Effect of temperature on life history traits of the invasive calanoid copepod *Arctodiaptomus dorsalis* (Marsh, 1907) from Lake Taal, Philippines

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**Abstract:** *Arctodiaptomus dorsalis* is an invasive calanoid copepod from America, and is now found in 23 out of 32 lakes and rivers in the Philippines. Live specimens of *A. dorsalis* were collected from Lake Taal and cultured in the laboratory. The specimens were reared under three different temperatures (25°C, 30°C, and 35°C) with the same food and light conditions, i.e. ~10^5 cells mL^−1 of *Chlamydomonas reinhardtii* and 12L:12D at ~60 lx, respectively. Post-embryonic development times from hatching to adult decreased from 31.5 d to 18.3 d as the temperature increased, while those during naupliar stages were quite similar, i.e. 4.4, 2.8 and 2.3 d at 25, 30 and 35°C, respectively. The naupliar durations were substantially shorter than the copepodid stages. Clutch sizes were almost the same, 8.7–9.2 eggs clutch^−1, among all temperatures tested, while hatching success decreased from 85.9% at 25°C to 24.2% at 35°C. Overall survival rates from hatching to adult decreased as well from 67% at 25°C to 23% at 35°C. This is the first successful attempt to culture *A. dorsalis* collected from a freshwater lake in the Philippines.

**Key words:** clutch size, hatching success, laboratory culture, non-indigenous zooplankton, post-embryonic development

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**Introduction**

*Arctodiaptomus dorsalis* (Marsh, 1907), a neotropical species, is known for its propensity for transcontinental invasion (Papa et al. 2012a). It was originally recorded to occur in the Americas, extending from the southern United States, through Central America, and to the north of South America (Reid 2007). This calanoid copepod was once mistakenly identified as *Tropodiaptomus vicinus* (Kiefer, 1930) (a native species in the Philippines) in Lake Taal (Amarasinghe et al. 2008). Detailed taxonomic studies on specimens collected from 2008 to 2010 revealed that it was actually *A. dorsalis*, and not *T. vicinus* (Papa et al. 2012b). Recent studies also showed that there has been a massive invasion of *A. dorsalis* in 18 out of 27 lakes investigated in the Philippines (Papa et al. 2012a). Introduction of this species may have been through ship drinking water reserves dumped into Laguna de Bay (Tuyor & Baay 2001) which was then, through aquaculture practices, dispersed to other parts of the country (Papa et al. 2012a). Recent studies by Metillo et al. (2014) and Rizo et al. (2015) added five more new locality records of *A. dorsalis* in the Bicol region of Luzon Island and Lake Lanao in Mindanao Island. These studies likewise failed to find existing *T. vicinus* and *T. gigantoviger* Brehm, 1933 (an endemic species in the Philippines) populations in their original habitats where the populations of *A. dorsalis* have become established.

Previous studies on *A. dorsalis*, formerly *Diaptomus dorsalis* Marsh, 1907, mainly focused on its distribution (Reid 2007) and a couple of them have also dealt with its development. Elmore (1982) observed that the development of *A. dorsalis* was affected by food concentration, wherein low food availability led to a decrease in developmental rates and body size, as well as lower clutch size and survival rates. Another study, focused on the factors
affecting its distribution in subtropical Florida, showed that food concentration clearly affected *A. dorsalis*’ ability to establish populations in oligotrophic and mesotrophic lakes (Elmore 1983). Although variations due to temperature were also shown, its effect on the development of *A. dorsalis* was not thoroughly discussed.

Temperature has been suggested as probably the most significant single parameter that affects the development of aquatic invertebrates (Heip 1974), and, specifically for copepods, strongly influences egg production (Ban 1994, Lee et al. 2003, Bonnet et al. 2009), embryonic development time (Yoshida et al. 2012), post-embryonic development time (Ban 1994, Jimenez-Melero et al. 2005, Devreker et al. 2007) and hatching success (Yoshida et al. 2012). It has been shown that increasing temperatures result in faster development of copepods under experimental conditions (Landry 1975, Ban 1994, Pinchuk & Paul 1998, Lee et al. 2003, Liu & Hopcroft 2006, Devreker et al. 2007, Bonnet et al. 2009) even when reaching 35°C—an extreme temperature simulated for tropical habitats (Burgis 1970, Li et al. 2012a). This is also the first attempt to culture expatriates of *A. dorsalis* outside of its original geographical distribution.

The aim of this study was to successfully culture *A. dorsalis* collected from Lake Taal, a large volcanic caldera (Ramos 2002) and the third largest lake in the Philippines (Hargrove 1991), at three different temperatures to evaluate the effects of temperature on life history parameters, such as post-embryonic development time, clutch size, and hatching success in this calanoid species. Anthropogenic activities, specifically aquaculture due to increasing food demand, can be attributed to Lake Taal’s eutrophication (Vista et al. 2006, White & San Diego-McGlone 2008, Papa & Zafaralla 2011), making conditions favorable for the thriving population of *A. dorsalis* (Reid 2007, Papa et al. 2012a). This is also the first attempt to culture expatriates of *A. dorsalis* outside of its original geographical distribution.

**Materials and Methods**

**Field collection**

Zooplankton was collected by performing four vertical net hauls using a conical plankton net (mesh size, 80 µm; mouth diameter, 30 cm) at a pelagic site (depth, 40 m) in Lake Taal, Philippines (14°00′40.6″N, 121°05′19.1″E), where *A. dorsalis* was previously documented (Papa et al. 2012a, b). In addition, one liter each of lake water from depths of 0, 5, 10, 20, 30, and 40 m was collected with a water sampler and then combined for use as the culture medium. The zooplankton samples collected were immediately transferred to 6-L carboy containers filled with filtered (Whatman GF/C) lake water, and transported back to the laboratory within ~1–2 h.

**Stock culture**

In the laboratory, ovigerous *A. dorsalis* females were

sorted from the samples placed in petri dishes filled with filtered lake water, and then observed using a compound microscope. Identification of *A. dorsalis* was based on the taxonomic keys, illustrations, and descriptions by Dussart & Defaye (2001), Papa et al. (2012a) and Petersen (2013). The isolated animals were then cultivated in 50 mL beakers, containing 30 mL filtered (Whatman GF/C) lake water and *Chlamydomonas reinhardtii* Dangeard 1899 (NIES-2235), which has been previously used in culture studies of *A. dorsalis* (Elmore 1982, 1983), with the concentration at ~10^5 cells mL^-1, which is more than the incipient limiting concentration (Elmore 1983). Cultures were kept at 29°C, with a photoperiod of 12L:12D for at least two generations (> four weeks) prior to the experiment. The light sources used were cool-white fluorescent tubes at a light intensity of ~60 lx, controlled by shading the tubes with cellophane. Culture media and food algae were changed three times a week. Newly hatched nauplii from the first generation of the stock culture were isolated and placed in new 50 mL beakers filled with the same food and medium. All individuals were transferred to new beakers filled with fresh food suspensions by Pasteur pipette every two days until they reached adult stage. Molts and dead animals were checked and removed every two days.

**Post-embryonic development**

In Lake Taal, the animals experience water temperatures ranging between 28–30°C (Perez et al. 2008), but may reach a minimum of 26°C to a maximum of 34°C (White & San Diego-McGlone 2008, Papa & Mamaril Sr 2011). The experimental temperatures were therefore selected at 25, 30 and 35°C, providing a range between the lowest and highest temperatures in Lake Taal. Thirty newly-hatched nauplii, hatched within 12 h from the eggs produced by the females acclimatized at each experimental temperature, were placed individually in 3-mL wells of a tissue culture plate at the same temperature as those of the mothers. Subsequently, development was recorded from naupliar to copepodid, and finally to adult stages. Each individual was observed under a stereoscopic microscope (Olympus, SZX12) every day to monitor for molts or dead animals. Time zero was defined as the time when the nauplii hatched. All experiments were performed under the same light conditions as the stock culture. The food suspension was changed every two days.

**Clutch size and hatching success**

When the individuals developed up to the adult stage, five pairs of the males and females were reared in a 50 mL beaker at each experimental temperature (25, 30 and 35°C) under the same food and light conditions as those in the experiments for post-embryonic development. The experiments were made in triplicate at each temperature. Food suspension was replenished every two days. Eggs laid by females and hatched nauplii were counted every day until all nauplii had hatched from the eggs in the first clutch
produced by all five females. Clutch size was defined as the number of eggs per clutch, and hatching success was the percentage of the number of nauplii hatched to the total number of eggs in a clutch. Unhatched eggs that were attached to the mother or had dropped to the bottom of the beaker for over 12 h after laying were defined as non-viable ones (based on Ban 1994, Mavuti 1994, Makino & Ban 2000, Liu et al. 2014, 2015).

Data analyses

The relationship between temperature \(T\) and development time \(D\) was described using Bělehrádek’s function:

\[ D = a(T - b)^c, \]

where \(a\), \(b\) and \(c\) are fitted constants. After linearization with log-transformed \(D\) and \(T\), values for \(a\) and \(c\) were calculated by linear-regression with iterative calculation of \(b\). Differences of post-embryonic development times from hatching to adult among the temperature treatments were analyzed using the Kruskal–Wallis test, and then multiple comparisons were made using Dunn’s method when the result indicated statistical significance. Variations among treatments concerning clutch size, hatching success and survival rates were analyzed by one way ANOVA, and then multiple comparisons were made using the Tukey post hoc test, when the result indicated significant difference. Spearman’s rank correlation analysis was made to evaluate the relationship between temperature and sex ratio. All data were analyzed using Origin 2016 (evaluation version from www.OriginLab.com) and SigmaPlot version 13.0 (www.sigmaplot.com).

Results

Post-embryonic development time (Post-EDT)

Results for the effect of temperature on the Post-EDT in \(A. dorsalis\) are summarized in Table 1. Mean post-EDTs from hatching to adult significantly decreased from 31.5 days at 25°C to 18.3 at 35°C with increasing temperature (Kruskal–Wallis test, \(df=2, H=32.535, p < 0.001\)). Durations of naupliar and copepodid stages varied from 4.4 and 25.9 d at 25°C to 2.3 and 15.0 d at 35°C, respectively. Ratios of naupliar to copepodid durations ranged from 0.13 to 0.17, indicating that a substantial period of the juvenile stages was spent as copepodes. The Kruskal–Wallis test showed significant differences between the treatments for both stage durations (\(df=2, H=38.735\) for nauplii and 27.28 for copepodides, \(p < 0.001\)), except for the naupliar stages at 30 and 35°C (Dunn’s method \(Q=1.359, p=0.522\)).

The development times \(D\) were described by the following Bělehrádek’s temperature \(T\) functions:

\[ D=1017.9(T-4.4)^{-1.80} (R^2=0.989) \]

for naupliar duration,

\[ D=12826.6(T+6.2)^{-1.80} (R^2=0.995) \]

for copepodid duration and

\[ D=15527.2(T+6.1)^{-1.80} (R^2=0.957) \]

for the post-EDT from hatching to adult.

The overall survival rates from hatching to adult decreased with increasing temperature, being 66.7, 53.3 and 23.3% at 25, 30 and 35°C, respectively (Table 1). The animals mostly died during copepodid stages, while relatively high survival rates during the naupliar stages were observed (77–97%).

Sex ratio

Sex ratio, the ratio of females to males, in the adult stages were 3.0, 1.7 and 1.3 at 25, 30 and 35°C, respectively (Table 1). Spearman’s rank correlation analysis showed negative correlation between temperature and sex ratio (Spearman’s \(r=-0.946, p < 0.001\)).

Clutch size and hatching success

Mean clutch sizes in \(A. dorsalis\) were 8.9, 9.2 and 8.7 eggs clutch\(^{-1}\) at 25, 30 and 35°C, respectively (Table 2). ANOVA indicated no significant difference in the clutch sizes among the temperatures tested (ANOVA, \(df=44, F=0.125, p=0.883\)).

Mean hatching successes were 85.9, 70.1 and 24.2% at 25, 30, and 35°C, respectively (Table 2). These differences were statistically significant (ANOVA, \(df=44, F=29.523, p < 0.001\)), with multiple comparisons tests indicating significant differences between 25 and 35°C (\(p < 0.001\)), as

| Stage      | Temperature (°C) | 25      | 30                 | 35                 |
|------------|------------------|---------|--------------------|--------------------|
|            | D    | sd   | s%    | n   | D    | sd   | s%    | n   | D    | sd   | s%    | n   |
| Naupliar   | 4.41 | 1.02 | —     | 30  | 2.84 | 1.37 | —     | 30  | 2.25 | 0.68 | —     | 30  |
| Copepodid  | 25.85 | 2.80 | 96.7  | 29  | 21.38 | 2.28 | 86.7  | 26  | 15.00 | 2.31 | 76.7  | 23  |
| Adult*     | 31.50 | 2.83 | 66.7  | 20  | 26.00 | 1.67 | 53.3  | 16  | 18.29 | 2.13 | 23.3  | 7   |
| Sex Ratio  | 3.00 | 1.67 |       |     |       |       |       |     | 1.33 |       |       |     |

\(n, n\) number of individuals in the stage, * the post-embryonic time from hatching to adult
well as 30 and 35°C ($p < 0.001$), but not for 25 and 30°C ($p=0.264$).

**Discussion**

**Post-embryonic development time and survival rate**

The results in this study on *A. dorsalis* echo previous work on other copepod species that showed a negative temperature function on post-EDTs (Ban 1994, Caramujo & Boavida 1999, Lee et al. 2003, Melão & Rocha 2004, Liu et al. 2014) and survival rates (Amarasinghe et al. 1997, Hall & Burns 2001, Jiménez-Melero et al. 2007). Although the same relationship between temperature and post-EDT was observed by Elmore (1983), the survival rates in this study follow a different trend. Comparison of results shows that the survival rates of *A. dorsalis* in this study have a similar negative relationship with temperature only when it was cultured in water taken from an oligotrophic-mesotrophic lake that *A. dorsalis* does not inhabit, and is not the same as when cultured in eutrophic lake water, wherein a slight increase in survival rates with increasing temperatures was observed.

*Arctodiaptomus dorsalis* spent more time in its copepodid stages than in its naupliar stages in this study, which has also been observed in *A. salinus* (Dayad, 1885) (Jiménez-Melero et al. 2007), unlike *Eodiaptomus japonicas* (Burckhardt, 1913) (Liu et al. 2014) and *Copodiaptomus numidicus* (Gurney, 1909) (Caramujo & Boavida 1999) which followed the equiproportional development model (Corkett 1984). The non-feeding early naupliar stages rely mostly on the yolk for nutrition (Mauchline 1998, Peterson 2001), thus requiring rapid molting to the feeding stages (Liu et al. 2014), unlike the copepodid stages that may have been influenced by food concentration (Ban 1994, Jiménez-Melero et al. 2007).

**Sex ratio**

A sex ratio skewed toward females was constantly observed at all three temperatures, which is common for many copepod species (Corkett & McLaren 1978) and also coincides with the general seasonal trend in Lake Taal (Papa et al. 2011). Increasing temperatures may have lowered the sex ratio of *A. dorsalis* due to low female survival, as previously observed in other copepods (Katona 1970, Halsband-Lenk et al. 2002). On the other hand, the higher proportion of males at higher temperatures may be compensatory measures for the low survival rates in order to increase the chances of copulation (Heinle 1970, Sabatini 1989) at temperatures considered to be non-optimal (Jiménez-Melero et al. 2014). Another probable reason for the decreased sex ratio may be sex change during juvenile development which has been linked to environmental temperature (Katona 1970, Voordouw and Anholt, 2002, Lee et al. 2003), although observations on this were not carried out in this study. These results should be investigated in future studies because sex ratios can be influenced by multiple factors aside from temperature (Gusmão et al. 2013, Jiménez-Melero et al. 2014).

**Clutch size and hatching success**

The results of this study showed no significant effect of temperature on clutch size in *A. dorsalis*, which echoes with previous studies on temperate calanoids such as *Copodiaptomus numidicus* (Caramujo & Boavida 1999), *Pseudocalanus newmani* Frost, 1989 (Lee et al. 2003) and *Eudiaptomus gracilis* (G.O. Sars, 1863) (Jiménez-Melero et al. 2005), although copepod embryonic development (Peterson 2001) and egg production (Hirche et al. 1997) generally depends on temperature. However, the clutch sizes in this study are considerably smaller than those recorded by Elmore (1983) for *A. dorsalis*. This fact is unexpected, since culture experiment conditions (i.e. food algal species and concentration) in this study were similar to those of Elmore (1983). The use of a monoalgal diet in this study, even at the incipient limiting concentration, may not have been enough to simulate eutrophic conditions used by Elmore (1983) wherein *A. dorsalis* was cultured using water from a lake that it inhabits.

On the other hand, mean hatching success was negatively affected by temperature, being just 24% at 35°C. The sudden decline in hatching success at the highest temperature tested can be attributed to severe thermal stress, as has been observed for other calanoids (Lee et al. 2003, Rhyne et al. 2009, Yoshida et al. 2012). The relatively high rates of hatching success at 25 and 30°C suggest that this is the optimal temperature range for hatching in *A. dorsalis*, and an increase in temperature beyond this range may

### Table 2. The mean values and standard deviations of reproductive parameters: clutch size (CS) and hatching success (HS) in *Arctodiaptomus dorsalis*.

| Reproductive parameter | Temperature (°C) | Mean | sd  | n  |
|------------------------|------------------|------|-----|----|
|                        | 25               |      |     |    |
| CS                     |                  | 8.9  | 3.0 | 15 |
| HS (%)                 |                  | 85.9 | 0.1 | 15 |
|                        | 30               |      |     |    |
| CS                     |                  | 9.2  | 2.4 | 15 |
| HS (%)                 |                  | 70.1 | 0.1 | 15 |
|                        | 35               |      |     |    |
| CS                     |                  | 8.7  | 2.1 | 15 |
| HS (%)                 |                  | 24.2 | 0.2 | 15 |

$n$, number of pairs observed and used in the experiment among the sex ratio of *A. dorsalis* (Papa et al. 2011). Increasing temperatures may have low-
limit its population growth.

Since higher metabolic losses at higher temperatures are considered more severe in food limited conditions (Liu et al. 2015), the reduced hatching success and low survival rates associated with low sex ratio in adults suggest that high temperatures over a certain threshold may exert a strong influence on an *A. dorsalis* population and can be a limiting factor for its population growth. This thermal stress experienced by *A. dorsalis* over 30°C could have caused energy acquired to be spent on survival rather than reproduction (Rhine et al. 2009) and may explain the slightly longer development time in copepodes and the small clutch sizes. The steady increase in water temperature in Lake Taal from 1948 to 2010 which may have been brought about by global climate change (Souissi 2012), could, therefore, severely affect the population of *A. dorsalis* if it goes beyond 30°C.

Although the food concentration used in this study is beyond the incipient limiting concentration as stated by Elmore (1983), the results resemble those from oligotrophic-mesotrophic setups wherein *A. dorsalis* does not thrive well, indicating that a food concentration of \(10^5\) cells mL\(^{-1}\) in this case may not have been enough to simulate a eutrophic setting. Food quality also affects the development of copepodes cultured in the laboratory (Burns 1985), especially mononaglial cultures, implying that mixtures of algae are better feed for laboratory-raised copepodes (Støttrup 2006, Jeyaraj & Santhanam 2013). These factors should be considered in future studies in order to attain better results.

Studies on the physiology and ecology of copepodes are necessary to predict their invasion of new habitats (Riccardi & Giussani 2006, Sullivan & Kimmerer 2013), as in the case for *A. dorsalis* in the Philippines (Papa et al. 2012a, Metillo et al. 2014, Rizo et al. 2015). It may have already displaced previously recorded endemic species from their habitats in the Philippines, and probably might displace unrecorded endemic calanoid species as well (Papa et al. 2012a). *Arctodiaptomus dorsalis’ small, transparent body (Reid 2007, Papa et al. 2012a), r-type life strategy (based on Elmore 1983, Reid 2007) and preference for eutrophic conditions (Elmore 1983, Reid 2007, Papa et al. 2012a) will enable it to escape predation pressure and significantly increase in number at temperatures below 30°C, potentially outlasting other larger, oligotrophic or mesotrophic-adapted endemic Philippine calanoid species.

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