of adults (Tyler, 1973; Holland, 1978; Clarke, 1979).

In contrast, very little is known about development and growth of larvae of *P. montagui*. While the larval development of several other pandalid species has been extensively studied both in the laboratory and in the natural environment (e.g., Modin and Cox, 1967; Wickins, 1972; Haynes, 1976, 1978, 1979, 1980, 1983, 1985; Rothlisberg, 1979, 1980; Stickney and Perkins, 1981; Wienberg, 1982a, b; Mikulich and Ivanov, 1983; Komai and Mizushima, 1993; Ouellet *et al.*, 1995, and earlier papers cited therein), only incomplete morphological descriptions and a few growth data have become available for larval Aesop shrimp (Pike and Williamson, 1964; older literature cited therein). Possibly also as a consequence of identification difficulties caused by the lack of a detailed morphological description, only scarce data are available on the seasonal and local distribution patterns of larvae of *P. montagui* in the plankton (Thorson, 1946; Lebour, 1947;

Rees, 1952; van der Baan *et al.*, 1972; Lindley, 1987; Wehrtmann, 1989).

In an unpublished investigation on the life cycle of *P. montagui* (see Schultze, 1993), different rearing techniques and food sources were tested, larval morphology and histology were described, and changes in the elemental and biochemical composition of larvae, early juveniles, and exuvial matter were measured; these data will be published elsewhere. In the present paper, patterns of larval growth (molting frequency, changes in body size and dry weight) are described and compared with those in other larval shrimps.

Materials and Methods

Ovigerous females of *P. montagui* were caught during winter (November through March, 1989–1991) with a shrimp net deployed from RV *Aade* in a deep channel southwest of the island of Helgoland ("Helgoländer Tiefe Rinne"; 40–60 m depth), North Sea. The shrimps were transported to the Helgoland Marine Biological Station and later maintained in flow-through plastic aquaria with 10 l of filtered sea water (1-μm pore size filters), at ambient temperature and salinity (3–6°C; 30–33‰), with an artificial 12:12 h light : dark cycle. Fresh mussel (*Mytilus edulis* L.) meat was given as food.

Hatching was observed during March and April, usually taking 3–5 subsequent nights in each clutch, with eclosion rates of about 300–500 larvae per night. Freshly hatched larvae were collected in sieves (300-μm mesh size) receiving the overflowing water from the aquaria. Within a few hours after hatching, the larvae were transferred with wide-bore pipettes to rearing vessels.

In order to obtain reliable data on the number of larval molting cycles, preliminary studies of larval morphology and growth were conducted in individual cultures (30-ml glass vials) at 6, 9, 12, 15, and 18°C. The larvae were checked daily for molting or mortality, when sea water (1-μm filtered; approximately 32‰ salinity) and food (freshly hatched brine shrimp nauplii, *Artemia* sp., San Francisco Bay Brand™ ± 10 nauplii per ml) were changed. Samples of larvae (at least 10 individuals per condition and developmental stage) were fixed in 4% formaldehyde-sea water solution for later examination of body size and morphology.

Since the individual rearing method yielded unsatisfactorily low survival rates (consistently less than 10% metamorphosis to the first juvenile), all later experiments were conducted in mass cultures: gently aerated 1–l glass beakers, with maximum larval densities decreasing stepwise from 150 (stage I) to 15 individuals/l (all stages later than VIII). Experimental temperatures, salinity, food, and frequency of water change were the same as in the individual rearing experiments.

When molting occurred, the larvae were staged (according to morphology and size) under a dissecting microscope and grouped in different rearing vessels, which then contained individuals in the same larval stage and of the same age within a given molting cycle. Within a few hours after each ecdysis, 10 larvae were taken from the cultures and their body size was measured microscopically with an eye-piece micrometer to the nearest 0.01 mm, as total length (*TL*, tip of the rostrum to the posterior margin of the telson) and carapace length (*CL*, tip of the rostrum to the posterior margin of the carapace). Eight other replicate samples were taken for the determination of initial larval dry weight (*W*) in each stage, with 5 (stage I), 2 (stage II), or 1 individual (all later stages) per sample. They were briefly rinsed in distilled water, blotted on fluff-free Kleenex® tissue (for optical use), transferred to preweighed tin cartridges, and freeze-dried overnight in a GT–2 Leybold-Heraeus® apparatus. *W* was then measured on a Mettler® UM–3 microbalance to the nearest 0.1 μg.

Consistent with the criteria presented by Williamson (1969, 1982), we avoid in our nomenclature the inconsistently applied and thus ambiguous term "postlarva" (in the literature indiscriminately used for late larval and early juvenile stages of shrimps). The name "zoea" is here applied to early larval stages which exclusively use thoracic appendages for locomotion; the term "decapodid" (as an equivalent of "megalopa"; Kaestner, 1980; Williamson, 1982) is used here for later larvae, which have already some juvenile characters (pereiopods and pleopods fully segmented and functional), but also retain larval features (functional exopods on at least some pereiopods). Juveniles, in contrast, lack such larval characters. The neutral term "instar" denotes a molting cycle, independent of the developmental phase (larval or juvenile) and the existence or lack of morphological changes associated with molting.

Statistical analyses followed standard methods as described by Sachs (1984). Since no significant deviations from a normal distribution were detected in our data (goodness-of-fit *G*-test), parametric tests were used consistently. Quantitative relationships between larval development time, number of stages, size, and weight were described by means of least-square regressions (with or without logarithmic transformation of data, depending on linearity). Correlation coefficients (r) were tested for significant deviations from zero. In pairwise comparisons of arithmetic mean values, Student's t-test was employed, while an ANOVA was used in multiple comparisons of mean values, as well as in those of the slopes of different regression lines. The following levels of statistical significance are distinguished in this paper: $P < 0.05$, $P < 0.01$, $P < 0.001$.

Linking nonlinear regression equations that describe the temperature-dependence of larval development time in the laboratory (present data; Fig. 1b) with polynomial equations that describe seasonal changes in the average surface sea-water temperature in the southern North Sea (Weigel, 1978), a simple simulation model can be derived (Anger, 1983). It is based on the computation and cumulative summing of temperature-dependent fractions of theoretical instar duration on consecutive calendar days; molting is assumed to occur when a value of ≥1.0 (i.e., 100%) is reached (see Anger, 1983, for more details). This simple model was used to predict the duration of larval development and the timing of settlement of *P. montagui* in the field as a function of the timing of hatching and subsequent changes in the ambient water temperature.

Results

The larval development of *P. montagui* consisted, in our material and under our experimental rearing conditions, of 6 zoeal and 2–5 decapodid stages, i.e., in a total of 8

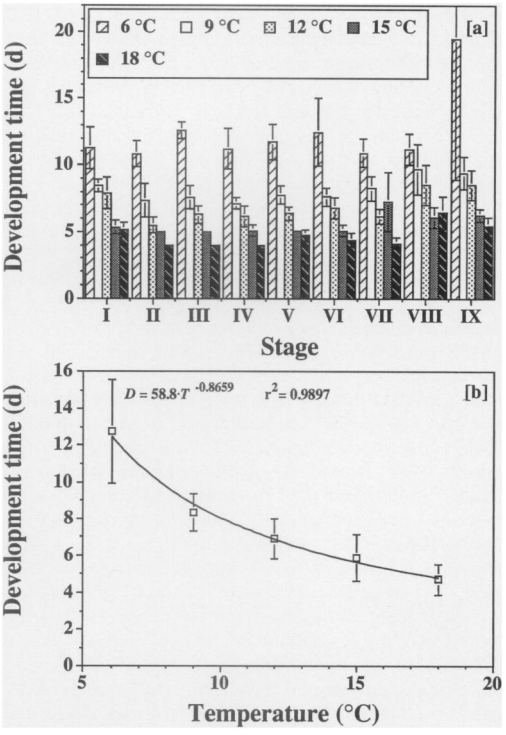

Fig. 1. *Pandalus montagui.* (a) Development duration ($\bar{x}$ ± SD) in successive larval stages reared at five different constant temperatures. (b) Fitted regression curve (power function) describing the relationship between average larval molt-cycle duration (*D*, in days; $\bar{x}$ ± SD) and temperature (*T*, °C); r^2 = coefficient of determination for regression equation.

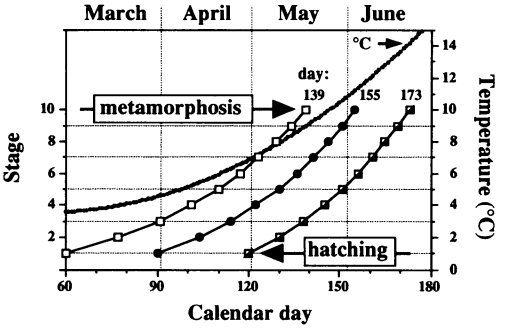

Fig. 2. Graphical model of simulated developmental sequences in three cohorts of larvae of *Pandalus montagui* in the plankton near Helgoland, southern North Sea, assumed to hatch in early March, April, and May, respectively. Sea-water temperatures estimated from average values given by Weigel (1978) and polynomial equations describing seasonal changes (Anger, 1983).

obligatory and 3 optional larval instars. The latter three stages were very similar to each other in morphology and body size. The morphology of all stages, as well as the frequency of different developmental pathways under different environmental conditions of temperature, salinity, and food, will be described elsewhere. No developmental differences except in survival rates were observed between different rearing methods (individual versus mass culture). Mortality increased drastically in all experiments, when the last zoeal stage (VI) molted to the first decapodid stage (instar VII). Highest survival to the first juvenile (67 %) was obtained in mass cultures kept at 15°C.

The average duration of larval instars decreased significantly with increasing temperature (ANOVA; $P < 0.001$), but did not differ significantly among subsequent instars (Fig. 1a). This low degree of variability in the average instar duration of Aesop shrimp larvae reared under constant temperature conditions allows the employment of another simple model of molting frequency: the number of molting cycles (or stages, *S*) passed can be described as a linear function of the time (*t*, in days) of larval development (Criales and Anger, 1986). For all temperatures tested in this study, highly significant regression equations were obtained for this relationship (all $r^2 \geq 0.9997$; $P < 0.001$); their slope parameter, which may be considered an index of molting frequency, increases with increasing temperature: 6°C: $S = 0.093 \cdot t + 0.94$; 9°C: $S = 0.101 \cdot t + 0.95$; 12°C: $S = 0.144 \cdot t + 0.94$; 15°C: $S = 0.169 \cdot t + 0.93$; and 18°C: $S = 0.200 \cdot t + 0.80$.

As a consequence of this regular molting pattern in larvae of *P. montagui,* mean instar durations (*D*) may be calculated and plotted against temperature (*T*). A hyperbola-shaped relationship is then obtained, which can be described with best fit of observed and predicted data as a power function (Fig. 1b). When this regression equation is linked with in situ water temperatures measured near the sampling site of our shrimp population (Weigel, 1978), a descriptive model is obtained, which predicts the theoretical development duration and time of settlement in the natural environment. Since we observed hatching exclusively during the months of March and April, we simulated the development of larval cohorts hatching at the beginning, in the middle, and at the end of this period (1 March, 1 April, and 1 May, or calendar days 60, 90, and 120, respectively; Fig. 2). Based

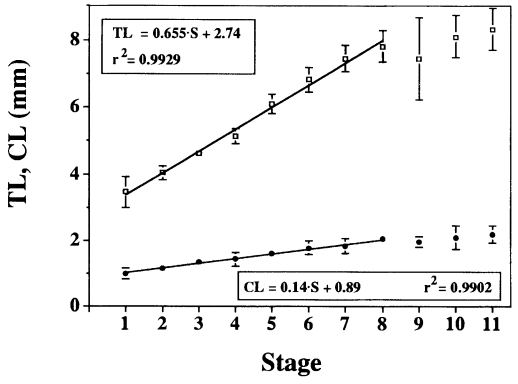

Fig. 3. Linear relationships between total length (*TL*), carapace length (*CL*), and the stage (*S*) of larval development in *Pandalus montagui*; size measurements from stages 9–11 not included in regressions. r^2 = coefficient of determination for regression equation.

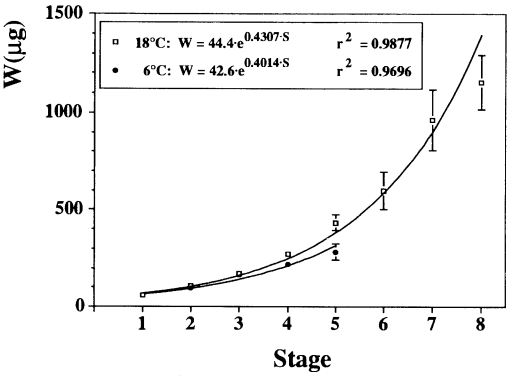

Fig. 5. Fitted regression curves (exponential functions) describing the relationship between larval dry weight (*W*, in µg; $\bar{x}$ ± SD) and the stage (*S*) of larval development in *Pandalus montagui* at two different temperatures (6°, 18°C). r^2 = coefficient of determination for regression equations.

on our laboratory observations, we assumed a development through an average number of nine larval stages.

As a consequence of rapidly increasing temperatures in the spring, the theoretical duration of subsequent instars decreases during the course of larval development, and the average duration of development from hatching to metamorphosis decreases in subsequently later hatching cohorts (Fig. 2). Since this acceleration effect is strongest at low temperatures (see slope in Fig. 1b), the shortening of total larval development duration is more conspicuous between the first two hypothetical cohorts as compared with the second and third. While hatching of subsequent cohorts was assumed to occur in one-month intervals, their predicted settlement follows in intervals of only 16 and 18 days, respectively (Fig. 2). According to this model, the larval development of our population of *P. montagui* should take place throughout the spring, at temperatures ranging from about 4–14°C, and settlement in late spring (from mid-May to mid-June), when local water temperatures range from approximately 9°–14°C (or perhaps slightly lower near the bottom).

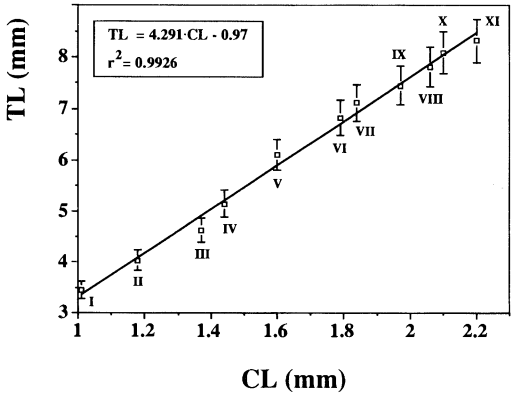

Fig. 4. Linear relationships between total length (*TL*) and carapace length (*CL*) in the larval stages (I–XI) of *Pandalus montagui*. r^2 = coefficient of determination for regression equation.

When body size (measured as total length, *TL*, or carapace length, *CL*) is plotted against the number of stages (*S*), a linear increase can be observed during the first eight, but not any longer in the last three larval instars (Fig. 3). This lack of growth in optionally occurring decapodid stages concurs with an apparent lack of morphological change (see above) and with an increased variability in size. The relationship between total length and carapace length does not change between the zoeal and the decapodid phase, remaining linear throughout larval development (Fig. 4). However, the morphometric relation between these two size dimensions (the quotient *TL*:*CL*) increases gradually from 3.3 to about 4.0 during the course of larval development.

The linear increase in body size of successive larval instars (Fig. 3) is in contrast to an exponential increase in body weight (Fig. 5). The latter relationship has been sometimes referred to in the literature as "Brook's law" (e.g., Kurata, 1962). While no significant differences in larval size were observed at different temperatures, significantly lower

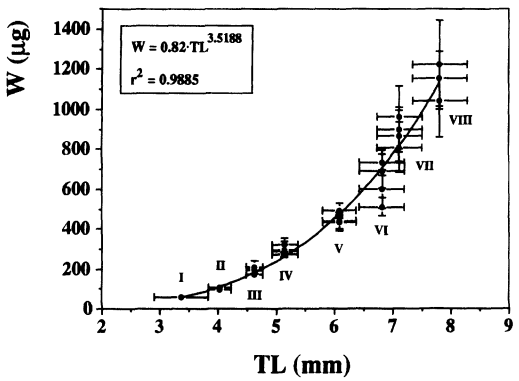

Fig. 6. Fitted regression curve (power function) describing the relationship between larval body size (total length, *TL*, in mm; $\bar{x}$ ± SD) and dry weight (*W*, in µg; $\bar{x}$ ± SD) in larval stages (I–VIII) of *Pandalus montagui*. r^2 = coefficient of determination for regression equation.

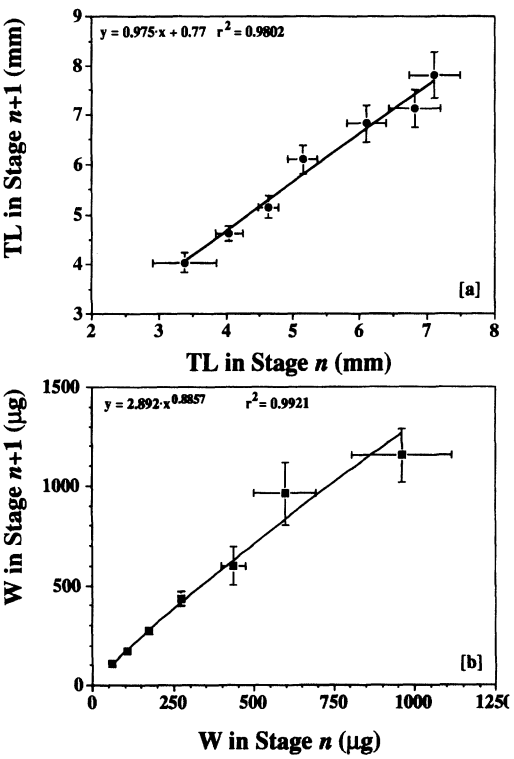

Fig. 7. Hiatt diagrams (Hiatt, 1948) describing (a) size increments, (b) weight increments in successive larval stages of *Pandalus montagui*. Size (total length, *TL*, in mm; $\bar{x}$ ± SD) and dry weight (*W*, in µg; $\bar{x}$ ± SD) in stage *n* plotted against values measured in the subsequent stage, *n* + 1. r^2 = coefficient of determination for regression equation.

dry weight was found in zoea IV and V larvae reared at 6°C as compared with those at all higher temperatures (pooled data; no significant differences could be detected at temperatures from 9–18°C). However, the exponents of the two curves in Fig. 5 were not significantly different (ANCOVA). In this experiment, all larvae reared at 6°C died after the fifth zoeal stage.

The allometric relationship between body size and weight of larvae of *P. montagui* is shown in Fig. 6. Both measures of growth reveal great individual variability among larvae originating from different females, and overlapping values were observed in the last three stages.

The average increase in size and weight in a series of successive instars can be depicted also in a Hiatt diagram (Hiatt, 1948). When total body length of subsequent stages is plotted against each other, the growth pattern appears to be linear (Fig. 7a), while the dry weight data showed a slight curvature (Fig. 7b). In consequence, best fit of observed and predicted data was obtained with a linear and a power function, respectively.

Discussion

With a total of up to 11 (eight obligatory and three facultative) morphological stages, the larval development of *P. montagui* in our laboratory experiments was similar to that described by Pike and Williamson (1964), who also found up to 11 larval instars, the last two of these being facultative. Thus, a total of eight or nine morphologically distinct stages, normally including six zoeal and two or three decapodid stages, may represent the typical developmental pattern in this species. Developmental variability, in particular in late (decapodid) stages, is common in caridean shrimps, where the number of larval stages can be influenced by both genetic and environmental factors (Knowlton, 1974; Williamson, 1982). The developmental sequence in *P. montagui* is similar to that in most other pandalid shrimp species, e.g., *P. borealis* (see Haynes, 1979; Wienberg, 1982a), *P. jordani* (see Modin and Cox, 1967; Rothlisberg, 1979, 1980), and in a number of other species (review: Haynes, 1985). An abbreviated type of larval development was observed less frequently in the Pandalidae: *Pandalus kessleri* Czerniavski (see Kurata, 1955), *P. prensor* Stimpson (see Mikulich and Ivanov, 1983), and probably most species of *Pandalopsis* (e.g., Kurata, 1964; Komai and Mizushima, 1993).

Larvae of *P. montagui* showed under constant conditions a very regular pattern of molting, that the sequence of successive stages could be described as a linear function of time, with increasing slope (i.e., an increasing molting frequency) at increasing temperatures (regression equations given above). The same pattern was observed also in the larvae of other caridean shrimp species: *P. borealis* (see Wienberg, 1982b; Shumway *et al.,* 1985), *P. jordani* (see Rothlisberg, 1979), *Palaemon longirostris* Milne Edwards (see Fincham, 1979), *Macrobrachium vollenhovenii* Herklots (see Willführ-Nast *et al.,* 1993), and *Crangon crangon* Linné and *C. allmanni* Kinahan (see Criales and Anger, 1986). It may thus be a typical trait of this group, but it occurs also in other decapod crustaceans with many larval instars and a gradual type of morphological development, e.g., in some Galatheidae and Raninidae (review: Anger, in press).

When the average duration of subsequent larval stages does not change significantly, overall mean values of instar duration can be given for defined conditions (e.g., different temperatures: Fig. 1b; cf. Rothlisberg, 1979). Extrapolation of these data allows for a prediction of approximate development duration in the field (Fig. 2). This can be further linked with data of larval migration and current speed, so that larval advection patterns can be predicted (Rothlisberg *et al.,* 1983). Although larvae of *P. montagui* may hatch during an extended period in the spring and summer (Thorson, 1946; Lebour, 1947), we observed hatching exclusively in the spring, i.e., during the time when water temperatures in the plankton begin to increase. Furthermore, Rees (1952) described a distinct peak in April. According to our simple model, development in the spring should cause a gradually decreasing molt cycle duration in successive larval instars, and the peak period of settlement should become shorter than that of hatching (Fig. 2). The same effect was predicted to occur also in a spider crab species which releases its larvae in late winter (Anger, 1983). Scarcity of data from the plankton, however, precludes at present a comparison of predicted and observed patterns of larval development and recruitment in Aesop shrimp (Wehrtmann, 1989; Wehrtmann and Greve, 1995).

The molting frequency of larvae of *P. montagui,* and the average size increment per larval molting cycle, can be considered rather constant under constant environmental conditions. As in a number of other caridean shrimp species (references: see above), this allows for a description of growth in larval size as a linear function of the number of instars (Fig. 3), or as a linear Hiatt diagram of size data (Fig. 7a). In such cases, where only little variation occurs in the relative growth increments of successive instars, independent of their size (cf. Rothlisberg, 1979; Wienberg, 1982b), average growth factors can be calculated for the larvae of different species or groups. For pandalid shrimp larvae, for instance, Gore (1985) gave an average size increase of about 17% per stage (based on data from seven species); our measurements in *P. montagui* (total lengths of stage I and VIII larvae) gave a surprisingly similar value: an average increase of 18% per molting cycle. In addition, the total growth factor (i.e., the quotient of size in the last to that in the first larval stage; Gore, 1985) is similar to the value calculated from our material (2.31 versus 2.26). This confirms that the larval growth characteristics of *P. montagui* are close to the average in pandalid shrimps. However, significant variability among different hatches or different environmental conditions can modify average growth increments and total growth rates (Rasmussen and Tande, 1995). Furthermore, late, facultative developmental stages appear to break the rule (Fig. 3: instars 9–11), because they may molt with a reduced or even without a size increment, and without further morphological change. The same pattern was observed also in late larvae of other caridean shrimps (Rothlisberg, 1979: *P. jordani*; Criales and Anger, 1986: *Crangon crangon, C. allmanni*).

The morphometric relations between different measures of body size (total and carapace length) show again a regular (linear) pattern in larvae of *P. montagui* (Fig. 4). Interestingly, however, the quotient *TL/CL* shows a decreasing trend in this species, whereas Rasmussen and Tande (1995) observed an increasing trend in *P. borealis.* Further data from other pandalid species should show the degree of interspecific variation, including possibly existing general tendencies in the developmental changes of this morphometric index. This variation should be important to know, since some authors use *TL,* while others prefer *CL* as a predictor of weight increments.

An exponential pattern of increase in biomass with an increasing number of instars (Fig. 5) has frequently been observed in decapod larvae, including shrimp and crab species (review: Anger, in press). The allometric relationship between measures of larval body size and weight (Fig. 6) is a common trait that has already been used for conversions of size to biomass data in larval decapods (Lindley, 1988). Thus, again, the larvae of *P. montagui* seem to reveal no unusual characteristics among the Caridea or, at least, among the Pandalidae. This should allow for exchanging some of the available information on pandalid larvae (e.g., Shumway *et al.,* 1985) and, hence, should help to complete our picture of larval development and growth in this ecologically and economically important group of marine shrimps.

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