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Egg development times of *Eurytemora affinis* and *Pseudodiaptomus forbesi* (Copepoda, Calanoida) from the upper San Francisco Estuary with notes on methods

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Egg development times (DTs) of copepods are used to scale DTs of life stages to temperature and to calculate egg production rate in sac spawners. Here, we report egg DTs at various temperatures for two copepod species from the upper San Francisco Estuary measured using video observations of individual egg sacs. The egg DTs (days) of *Eurytemora affinis* and *Pseudodiaptomus forbesi* were related to temperature (T, °C) by $DT = 11.5e^{-0.106T}$ and $DT = 22.7e^{-0.121T}$, respectively. Video observations decreased manpower requirements, increased the frequency of observations and provided more detailed observations of individual hatching patterns compared with historical techniques including direct observations and regression analysis.

KEYWORDS: egg duration; embryonic duration; hatching time

INTRODUCTION

The egg development time (DT) of copepods is important for understanding the basic ecology of individual species, as well as interactions among species. Egg DT is a useful scaling factor for the influence of temperature on the DTs of other life stages (Corkett and McLaren, 1970). For egg-

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bearing copepods, egg DT is an essential parameter for calculating egg production rate (EPR) by the egg ratio method (Edmondson, 1971; Ohman *et al.*, 1996). EPR, calculated by this method, is the ratio of eggs to females (egg ratio) in a sample divided by the egg DT. Additionally, species with shorter egg DTs have shorter interclutch periods and can reach maturity faster (Maier, 1989; Caramujo and Boavida, 1999). The DT of eggs also influences the mortality rates of females, as ovigerous females are more susceptible to predation (Vuorinen *et al.*, 1983; Winfield and Townsend, 1983; Bollens and Frost, 1991).

Egg DTs vary among species and locations (McLaren *et al.*, 1969; Vijverberg, 1980; Herzig, 1983). They are strongly influenced by temperature (McLaren, 1966; Corkett and McLaren, 1970; Maier, 1989) and can be affected by other environmental factors including salinity (McLaren, 1966; Uye, 1980; Ishikawa *et al.*, 1999), light (Landry, 1975a; Uye and Fleminger, 1976; Uye, 1980) and oxygen concentration (Uye and Fleminger, 1976). To accurately assess egg DT, it is therefore necessary to quantify egg DTs for each target species, location and temperature, under prevailing environmental conditions.

Here we report egg DTs for two calanoid copepods, *Eurytemora affinis* Poppe, 1880 and *Pseudodiaptomus forbesi* Poppe and Richard, 1890, from the upper San Francisco Estuary (SFE), which includes Suisun Bay and the Sacramento-San Joaquin Delta. *Eurytemora affinis* is a euryhaline cosmopolitan copepod species that has successfully invaded numerous freshwater lakes and reservoirs (Lee, 1999). Before 1987, it dominated copepod biomass in the upper SFE for much of the year (Ambler *et al.*, 1985; Orsi and Mecum, 1986). Currently, it is limited spatially to upstream regions and seasonally to spring (Kimmerer and Orsi, 1996). Because of its wide distribution and importance in numerous estuarine and freshwater systems, much is known about the basic biology of *E. affinis*, and egg DTs have been measured in numerous locations (Andersen and Nielsen, 1997; Ishikawa *et al.*, 1999; Devreker *et al.*, 2009, 2012). Although *E. affinis* is now considered a sibling species complex containing numerous subclades (Lee, 2000) and at least two species (Alekseev and Souissi, 2011), egg DT, unlike other reproductive parameters, has not been reported to differ among clades (Devreker *et al.*, 2012).

In contrast to *E. affinis*, little is known about *P. forbesi*. Native to the Yangtze River, China, *P. forbesi* was first detected in the SFE in 1987 (Orsi and Walter, 1991). Since its introduction, *P. forbesi* has replaced *E. affinis* as the biomass dominant species during summer and autumn (Kimmerer and Orsi, 1996; Kimmerer, 2002; Winder and Jassby, 2011). Recently, *P. forbesi* has been reported in the Columbia-Snake River system in Washington, USA, where it also dominates late-summer zooplankton abundance in the lower river and estuary (Cordell *et al.*, 2008).

METHOD

Experimental observations

Egg DTs were determined in laboratory incubations over a range of temperatures for *E. affinis* (~10, 15 and 20°C) and *P. forbesi* (~16, 18 and 22°C). Adult copepods were collected from the upper SFE, California, USA (salinity ≤2) between Chipps Island (38°2′45″N; 121°54′23″W) and Rio Vista (38°8′54″N; 121°41′17″W) on the Sacramento River and Twitchell Island (38°5′30″N; 121°39′7″W) on the San Joaquin River. Adult *E. affinis* were collected between February and May 2001. Adult *P. forbesi* were collected between July 2011 and February 2012. *Pseudodiaptomus forbesi* were collected over a longer time period in order to measure egg DT from copepods acclimated to a wide range of temperatures (10.5–21°C), and egg DT was measured at a minimum of two temperatures for each environmental temperature regime. Copepods were collected using short (3–10 min) horizontal tows with a 0.5-m diameter 200-μm net and resuspended in insulated 20-L containers for transport. Temperature and salinity *in situ* were measured with a handheld meter (YSI, Model 30).

In the laboratory, males and non-ovigerous females (~20 individuals each) were sorted into three to five replicate 1-L glass beakers containing 35-μm filtered water from the site of collection. The copepods were then acclimated to the designated temperature in a temperature-controlled room or water bath on a 12 h light: 12 h dark cycle. The water in each beaker was aerated lightly and copepods were fed daily in excess (>500 μg C L^{-1}). Diets were chosen to maximize egg production based on past experience culturing each species and therefore differed between species. *Eurytemora affinis* was fed a mixture of live phytoplankton (*Rhodomonas salina* CCMP 1319, *Skeletonema marinoi*, formerly *S. costatum* CCMP 1332, and *Thalassiosira weissflogii* CCMP 1587 and 1336). *Pseudodiaptomus forbesi* was fed a mixture of live (*Chlamydomonas reinhardtii* UTEXID 90 and *Scenedesmus obliquus* UTEXID 393) and cryopreserved (Shellfish Diet®, Reed Mariculture Inc.) phytoplankton.

The acclimation duration was dependent on the magnitude of the difference (ΔT) between the temperature at the time of collection and the incubation temperature. Monitoring for eggs began after 24 h ($\Delta T \leq 2$°C) to 48 h ($\Delta T > 2$°C), and any eggs produced during the acclimation period were discarded. To monitor the production of eggs, copepods were removed from each beaker with a 100-μm sieve every 2 h for *E. affinis* and every 1–4 h (≥18°C) or every 6–8 h (<18°C) for *P. forbesi*. The initial

time for egg development (i.e. egg-laying) was calculated as the midpoint of the interval between successive sampling periods. Females that had produced eggs during the interval were transferred individually to six-well plates containing ~12 mL fresh 35-μm filtered water and ample food. Females that had not produced eggs and males were returned to the beaker. For each species, 8–15 clutches were observed at each temperature.

Several hours (~10 h) before hatching was expected based on preliminary observations, clutches were removed from females with fine dissecting needles. The clutches were then placed in a 50-mL crystallization dish or the inner chamber of a miniature water bath (~12 mL) filled with GF/F filtered water. Clutches that were visibly damaged during the removal processes were discarded. The duration of separation between eggs and females was minimized to avoid oxygen deficiency and microbial infestation.

Egg hatching was then monitored under a dissecting microscope (Wild M5A) on a transmitted light base equipped with a fiber optic light source (JH Technologies Inc., Model MO150) and combination gooseneck (Schott, Model A08520) at ×12 or ×25 magnification with a digital video camera (Industrial Vision Source CCD Color Camera) attached with a beam splitter/photo port. For *E. affinis*, the camera was connected to a video monitor (Sony Trinitron, Model PVM-20N2U) and a video cassette recorder (Sony, Model SLV-N50), and egg hatching was recorded on VHS tapes. For *P. forbesi*, the camera was connected to a MacBook Pro (OS 10.6.8) laptop computer with a digital video converter (Datavideo DAC-200 Digital-to-Analog Converter), and egg hatching was recorded with time-lapse recording software (Gawker 0.8.3). Temperature was monitored at 10 min intervals with a temperature recorder (Ever Ready Thermometer Company, Ertco, Temp101) and confirmed with a thermometer. The temperature during egg development was estimated as the mean temperature from 24 h before egg production to the end of egg hatching. Egg diameter (μm) was measured on a dissecting microscope equipped with an ocular micrometer at ×50 magnification for a subset of individuals (10–12) of each species.

Monitoring of *E. affinis* egg development was continuous, and all egg hatching events were captured. Therefore, the DT of *E. affinis* was calculated as the time from egg-laying (i.e. the midpoint of the interval between successive sampling periods) to the actual hatch time. Monitoring of *P. forbesi* egg development was not continuous (i.e. time-lapse recordings) in order to decrease effort and minimize file sizes, so hatch time was calculated at 10 min intervals. Additionally, some hatching events were missed for 17 of the 61 *P. forbesi* clutches monitored because of equipment malfunctions. Therefore, the median hatch time was estimated for clutches in which all hatches were observed (~36% of the total time from the first hatch to the last, not including extreme laggards), and the ratio of the median time to the total duration of hatching was used to estimate the median hatch time of the clutches with missing observations. DT for these clutches was then calculated as the time from egg-laying to the median hatch time.

Model fitting

Various functions have been proposed to fit DT or rate, its inverse, to temperature (Nielsen *et al.*, 2002). These include the Bělehrádek function

$$\mathrm{DT} = a(T - T_0)^b \quad (1)$$

where T is temperature, and a, b and T_0 are fitting parameters. The Bělehrádek function has been widely used (McLaren, 1995), but has been criticized on several grounds (Guerrero *et al.*, 1994). Specifically, this function does not converge well in nonlinear fitting routines. Fitting our data for each of the copepods gave nonsensical values of b (−6) and T_0 (<−30), and very strong correlations (>0.999) between pairs of parameters indicating over-fitting. A fixed value of $b \approx -2$ is often used to minimize this problem (McLaren, 1995; Leandro *et al.*, 2006), but this value is arbitrary and difficult to justify. Nielsen *et al.* (Nielsen *et al.*, 2002) fitted a linear relationship of development rate to temperature for *Oithona similis* over a wide temperature range, but our development rates were nonlinear with regard to temperature. Another alternative is an exponential function

$$\mathrm{DT} = ae^{bT} \quad (2)$$

which relates directly to Q_{10} [$b = 0.1 \ln(Q_{10})$]. The corresponding equation from the metabolic theory of ecology (MTE) (Brown *et al.*, 2004) is

$$\mathrm{DT} = \alpha e^{\mathrm{E}/kT} \quad (3)$$

where α is a fitting parameter, E is the activation energy, k is Boltzmann's constant, and T is the temperature in degrees Kelvin. We fitted equation (2) to temperature and equation (3) to $1/T$ to compare these relationships. Both were fitted using a generalized linear model with a log link function and constant variance in *R* (version 2.12.1).

Simulation

We also conducted a simple simulation based on our results for *P. forbesi* to compare our individual-based

method (i.e. video observations) to the bulk method (Andersen and Nielsen, 1997; Nielsen *et al.*, 2002; Gould and Kimmerer 2010) for a single temperature. To simulate individual measurements, we used temperature-dependent rates from equation (2) and added error from the initial sampling window and from the variability among individual females:

$$\mathrm{DT_s} = \mathrm{DT} + U(-t/2,\ t/2) + N(0, \mathrm{SD}) \qquad (4)$$

where $\mathrm{DT_s}$ is the simulated DT of an individual female's eggs, DT is the mean for all females, U is a uniform distribution to represent a sampling window for egg-laying of t hours, and N is a normal distribution with mean of zero and standard deviation, SD. DT was set to 2 days, t to 4 h and SD was determined by fitting equation (2) to our data. For each simulation, 5 to 120 values of $\mathrm{DT_s}$ were calculated using a sampling window $t = 4$ h, and averaged to get a mean DT.

For the bulk method, we assumed that 120 egg sacs would be examined at eight equally spaced time points. For each egg sac, the actual DT was determined by sampling from equation (4) with $t = 0$ (since egg-laying is not observed). Then the stage of development of each individual was determined by sampling from a uniform distribution between 0 (ready to hatch) and this DT. Time of observation was regressed against the proportion that had not hatched at each time point to get the intercept as an estimate of total hatching time. Each of the above simulations was repeated 1000 times.

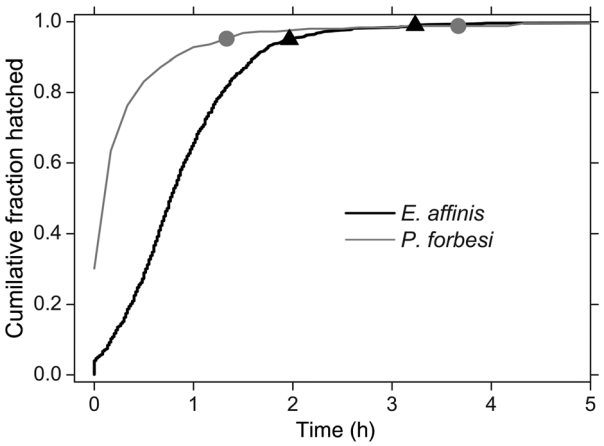

Fig. 1. Cumulative fraction of eggs hatched versus time (h) after the first egg in each clutch had hatched. All data pooled for *Eurytemora affinis* (751 eggs) and *Pseudodiaptomus forbesi* (249 eggs). Lines are the cumulative fractions. Symbols are the 95th and 99th percentiles of hatch time, respectively.

RESULTS

Hatch duration (i.e. the time interval between hatching of the first egg and the last) ranged from <0.1 to >10 h for both species. The distribution of individual egg hatching times within a clutch was skewed such that the majority of the eggs hatched early, while a few hatched late (Fig. 1). Hatch durations for *E. affinis*, which carries a single large clutch, were longer than those of *P. forbesi*, which carries two smaller clutches, but hatching was 95% complete for both species within 2 h.

Pseudodiaptomus forbesi egg DTs were similar in paired clutches, so DTs were averaged for each pair. The egg DTs of *E. affinis* and *P. forbesi* were related to temperature as $\mathrm{DT} = 11.5\mathrm{e}^{(-0.106 \pm 0.008)T}$ and $\mathrm{DT} = 22.7\mathrm{e}^{(-0.121 \pm 0.018)T}$, respectively, including 95% confidence intervals (Fig. 2). The fits of the exponential and MTE equations were very similar; the residual deviance for *E. affinis* was 0.58 day for the exponential and 0.57 day for the MTE equation, and equivalent values for *P. forbesi* were both 1.99 days. Egg DT of *P. forbesi* was independent of the field temperature at the times when copepods were collected (Fig. 3, linear regression slope = 0).

Pseudodiaptomus forbesi eggs were 108 ± 6 μm (mean ± 95% CI) in diameter and *E. affinis* eggs were 80 ± 2 μm in diameter. *Pseudodiaptomus forbesi* carried approximately 6 (4–8) eggs per sac, while *E. affinis* carried 24 (4–57) eggs per sac.

Simulations showed that both methods of determining egg DT gave unbiased results (Table I). The individual-based method could achieve similar results to those from bulk incubation ($n = 120$) with fewer than 10 egg sacs (Table I).

DISCUSSION

These data include the first report of egg DTs for *P. forbesi*, and the first report from the SFE for *E. affinis*. The egg DTs of *P. forbesi* were approximately 50% longer than those of *E. affinis* at the same temperature, although this difference in egg DT decreased as temperatures increased. However, these longer DTs are similar to those previously reported for other *Pseudodiaptomus* spp. (Hart, 1981; Uye *et al.*, 1982; Jerling and Wooldridge, 1991; Beyrend-Dur *et al.*, 2011). In general, *Pseudodiaptomus* spp. carry a smaller number of larger eggs (Liang and Uye, 1997; McKinnon and Klumpp, 1998; this study) than does *Eurytemora* spp. (Crawford and Daborn, 1986; Hirche, 1992; Conway *et al.*, 1994; Berasategui *et al.*, 2012; this study). The larger egg may contribute to the longer DTs, as increases in DT with egg size have been reported among closely related species of copepods (McLaren *et al.*, 1969; Corkett and McLaren, 1970; Corkett, 1972; Vijverberg, 1980). The longer DTs, and possibly the larger eggs, may also be related to the loss or abbreviation of the first naupliar stage

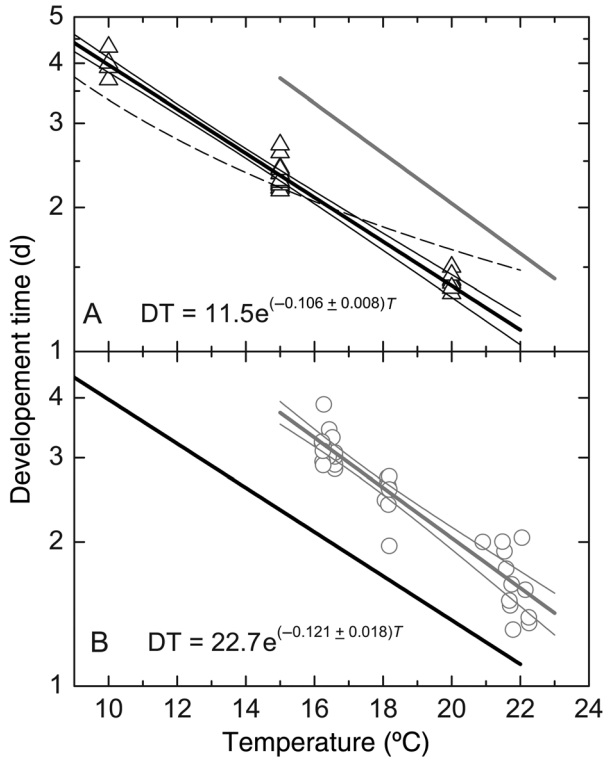

Fig. 2. Egg DT (d) as a function of temperature (T, °C) for (**A**) *Eurytemora affinis* including a reference line (thick gray) for *Pseudodiaptomus forbesi* and (**B**) *P. forbesi* including a reference line (thick black) for *E. affinis*. Points are the median hatching times of individual clutches for *E. affinis* and paired clutches for *P. forbesi*. Lines are the exponential response of egg DT to temperature fit using a generalized linear model with a log link function and constant variance, shown with 95% CI. Dashed black line (A only) is a curve representing data from a variety of studies of *E. affinis* (Andersen and Nielsen, 1997, their Fig. 5).

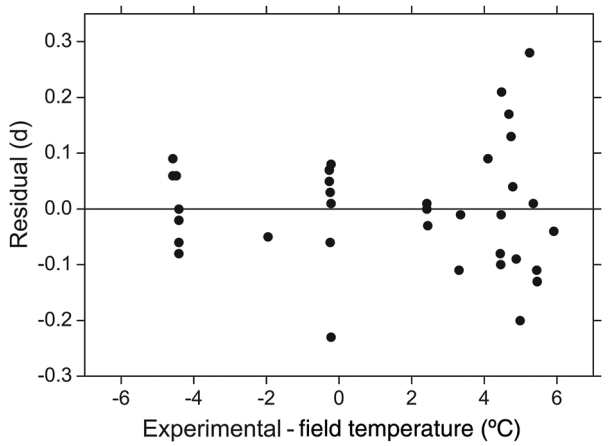

Fig. 3. Residuals (d) from the generalized linear model of egg DT for *Pseudodiaptomus forbesi* as a function of the difference between experimental and field temperature (°C). Deviation from the generalized linear model is independent of the temperature difference (linear regression slope = 0).

Table I: Simulation results comparing the individual-based and bulk methods of estimating DT with various numbers of egg sacs incubated (n)

	95% Confidence limits	
Method (*n*)	Lower	Upper
Individual		
5	1.90	2.11
10	1.93	2.07
15	1.94	2.06
20	1.95	2.05
120	1.98	2.02
Bulk		
120	1.90	2.12

Values are lower and upper 95% CI determined as quantiles of 1000 simulated samples.

among pseudodiaptomids (Goswami, 1978; Hart, 1981; Golez *et al.*, 2004).

The egg DTs of *E. affinis* reported here fall within the range previously reported for this species complex from other locations (Corkett and McLaren, 1970; Andersen and Nielsen, 1997; Ishikawa *et al.*, 1999; Devreker *et al.*, 2009), although the fitted relationships differed slightly among these studies (Fig. 2). Small differences between the egg DTs of *E. affinis* observed between this study and others may be the result of differences in environmental conditions. Egg DT has been reported to vary with salinity (McLaren, 1966; Uye, 1980; Ishikawa *et al.*, 1999); however, the salinity range over which copepods were collected and egg DT was observed in this study was small (0.1−1.7). Temperature acclimation, both short- and long-term, has also been observed to affect egg DT (Landry, 1975b; Tester, 1985; Hansen *et al.*, 2010). The time necessary for short-term acclimation depends on both the magnitude and direction of the temperature change (Tester, 1985). Although we limited the temperature change during acclimation (± 6°C), the acclimation time of field-collected adults to experimental temperatures in this study (24−48 h) was shorter than the 84 h to 8 d recommended by Tester (Tester, 1985). This may account for the increase in variability among egg DTs at the highest and lowest temperatures where the temperature change was largest. Long-term acclimation effects were not examined for *E. affinis*; however, the egg DTs of *P. forbesi* did not appear to be significantly influenced by the temperature at the time of collection.

The exponential model is clearly superior to the Bělehrádek model because of the difficulty in fitting that model without arbitrary constants. Although substantial differences have previously been reported between the exponential and MTE formulations for the temperature response of vital rates (Gillooly *et al.*, 2001), we found no

difference between them. Furthermore, aspects of the MTE have been criticized on grounds of both theory and model fitting (Price *et al.*, 2012). This leaves the choice between the exponential or power function (Nielsen *et al.*, 2002) or some other monotonic function up to the experimenter, since the principal objective of developing such a model is to allow accurate interpolation to temperatures at which DTs were not measured.

Egg DTs of copepods have been assessed using two general approaches: bulk incubation followed by regression analysis, and individual-based observations (Andersen and Nielsen, 1997). Although several studies have shown no difference among egg DTs measured using both methods (Burgis, 1970; Maier, 1989; Ozaki and Ikeda, 1997), small differences could alter estimates of egg DT, and thus calculations of population dynamics. Bulk incubation requires incubating large numbers of ovigerous females, monitoring hatching over time, and determining DT from the intercept of the relationship between percent hatching and incubation time. This method minimizes handling, but presumes that the copepods incubated are randomly distributed through their egg-carrying cycle, which may not always be the case.

Conversely, direct observations of individual eggs from laying to hatching are time-consuming and require more handling than the bulk incubation method, especially if the egg sacs are removed from the female for observation. However, equivalent results can be achieved with far fewer females, as our simulations showed (Table I). Direct observations also provide information on the variability of egg hatching among individuals, which is not provided by bulk incubation. The use of video to monitor egg develop in this study eliminated some of the manpower requirements associated with direct observations and increased the frequency of observation, making it a more appealing and accurate technique.

The individual-based method may be preferable when egg development is rapid and EPR is high, conditions under which sufficient numbers of females become ovigerous during short-time periods. In contrast, slow development and a low proportion of ovigerous females in the population favor using the bulk incubation method, since there is no need to hold the females until they produce eggs. Our laboratory previously used the bulk method to determine egg DT in the cyclopoid *Limnoithona tetraspina*, which develops slowly and has a low reproductive rate (Gould and Kimmerer, 2010).

The use of video in science is becoming more common as the technology associated with video capture, storage and analysis improves and becomes less expensive. However, few studies have employed video techniques to monitor egg development in copepods (McKinnon and Klumpp, 1998; Yoshiki *et al.*, 2006, 2011). In addition to reducing manpower requirements and increasing the frequency of observations, the use of video in this study provided detailed information on the variability of egg hatching among clutches. The duration of hatching in this study varied greatly among eggs within a clutch. Large variability and asymmetrical distribution in hatching among clutches has also been observed in other studies (McLaren, 1966; Hart and McLaren, 1978; Uye *et al.*, 1982; Bonnet and Carlotti, 2001; Nielsen *et al.*, 2002). Hart and McLaren (Hart and McLaren, 1978) attributed some of this variability to female behavior (urosome flexing) and to the position of eggs within the clutch, with peripheral eggs hatching earlier. We did not observe any obvious influence of position on hatching for *P. forbesi*, but these sacs are geometrically simple, and although similar behaviors were observed by Uye *et al.* (Uye *et al.*, 1982) for *P. marinus*, they observed no difference in hatching among clutches in both attached and detached eggs. The variation in hatching durations observed in this and other studies could significantly influence calculations of reproductive parameters, including egg DT, interclutch duration (time between spawning of successive clutches), stage duration and generation time (time from egg to maturity) which are all used to model population dynamics. However, this variability is more a result of actual individual variability than experimental error, and is therefore useful in developing individual-based or other models that address variability explicitly.

Accurate information on the basic biology of these and other species of copepods is becoming more important as they continue to invade new habitats, and scientists try to predict or determine their roles in these systems. Large differences among species and environmental conditions support the use of egg DTs determined specifically for each target species and location. Video observations proved to be an easy technique for increasing the accuracy of these measurements and for decreasing the effort required.

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