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# Effects of food concentration on the reproductive capacity of the invasive freshwater calanoid copepod *Arctodiaptomus dorsalis* (Marsh, 1907) in the Philippines

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## ABSTRACT

The relationship between food concentration and reproductive capability has been reported for many copepods. Such information can indirectly provide insight as to how species invade new habitats. *Arctodiaptomus dorsalis* (Marsh, 1907), originally described from the United States, has been found to be present in more than 20 Philippine inland water bodies and has also been documented to prefer eutrophic conditions. By feeding this copepod different concentrations of *Chlamydomonas reinhardtii* Dangeard, 1888 ($4 \times 10^3$ cells ml$^{-1}$, $5 \times 10^4$ cells ml$^{-1}$, $10^5$ cells ml$^{-1}$, and $2 \times 10^5$ cells ml$^{-1}$), we investigated the effect of food concentration on different reproductive parameters of *A. dorsalis*: hatching success (HS), clutch size (CS), latency time (LT), inter-clutch duration (ICD), egg production rate (EPR), and fecundity (F). With increasing food concentration HS varied from 13.64% to 50.74%, and CS from 8.50 to 10.57 eggs clutch$^{-1}$, but these differences were not statistically significantly. EPR significantly increased with food concentration from 3.00 to 7.54 eggs female$^{-1}$ d$^{-1}$, while ICD and LT both significantly decreased from 2.00 to 1.71 d and 1.58 to 0.71 d, respectively. F significantly increased from 3.4 to 59.2 eggs female$^{-1}$ with increasing food concentration, with a maximum of 104 eggs in nine clutches for one individual. The spawning interval thus became shorter and clutches are produced at higher rates at high food concentrations. The successful invasion of *A. dorsalis* into the inland waters of the Philippines, therefore, could be attributed to the natural eutrophic conditions of these habitats, which has been further aggravated by anthropogenic nutrient inputs into the ecosystem.

**Key Words:** eutrophication, feeding experiments, freshwater zooplankton

## INTRODUCTION

Copepods play a crucial role in aquatic ecosystems as primary consumers providing a link between producers and higher trophic levels (Amarasinghe *et al.*, 1997; Richardson, 2008; Liu *et al.*, 2015). Copepod production, population dynamics, and life history are therefore important in investigations of lake ecosystems (Jiménez-Melero *et al.*, 2012; Liu *et al.*, 2015), as well as investigations of the environmental factors affecting their biology (Makino & Ban, 2000). Together with temperature, food concentration has been considered as one of the most important parameters affecting the reproduction (Ban, 1994; Jiménez-Melero *et al.*, 2012; Liu *et al.*, 2015) and population growth (Sullivan & Kimmerer, 2013) of copepods.

Previous studies have shown that food concentration affects egg production (Ban, 1994; Jónasdóttir, 1994; Liu *et al.*, 2015), clutch emergence (Chaudron *et al.*, 1995; Jiménez-Melero *et al.*, 2012; Liu *et al.*, 2015) and hatching success (Chaudron *et al.*, 1995; Liu *et al.*, 2015) of copepods. Makino & Ban (2000) used different concentrations of the alga *Cryptomonas tetrapyrenoidosa* Skuja, 1948 to simulate an oligotrophic environment and observed that clutch size, egg production rate and hatching success of *Cyclops* sp. were affected by an increase in concentration of algae from 1 × $10^3$ to 4 × $10^4$ cells $ml^{-1}$. Most of these studies were done on temperate copepods, and only meagre information concerns tropical species (Amarasinghe *et al.*, 1997).

Published studies on the freshwater zooplankton in the Philippines have primarily focused on taxonomy (Papa & Briones, 2014), ecology (Papa & Zafaralla, 2011; Papa *et al.*, 2011, 2012b), and development (Tordesillas *et al.*, 2016). Studies on Philippine lakes focusing on trophic ecology in relation to the phytoplankton community and/or levels of chlorophyll a (Chl-a) are scant, mostly focusing on aquaculture development in major lakes (Tamayo-Zafaralla *et al.*, 2002) such as Laguna de Bay, the largest in the country, Lake Taal, Batangas province, and the seven maar lakes of San Pablo City, Laguna province, all on the island of Luzon, and Lake Lanao on the southern island of Mindanao. Available data on these lakes include evaluations of their mesotrophic to hypereutrophic status (Tamayo-Zafaralla *et al.*, 2002; Cuvin-Aralar *et al.*, 2004; Baldia *et al.*, 2007; Perez *et al.*, 2008), measurements of their Chl-a levels (2 ug $l^{-1}$ to 150.63 ug $l^{-1}$) (Laguna Lake Development Authority, Environmental Quality Research Division, 2008; Perez *et al.*, 2008), and descriptions of their phytoplankton communities (Lewis, 1978; Tamayo-Zafaralla *et al.*, 2002; Papa & Mamaril, 2011), but no information on how these factors affect the reproduction of zooplankton. Only Papa *et al.* (2012b) correlated Chl-a levels to zooplankton spatial abundance in Laguna de Bay, although exact figures for Chl-a were not given.

We investigated the effects of different concentrations of food on the rates of egg production, egg development, and hatching success of the calanoid copepod *Arctodiaptomus dorsalis* (Marsh, 1907) reared in the laboratory under food-limited, abundant and overabundant conditions. This copepod, described from Louisiana, USA (Marsh, 1907), and known through Central America to northern South America (Reid, 2007), was recorded in 23 out of 32 lakes, rivers and dams in the Philippines from 2011 to 2015 (Papa *et al.*, 2012a; Metillo *et al.*, 2014; Rizo *et al.*, 2015; Tordesillas *et al.*, 2016). Our study was aimed at investigating whether *A. dorsalis* could have presumably displaced calanoid copepods endemic to the Philippines (Papa *et al.*, 2012a; Metillo *et al.*, 2014) owing to its preference for eutrophic waters (Elmore, 1983; Reid, 2007; Papa *et al.*, 2012b), a preference which has been observed to affect its distribution in Florida, USA (Elmore, 1983). We also add to the sparse available data on tropical copepods (Elmore, 1982; Amarasinghe *et al.*, 1997), specifically on their reproduction, and provide information on the life history of an invasive species.

## MATERIALS AND METHODS

### Stock cultures

A mean of 20.67 adults and 73.33 in various naupliar and copepodid stages of *Arctodiaptomus dorsalis*, which had been cultivated in the Biology Laboratory of the Thomas Aquinas Research Complex, University of Santo Tomas, Manila, Philippines since August, 2014, were grown in three 250 ml beakers containing 150 ml of sterile tap water and fed with ~1.5 × $10^5$ cells $ml^{-1}$ of a suspension of the green alga *Chlamydomonas reinhardtii* Dangeard, 1888 (strain NIES 2235) for four weeks prior the experiment. The stock cultures were maintained at a constant temperature of 30 °C with a photoperiod of 12L:12D with a light intensity of ~60 lux using a cool-white fluorescent tube shaded with a sheet of blue cellophane. The culture medium was replaced, and moults and dead individuals were removed every two days.

### Experimental procedure

A mono-algal diet of *C. reinhardtii* was used as food at concentrations of approximately 4 × $10^3$ cells $ml^{-1}$, 5 × $10^4$ cells $ml^{-1}$, $10^5$ cells $ml^{-1}$ and 2 × $10^5$ cells $ml^{-1}$. Concentrations were measured using a hemocytometer. The lowest concentration represents an oligotrophic condition (Makino & Ban, 2000), and the last three represent different levels of eutrophic conditions (Gastrich *et al.*, 2004). Male/female pairs in the fifth copepodite stage were isolated from the stock culture and placed in a 5 ml well of a tissue culture plate with 4 ml of algal suspension. No acclimation was done following Chow-Fraser & Sprules (1992) and Gentleman & Neuheimer (2008). Five pairs of copepods were observed for each experimental food concentration. All setups were maintained at the same temperature and light conditions as those of the stock culture. The culture medium was replaced with fresh algal suspension every other day. Spawning and number of newly hatched nauplii were recorded every day using stereoscopic (Swift SM90) and compound (Olympus CX21) microscopes for twelve days from the first clutch of eggs spawned (modified from Jeyaraj & Santhanam, 2013). Dead males were replaced with live ones whenever found.

### Reproductive parameters

The following parameters were observed: hatching success (HS), the percentage of successfully hatched nauplii from each clutch; clutch size (CS), the total number of eggs in a particular clutch produced by an ovigerous female; latency time (LT), the number of days between the hatching of a clutch of eggs and the spawning of the next clutch; inter-clutch duration (ICD), the time interval between the spawnings of two consecutive clutches; and egg-production rate (EPR), the number of eggs produced by each female per day determined using the quotient CS/ICD for each clutch of each individual. Nauplii that emerged within three days of the first hatching per clutch were fixed with 70% ethanol and stained with Rose Bengal for counting (based on a modification of Ask *et al.*, 2006). The fecundity (F) of a female was quantified as the total number of eggs it produced during the study period.

**Table 1.** Mean and standard deviations (SD) of reproductive parameters in *Arctodiaptomus dorsalis* reared under four different food concentrations; CS, clutch size (eggs $clutch^{-1}$); LT, latency time (days) (* no data for the 4.0 × $10^3$ food concentration); HS, hatching success (%); ICD, inter-clutch duration (days); EPR, egg production rate (eggs $female^{-1}$ $day^{-1}$).

| | Food concentration (cells ml–1) | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 4 × $10^3$ | | | 5 × $10^4$ | | | $10^5$ | | | 2 × $10^5$ | | |
| Parameters | Mean | SD | *N* | Mean | SD | *N* | Mean | SD | *N* | Mean | SD | *N* |
| No. of pairs | | | 1 | | | 4 | | | 5 | | | 4 |
| HS (%) | 13.64 | | 17 | 39.67 | | 149 | 44.60 | | 154 | 50.74 | | 296 |
| CS | 8.50 | 2.50 | 2 | 9.31 | 3.33 | 16 | 8.11 | 4.52 | 19 | 10.57 | 3.13 | 28 |
| EPR | 3.00 | 0.00 | 1 | 3.83 | 2.54 | 12 | 5.33 | 3.59 | 15 | 7.54 | 4.17 | 24 |
| ICD | 2.00 | 0.00 | 1 | 2.92 | 1.38 | 12 | 2.20 | 1.33 | 15 | 1.71 | 0.73 | 24 |
| LT | – | – | – | 1.58 | 1.08 | 12 | 1.10 | 0.69 | 15 | 0.71 | 0.35 | 24 |

### *Statistical analyses*

Significant differences in each reproductive parameter (CS, HS, EPR, ICD, and LT) among the food concentrations were analysed with a Kruskal-Wallis test, followed by a post-hoc Dunn's method. when the results of the Kruska-Wallis test indicated a significant difference. Values for F were tested using a one-way ANOVA with a post hoc Tukey's pairwise test. All statistical analyses were made using SigmaPlot (Version 13.0, Systat Software, San Jose, CA, USA; www.systatsoftware.com).

## RESULTS

The effects of food concentration on the reproductive parameters of *A. dorsalis* are summarized in Table 1. HS varied from 13.64% to 50.74%, and CS from 8.50 to 10.57 eggs clutch$^{-1}$. Although increasing trends were found in both HS and CS (Fig. 1A, 1B), Kruskal-Wallis tests showed no significant differences for both parameters among food concentrations (Table 2).

For EPR, ICD and LT, only data from the food concentrations of 5 × 10$^4$, 10$^5$, and 2 × 10$^5$ cells ml$^{-1}$ (Fig. 1) were analysed because only one individual was able to produce eggs at the 4 × 10$^3$ cells ml$^{-1}$ concentration. EPR increased from 3.83 to 7.54 eggs d$^{-1}$ with increasing food concentration (Fig. 1C), and the difference was statistically significant (Table 2) between food concentrations of 5 × 10$^4$ and 2 × 10$^5$ cells ml$^{-1}$ (Dunn's method $Q = 2.96$, $p < 0.05$).

There was a significant decrease in ICD (Fig. 1D), from 2.92 to 1.71 d, with food concentration (Table 2). The period between the hatching of the eggs in a clutch and the spawning of the next clutch of eggs especially shortened between the 5 × 10$^4$ and 2 × 10$^5$ cells ml$^{-1}$ food concentrations ($Q = 2.26$, $P < 0.05$).

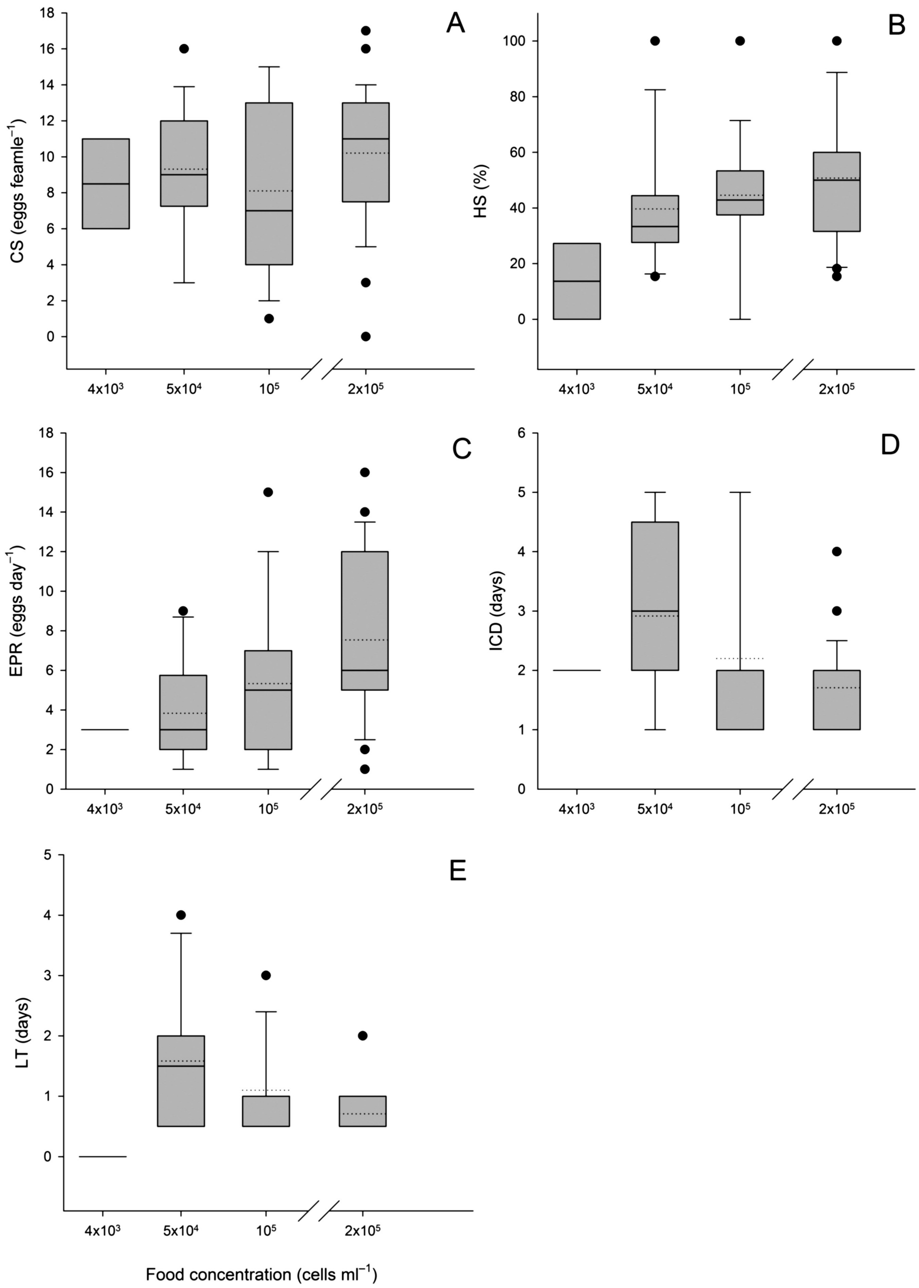


**Figure 1.** Reproductive parameters of *Arctodiaptomus dorsalis* maintained in increasing food concentrations (cells ml$^{-1}$) at constant temperature of 30 °C. Dotted lines represent mean values, solid lines median values. Only one individual successfully produced clutches at the lowest food concentration (**C**, **D**, and **E**).

A significant decrease from 1.58 to 0.71 d was also observed for LT (Table 2, Fig. 1E), with the most substantial difference occurring between concentrations of $5 \times 10^4$ and 2 x $10^5$ cells $ml^{-1}$ ($Q = 2.47$, $P < 0.05$).

The mean fecundity (F) of *A. dorsalis* steadily increased from 3.4 to 59.2 eggs $female^{-1}$ with increasing food concentration (Fig. 2), reaching a maximum of 104 eggs produced in nine clutches for one individual fed on $2 \times 10^5$ cells $ml^{-1}$. There was a significant difference among the *Chlamydomonas* concentrations (ANOVA, $df = 19$, $F = 3.242$, $P < 0.05$), particularly between the $4 \times 10^3$ and $2 \times 10^5$ cells $ml^{-1}$ concentrations (Tukey's Pairwise Test, $q = 4.408$, $P < 0.05$). Only one female produced eggs at the lowest food concentration.

## DISCUSSION

*Arctodiaptomus dorsalis* produced more eggs per day at shorter intervals at higher food concentrations. This sharp increase in mean fecundity is the result of more eggs being produced at higher food concentrations, despite the sizeable but statistically insignificant variation in clutch size. These results suggest that oocyte maturation and subsequent egg production of *A. dorsalis* was positively affected by food concentration, in agreement with previous studies on other planktonic copepods (Uye, 1981; Ban, 1994; Hirche *et al.*, 1997; Ohs *et al.*, 2010; Jiménez-Melero *et al.*, 2012; Jeyaraj & Santhanam, 2013; Liu *et al.*, 2015). Elmore (1983) suggested that at the most inadequate food levels, *A. dorsalis* was unable to reproduce. We observed such a situation at the $4 \times 10^3$ cells $ml^{-1}$ concentration and suggest that this is the approximate low incipient limiting concentration for successful reproduction in this species. Furthermore, since egg production incurs a significant energy cost (Jónasdóttir, 1994), females may require more time to feed during conditions of low food concentration in order to save enough energy for reproduction (Jiménez-Melero *et al.*, 2012).

**Table 2.** Kruskal-Wallis test results on the different reproductive parameters measured in the rearing of *Arctodiaptomus dorsalis* under four different food concentrations. No significant differences were found for egg production rate (EPR), inter-clutch duration (ICD), and latency time (LT) at $4 \times 10^3$ cells $ml^{-1}$ because only one individual was able to produce clutches, and was only able to do so twice. Multiple comparison tests using Dunn's method showed significant difference between $5 \times 10^4$ and $2 \times 10^5$ for EPR, ICD, and LT. CS, clutch size; HS, hatching success (%).

| Parameters | df. | H | *P* |
|---|---|---|---|
| CS | 3.00 | 4.03 | > 0.05 |
| HS | 3.00 | 7.76 | > 0.05 |
| EPR* | 2.00 | 7.14 | 0.03 |
| ICD* | 2.00 | 7.19 | 0.03 |
| LT* | 2.00 | 8.39 | 0.01 |

*Significant difference at < 0.05 level

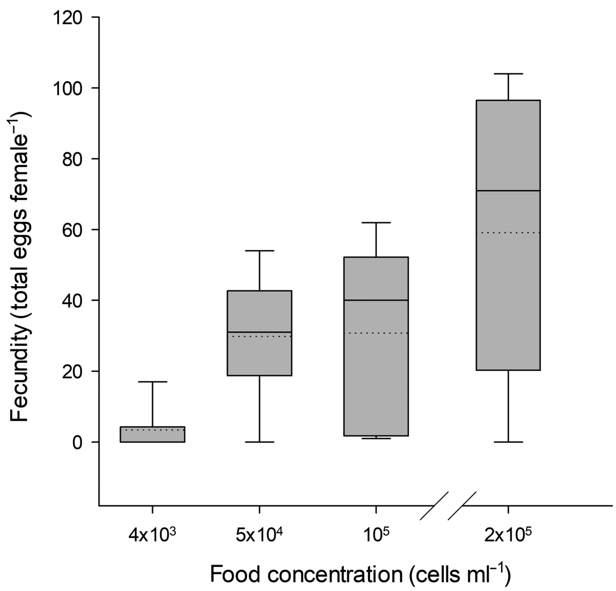


**Figure 2.** Fecundity of *Arctodiaptomus dorsalis* in increasing food concentrations. Dotted lines represent mean values; solid lines represent median values.

Clutch size was not significantly affected by the concentration of food, contrary to studies on other planktonic crustaceans (Hopcroft & Roff, 1996; Amarasinghe *et al.*, 1997; Liu *et al.*, 2015). A decrease in clutch size under low food concentration has been observed in *Arctodiaptomus salinus* (Daday de Deés, 1885) (Jiménez-Melero *et al.*, 2012). The clutch sizes of *A. dorsalis* we observed were considerably smaller than those reported by Elmore (1983), even though the algal food used was the same, and concentrations of $10^5$ cells $ml^{-1}$ and $2 \times 10^5$ cells $ml^{-1}$ were beyond the incipient limiting concentration. The surprisingly slight increase in hatching success when compared to that of other copepods (Irigoien *et al.*, 2002; Ask *et al.*, 2006) could be due to the direct relationship of this reproductive parameter with temperature (Tordesillas *et al.*, 2016).

The presence of *Chlamydomonas* in Philippine lakes such as Laguna de Bay (Tamayo-Zafaralla *et al.*, 2002; Cuvin-Aralar *et al.*, 2004), Lake Taal (Perez *et al.*, 2008; Papa & Mamaril, 2011), and Lake Lanao (Lewis, 1978) has been well documented, suggesting that this alga is available as a food source for *A. dorsalis* in these lakes, where the copepod has also been reported (Tuyor & Baay, 2001; Papa *et al.*, 2012a, 2012c; Metillo *et al.*, 2014). Although *C. rheinhardtii* has been used as food for the culture of *A. dorsalis* in previous studies (Elmore, 1982, 1983; Tordesillas *et al.*, 2016), the nutrient quality of mixtures of different species of algae have been regarded as better for the culture of copepods (Støttrup, 2006; Jeyaraj & Santhanam, 2013) and to have positive effects on clutch size (Jónasdóttir, 1994), hatching success (Guisande & Harris, 1995), egg-production rate (Makino & Ban, 2000), and inter-clutch duration (Caramujo & Boavida, 1999). The nutrient content of algal food should be considered in any future studies since it can be a limiting factor in the reproduction of copepods (Jónasdóttir, 1994; Chaudron *et al.*, 1995; Koski & Kuosa, 1999), and could affect the results of laboratory experiments.

Our relatively limited knowledge of the reproduction of tropical calanoid copepods (Elmore, 1982; Amarasinghe *et al.*, 1997) makes it difficult to make comparisons with similar species, most especially from southeastern Asia. But based on the study by Papa (2012a) lakes formerly occupied by Philippine endemic calanoids such as *Filipinodiaptomus insulanus* (Wright, 1928) and *Tropodiaptomus* spp. have been replaced by *A. dorsalis*, it seems that eutrophication plays a role, as observed by Elmore (1983). Because there is no knowledge of the feeding and adaptations to eutrophication of endemic species of calanoid copepods, it is still unclear whether the increase in algal densities gave *A. dorsalis* an advantage over endemics in terms of reproductive potential, or proved to be a disadvantage to oligotrophic to mesotrophic endemics, allowing *A. dorsalis* to occupy vacated niches. Nevertheless, the naturally eutrophic waters of Philippine lakes (Ong *et al.*, 2002), with nutrient input from anthropogenic sources (Metin, 2005), could have provided the right food conditions for *A. dorsalis* to successfully establish populations in Philippine inland waters and for its spread throughout the country.

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