

Response of *Chrysoperla nipponensis* (Okamoto) (Neuroptera: Chrysopidae) Under Long and Short Photoperiods

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Abstract

Photoperiod is an important factor influencing many biological processes including population dynamics of many insect species in temperate zones. To determine the population response of *Chrysoperla nipponensis* under altered conditions (high temperature and short photoperiod) and to test whether the short photoperiod was suitable for artificial storage, the life table data of *C. nipponensis* were collected at 25°C under a long photoperiod, 15:9 h (L:D), and a short photoperiod, 9:15 h (L:D) and analyzed using the age-stage, two-sex life table approach. We found that *C. nipponensis* developed faster under the long photoperiod than under the short photoperiod. The shorter developmental time, higher fecundity, and higher proportion of females found during the long photoperiod resulted in higher intrinsic and net reproductive rates, but a shorter mean generation time and life expectancy compared to those reared during the short photoperiod. Individuals reared under the short photoperiod also had a high reproductive value. Population projection demonstrated that *C. nipponensis* reared at the long photoperiod would complete four generations in 150 d, while reared under the short photoperiod would just be entering the second generation. Our results demonstrated that the different fitness values obtained for *C. nipponensis* individuals by varying photoperiod lengths, were readily distinguishable when using the age-stage, two-sex life table. **High winter temperatures would be detrimental to a diapausing population, and diapause induced by the short photoperiod would be beneficial to the storage of natural enemies.**

Key words: two-sex life table, photoperiod, *Chrysoperla nipponensis* (Okamoto)

Many organisms, including insects, react to seasonal changes by adaptive responses in their development and reproduction (Wilde 1962, Tauber et al. 1986, Danks 1987, 1994, Nelson et al. 2010). Insects are ectothermic organisms that are affected by numerous seasonal and diurnal changes under abiotic conditions, of which photoperiod is the most predictable and probably the most important physical variable of nature. It is well known that photoperiodic signals can be responsible for inducing environmental tolerances in insects to upcoming deleterious seasonal conditions (Koštal 2011). The photoperiod-sensitive stage varies in different insect species (Danks 1987), short day length often induces diapause, while a lengthening photoperiod may lead to uninterrupted development and reproduction (Veerman 2001). The photoperiodic response, however, is a complex event entailing a series of physiological and behavioral processes. The effects of shortened photoperiods on insects have been studied in various ways, Howarth and Duman (1983) showed that shortened day length can enhance cold tolerance

in *Dendroides canadensis* Latreille beetles, while Hodková et al. (1999) showed that short photoperiod changed the cell membrane phospholipid composition of *Pyrrhocoris apterus* (L.). Short photoperiod can also increase food conversion efficiency (Doležal et al. 2007). Chen et al. (2013) also found that a short photoperiod can improve the material content (e.g., protein and glycogen) of *C. nipponensis*. Although each of these studies has been useful in determining various physiological aspects resulting from shortened photoperiods, only demographic studies are capable of revealing the overall effect of photoperiod on the survival, development, and reproduction at the population level. Previous studies also confirm that photoperiod is the most reliable external factor affecting life history timing (Bradshaw and Holzapfel 2007). The possibility of climate change increasing winter temperatures caused us to examine the negative effects that a shortened photoperiod and elevated temperature would have at the population level of a species in nature. Understanding how the population might fluctuate under these

conditions and whether these conditions were ultimately harmful to the species survival were the essence of our investigation.

Larvae of the cosmopolitan family Chrysopidae (Neuroptera) are known to be predators of plant-sucking insect pests and have also served as valuable indicator species in ecological assessments of natural and semi-natural habitats (Stelzl and Devetak 1999). *Chrysoperla nipponensis* (Okamoto) is a common and important natural enemy of agricultural and forest pests in China that has been successfully mass-reared for use in biological control programs (Xu et al. 1999). As in *Chrysoperla carnea* and other *Chrysoperla* species that undergo reproductive diapause (Tauber et al. 1993, Chang et al. 1995), *C. nipponensis* overwinters in the adult stage (Xu et al. 2002). In the field, adults began to enter diapause from late October, with the reproductive diapause ending in late March when the daylight is lengthening (Xu et al. 1999). Xu et al. (2004) found that, the adult stage was the most sensitive stage for diapause induction while the third instar and prepupal stages were more sensitive to photoperiodic change than other immature stages; the critical photoperiod of *C. nipponensis* was between 12.5L-11.5D and 13L-11D. Diapause is a genetically inherited behavior controlled by photoperiod and regulated by temperature (Philogène 2008). Reproductive diapause can extend an insect's lifespan and delay the oviposition period. The focus of the present research was to determine if a shortened light treatment (9L: 15D) has a detrimental impact on the *C. nipponensis* population.

To illustrate the effect of photoperiod on the demographic traits of *C. nipponensis*, raw life table data of *C. nipponensis* under short (9L:15D) and long (15L:9D) photoperiods were collected and analyzed using the age-stage, two-sex life table, to compare the development, survival rate, fecundity, life expectancy, reproductive value, and population projection in order to determine the effects of photoperiod at the population level. The age-stage, two-sex life table, which is unique because it includes both sexes as well as variable development rates among individuals, is an ideal tool for studying population dynamics (Chi and Liu 1985, Chi 1988). To date, it has been used on a number of diverse insect species, including the sweetpotato weevil (Reddy and Chi 2015), *Aphis fabae* (Akca et al. 2015), coccinellid species (Mou et al. 2014), etc. Because traditional life table research is extremely time- and labor-intensive, making replication impractical, most past researchers have ignored stage differentiation, and have also excluded the contribution that male individuals make to the population, instead using sex ratio to calculate the "female" offspring, and this practice has inevitably resulted in errors in their life table analysis and interpretation (Huang and Chi 2012, Yu et al. 2013, Akca et al. 2015). Survival rate and fecundity data from the age-stage, two-sex life table can be used to predict population emergence trends (Tuan et al. 2014a, Reddy and Chi 2015, Saska et al. 2016) – a parameter critical to predicting behavior of groups exposed to unfavorable environments.

The two major questions we hoped to solve with this research were: 1) what would be the overall developmental trend when a population experiences an unfavorable environment change such as elevated temperatures combined with a shortened photoperiod; 2) the lacewing goes into reproductive diapause in response to the shortened photoperiod and delay their oviposition period, we hoped to determine whether it would be appropriate to subject these predators to shortened photoperiods when they were being mass-stored. The results would provide an academic bases and reference for overwintering protection and mass artificial storage of reproductive diapausing predatory insects such as *C. nipponensis*.

Materials and Methods

Insects

C. nipponensis adults were collected in May 2010 from a plant nursery in Taian, Shandong Province, China (36°15' N, 116°59' E). Adults were paired in glass cylinders (18 cm high, 9 cm in diameter) and supplied with a dry powdered mixture of yeast-sugar (yeast: sugar = 10: 8) and a 10% honey-water solution as food. The cylinders were kept in an environmental chamber (RSZ Artificial Intelligence Phytotron, Changzhou, Jiangsu, China) set at a photoperiod of 15:9, with constant 25 °C temperature and 60% humidity. Eggs were collected daily and the larvae reared individually on *Aphis craccivora* Koch in glass tubes (2 cm in diameter, 7 cm in length) under the above conditions. After two generations, eggs laid within a 24 h period were collected from the same 10 pairs and randomly divided into two groups for the life table studies. During the life table study, the two groups were simultaneously kept in a separate environmental chamber (LRH-150-G Illuminating Incubator, Medical Apparatus Factory, Guangdong province, China) set at 25 °C and the designated photoperiod (L:D = 15:9 or L:D = 9:15). A total of 189 eggs were used for the long photoperiod life table study, while 55 eggs were used in the short photoperiod study. Larval mortality and development were recorded daily. Newly emerged adults were paired and reared using the procedure described above. The daily survival and fecundity were recorded until the death of all individuals.

Life Table Analysis

Life history raw data were analyzed using the age-stage, two-sex life table theory (Chi and Liu 1985) and the method described by Chi (1988). The age-stage specific survival rate (s_{xj} , where x = age and j = stage) is the probability that a newborn individual will survive to age x and stage j . The age-stage specific fecundity (f_{xj}), the age-specific survival rate (l_x), the age-specific fecundity (m_x), the life expectancy (e_{xj}) (the lifespan that an individual of age x and stage j is expected to achieve) and the reproductive value (v_{xj}) (the contribution of individuals at age x and stage j to the future population), were calculated according to the method described by Chi and Su (2006). The following population parameters were calculated: r , intrinsic rate of increase, λ , finite rate of increase, R_0 , net reproduction rate, and T , the mean generation time. The net reproductive rate was calculated as:

$$R_0 = \sum_{x=0}^{\infty} l_x m_x \quad (1)$$

The cumulative net reproductive rate R_x was calculated as:

$$R_x = \sum_{i=0}^x l_x m_i \quad (2)$$

The intrinsic rate of increase was estimated using the iterative bisection method from the Euler-Lotka formula:

$$\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1 \quad (3)$$

with age indexed from 0 (Goodman 1982). The finite rate (λ) was calculated as $\lambda = e^r$. The mean generation time is defined as the period of time that a population needs to increase to R_0 -fold of its initial size (i.e., $e^{rT} = R_0$ or $\lambda^T = R_0$) at the stable age-stage distribution and was calculated as $T = (\ln R_0)/r$. The bootstrap method (with 200, 000 bootstraps) was used to achieve precise estimates of the variance and standard errors of the developmental time, survival

Table 1. Developmental time and preadult survival (mean \pm SE) of *C. nipponensis* at 25°C under short (L: D=9: 15 h) and long (L:D= 15: 9 h) photoperiods

Statistics	Long photoperiod		Short photoperiod		P
	n	Mean \pm SE	n	Mean \pm SE	
Egg duration (d)	189	3.99 \pm 0.005	55	4.0 \pm 0.0	0.631
1st instar duration (d)	156	3.21 \pm 0.07	50	4.36 \pm 0.14	<0.0001
2nd instar duration (d)	139	2.70 \pm 0.06	46	3.43 \pm 0.18	<0.001
3rd instar duration (d)	115	3.79 \pm 0.11	44	4.04 \pm 0.17	0.219
Prepupal duration (d)	109	3.31 \pm 0.08	44	3.66 \pm 0.18	0.072
Pupa duration (d)	62	4.76 \pm 0.09	33	6.09 \pm 0.24	<0.0001
Preadult survival rate (s_d)	189	0.328 \pm 0.034	55	0.600 \pm 0.066	<0.001

Standard errors were estimated by using 200,000 resampling. Differences between two treatments were compared by using paired bootstrap test.

rate, fecundity, and population parameters. Differences between treatments were examined by using the paired bootstrap test based on the confidence interval of differences (Efron and Tibshirani 1993, Yu et al. 2013, Akca et al. 2015, Polat Akköprü et al. 2015). The TWOSEX-MSChart computer program (available at <http://140.120.197.173/Ecology>) was used in the analysis (Chi 2016).

Population Projection

Survival rate and fecundity data were used to predict population growth according to Chi and Liu (1985) and Chi (1990). The computer program TIMING-MSChart (<http://140.120.197.173/Ecology>) used in this projection (Chi 2016) is also available at the above-mentioned web site.

Results

The development durations of different stages of *C. nipponensis* under the long and short photoperiods are shown in Table 1. The developmental durations of the first and second instars reared under short photoperiod were significantly longer than those reared under long photoperiod, but no differences were found in the third instar and prepupal stage. At the short photoperiod, the pupal stage was significantly longer than it was during the long photoperiod. The adult pre-oviposition period (APOP), total pre-oviposition period (TPOP), and adult longevity were all significantly longer in the short photoperiod than those from the long photoperiod (Table 2). On average, females produced significantly less eggs when reared under the short photoperiod than under the long photoperiod, although no significant differences ($P = 0.08803$) were noted in the oviposition-days in the two treatments.

In the long photoperiod treatment, 62 adults (40 females and 22 males) successfully completed development from the 189 eggs used at the beginning of the life table study, while in the short photoperiod, 33 individuals (12 females and 21 males) successfully developed to the adult stage from the initial 55 eggs. The ♀ to ♂ sex ratios resulting from the long photoperiod (1.82: 1) were slightly higher than at the short photoperiod (1: 1.75). The preadult survival rate of individuals reared under the long photoperiod was significantly lower than that under the short photoperiod (Table 1). The probabilities that an individual would survive from egg to adulthood

Table 2. The adult preoviposition period (APOP), total preoviposition period (TPOP), adult longevity, total longevity, oviposition days, and fecundity of *C. nipponensis* at 25°C at short (L: D=9: 15) and long (L:D= 15: 9) photoperiods

Statistics	Long photoperiod		Short photoperiod		P
	n	Mean \pm SE	n	Mean \pm SE	
APOP (d)	39	12.21 \pm 1.63	11	65.08 \pm 5.65	<0.0001
TPOP (d)	39	33.97 \pm 1.62	11	90.90 \pm 5.07	<0.0001
Adult longevity (d)	62	68.47 \pm 3.66	33	124.84 \pm 5.94	<0.0001
Oviposition-days (d)	39	38.05 \pm 2.71	11	27.44 \pm 5.60	0.08803
Fecundity (eggs/female)	40	298.02 \pm 32.11	12	158.68 \pm 41.51	<0.01

Differences between two treatments were compared by using paired bootstrap test.

under the long photoperiod were 21.2% for males and 11.6% for females, respectively; while the corresponding values for the short photoperiod survival were 38.2% (♂) and 21.8% (♀). Due to the variable developmental rate that occurred among individuals, there were significant stage overlaps in the survival rate (s_{xj}) during both photoperiods (Fig. 1).

During the short photoperiod, the age-specific female fecundity (f_{xj}) was substantially delayed until age 72 d compared to the 25 d required during the long photoperiod (Fig. 2). The peak value of female age-specific fecundity (f_{xj}) that occurred during the long photoperiod (7.56 eggs) was somewhat higher than the value found in the short photoperiod (6.67 eggs). Due to the higher sex ratio, the m_x curve was much closer to f_{xj} in the long photoperiod in contrast to the curve in the short photoperiod. The curve of the cumulative reproductive rate R_x was also higher for the long photoperiod than in the short photoperiod.

When the survival rates of all stages at the same age are combined, we would obtain the age-specific survival rate (l_x) (Fig. 3). The age-specific survival rate of *C. nipponensis* during the long photoperiod was lower than in the short photoperiod, while the net maternity ($l_x m_x$) started much earlier and was higher in the long photoperiod than in the short photoperiod.

The calculated life expectancy during the short photoperiod was longer than that occurring during the long photoperiod (Fig. 4). The life expectancies for a newly laid egg, newly emerged female adult, and male adult during the long photoperiod were 40, 65, and 78 d, respectively. Due to the shorter longevity and higher mortality in earlier instars during the long photoperiod, the above life expectancy values were shorter than those found in the short photoperiod 98, 117, and 134 d for a newly laid egg, newly emerged female and male adult, respectively.

The reproductive values (v_{xj}) of individuals at age x and stage j (defined as the contribution of an individual to the future population (Fisher 1930)) of *C. nipponensis*, are shown in Fig. 5. The value of v_{xj} for *C. nipponensis* reared at a long photoperiod increased to 28.92 d⁻¹ at 20 d when female adults emerged. When reared under a short photoperiod, the v_{xj} value only increased to 9.73 d⁻¹ when female emerged later at 23 d. The largest v_{xj} values (68.97 d⁻¹) occurred at 34 d when reared at a long photoperiod, and 75.45 d⁻¹ at 92 d under the short photoperiod.

The population parameters are listed in Table 3. The values for the intrinsic rate of increase (r), and finite rate of increase (λ) during the long photoperiod were higher than those from the short photoperiod (paired bootstrap test: $P < 0.001$), while the mean generation

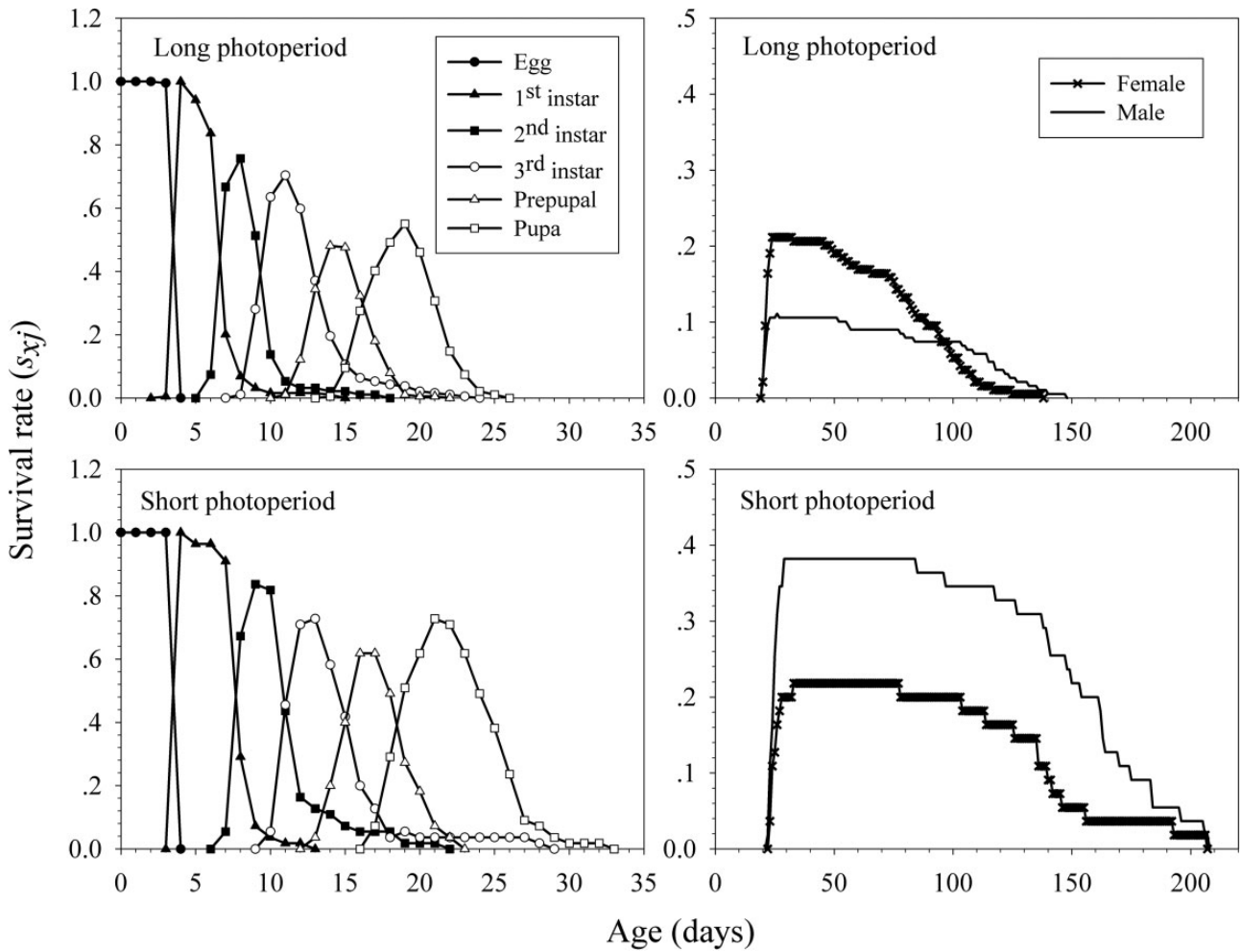


Fig. 1. Age-stage specific survival rate of *C. nipponensis* at 25°C under long (15L: 9D) and short photoperiods (9L: 15D).

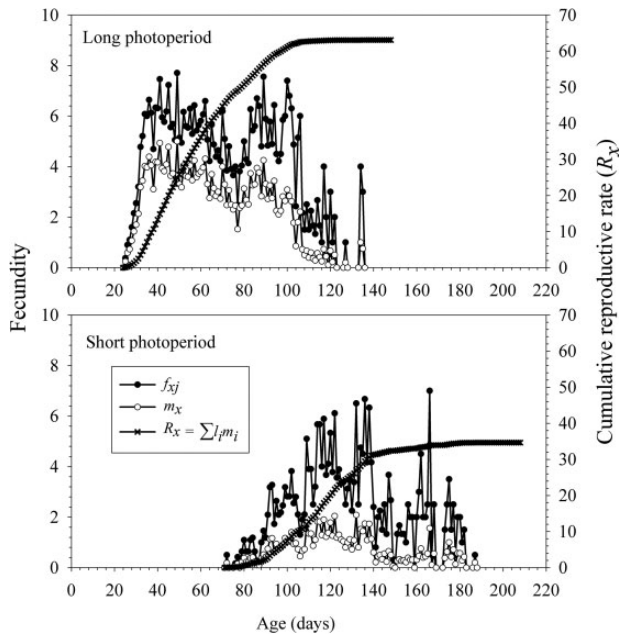


Fig. 2. Female fecundity f_{xj} (j , female), age-specific fecundity m_x and R_x of *C. nipponensis* at 25°C under long (15L: 9D) and short photoperiods (9L: 15D).

time (T) from the long photoperiod was significantly shorter than it was in the short photoperiod (paired bootstrap test: $P < 0.001$). The net reproduction rate (R_0) found for the long photoperiod was higher than in the short photoperiod, but not significantly different.

The population projection based on the basic data (s_{xj} and f_{xj}) of a life table offers a comprehensive understanding of the age and stage composition of a population during its growth. The projection for *C. nipponensis* suggested that a population would grow much faster when reared at a long photoperiod than it would at a short photoperiod (Fig. 6). Beginning with an initial 10 eggs, the population growth curves approach linearity after approximately 150 days under long photoperiod, meaning that the population can reach a “stable age” at 150 d, although populations reared under a short photoperiod did not reach a stable age. If *C. nipponensis* reared at a long photoperiod were allowed to successfully propagate for 150 days, the total population would exceed one million individuals and be in the fourth generation, while the population reared under a short photoperiod would just be entering the second generation.

Discussion

The effect of environmental factors on populations has been studied from ecological or physiological viewpoints. For example, larvae of *Sesamia nonagrioides* (Lefebvre) delayed pupation when reared under short day conditions compared to longer photoperiods (Pérez-

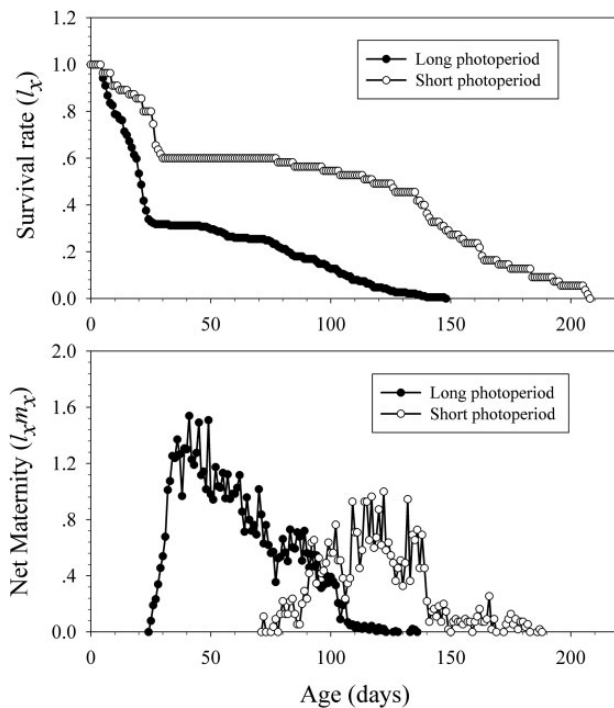


Fig. 3. Age-specific survival rate (l_x) (A) and age-specific maternity ($l_x m_x$) (B) of *C. nipponensis* at 25°C under long (15L: 9D) and short photoperiods (9L: 15D).

Hedo et al. 2011), while larvae of *Leptinotarsa decemlineata* (Say) developed faster under short-day than under long-day conditions (Doležal et al. 2007). Our results showed that a shortened photoperiod significantly extended the developmental time of the early stages of *C. nipponensis* and that the durations of the 1st and 2nd instars were significantly longer than those reared under a longer photoperiod. Although no significant differences were found between the two photoperiods in the developmental times of the third instar and prepupal stage, the total preadult developmental time under a short photoperiod was significantly longer than it was during the extended photoperiod, showing that *C. nipponensis* larvae took a longer period of time to complete their development (Table 1) during a short photoperiod. Moreover, the adult lifespan during the short photoperiod was almost doubled that of the long photoperiod as shown in Table 2. Adults also showed obvious diapause characteristics. Diapause is an adaptative strategy for survival in unfavorable environmental conditions (Suzuki et al. 1999). This extended adult longevity that occurred under the short photoperiod, however, was still nearly two months shorter than the 6-7 month-long diapause period that occurs under natural conditions (Xu et al. 2004). In Shandong, China where winter temperatures are often below 0°C coupled with a short photoperiod, green lacewings normally survive the conditions through induced reproductive diapause. The extended reproductive behavior resulting from the increased temperature will likely result in shortages of food resources, scarcity of water, etc., which would have negative consequences on the lacewing population.

Under the long (L:D = 15:9) and short (L:D = 9:15) photoperiods, the sex ratio of the stable *C. nipponensis* population was higher at the long photoperiod than it was during the short photoperiod. According to our laboratory rearing data and field sampling, we found that there were more females present during the summer, while males predominated in the autumn. Cortés et al. (2008)

demonstrated the effect of photoperiod on sexual and parthenogenetic reproduction in *Acyrtosiphon pisum* (Hemiptera: Aphididae) by using a transcriptomic approach. Other studies also noted that a shortened photoperiod was a key factor for inducing parthenogenesis in aphids to produce males (Simon et al. 2002, Cortés et al. 2008). Our study showed that the excess of female *C. nipponensis* produced under long photoperiod conditions would consequently produce more offspring to achieve the highest population growth rate, while the predomination of males in the population under short photoperiod conditions would probably compensate for the high mortality rate occurring in overwintering male adults.

Photoperiod and temperature are two critical factors affecting life histories in temperate ectotherms (Śniegula et al. 2016). During winter (low temperatures and short photoperiod), the diapausing adults that would be found in protected habitats that were sheltered from the wind but exposed to the sun, survived by consuming energy stored during the fall months. During the growing season (high temperature and long photoperiod), however, the lacewing larvae actively prey and the adults feed on nectar, allowing the population to maintain itself. Our results showed that the intrinsic rate (r), net reproductive rate (R_0), and finite rate (λ) values were all higher in individuals reared during a long photoperiod than in those reared under a short photoperiod, although the mean generation time (T) was significantly shorter in the long photoperiod than in the short photoperiod. All statistical values showed significant differences between the two photoperiods (Table 3). This would imply that with increases in winter temperature, adult females would be prone to oviposit earlier to improve the intrinsic rate, net reproductive rate and finite rate, although these values would still be less than those under a long photoperiod. The inevitable result due to the expected global warming would negatively impact the population structure.

An interesting finding was that the peak reproductive value of *C. nipponensis* reared at a long photoperiod was lower than that in a short photoperiod, but the age-specific fecundity (m_x) was higher in the longer photoperiod than in the short one. A similar phenomenon has been found in other insects: Reddy and Chi (2015) noted that sweetpotato weevils reared on a normal host (*Ipomoea batatas*) have a lower peak reproductive value than those reared on an alternative host; while Saska et al (2016) found that the highest age-stage reproductive value was estimated to occur in offspring of *Metopolophium dirhodum* reared under a high concentration of glyphosate-based herbicide treatments. Since the v_{xj} is calculated using only s_{xj} and f_{xj} (Huang and Chi 2011, Tuan et al. 2014b), the high reproductive value but low fecundity may be due to the high s_{xj} value found in *C. nipponensis* during short photoperiods.

Yu et al. (2013) and Tuan et al. (2014b) demonstrated the usefulness of population projection and pest damage prediction using life tables in biological control projects. In our study, population projection was conducted for a test population response under unfavorable conditions. *C. nipponensis* reared under a long photoperiod would complete four generations by 150 d, while populations reared under a short photoperiod were only in their second generation at the end of the same time period. Similar results were reported for the sweet potato weevil. Reddy and Chi (2015) found that *Cylas formicarius* would grow much faster on the normal host than on an alternative host. *Aphis fabae* populations increased significantly faster when reared at 20 and 25°C than those at higher or lower temperatures (Akca et al. 2015).

Although the mass rearing of chrysopids initially began several decades ago (Finney 1948), the practice has been decreasing in recent years due to difficulties encountered in mass storage (Nasreen et al. 2011). The effective storage of large numbers of natural

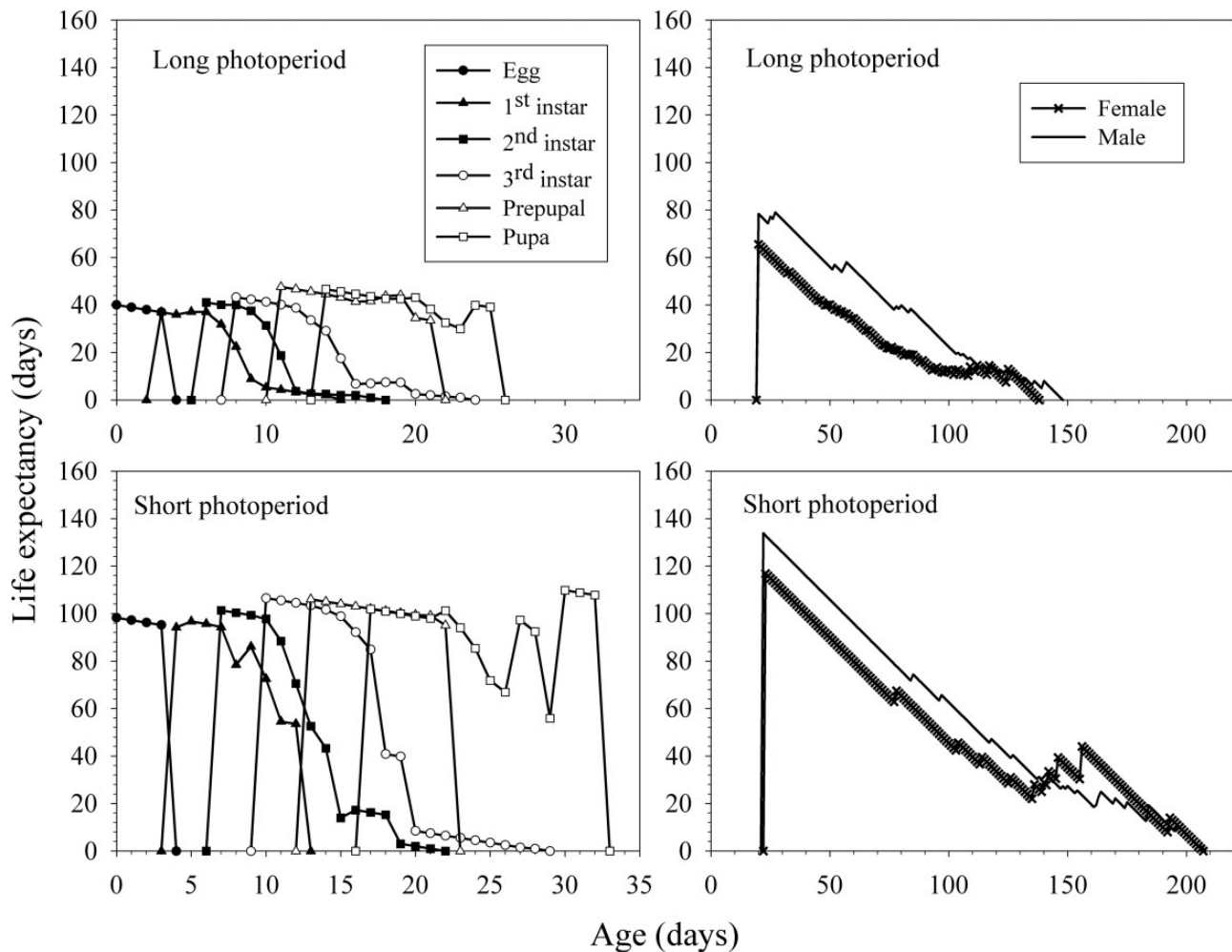


Fig. 4. Life expectancy of each age-stage group of *C. nipponensis* at 25°C under long (15L: 9D) and short photoperiods (9L: 15D).

enemies is a key factor in ensuring the mass propagation and release of the species being cultured (Tauber et al. 1993). As in other species of the genus *Chrysoperla* (Gibson and Hunter 2005), e.g., *C. carnea* (Stephens) (Porcel et al. 2011), and in most other genera e.g., *Mallada* (*basalis*) (Wu 1995, Cheng et al. 2010), larvae of *C. nipponensis* are generalist predators, while the adults feed only on nectar, honeydew, and pollen. Use of an artificial diet (such as a powdered mixture of yeast-sugar along with a 10% honey-water solution) has been found to supply adequate nutrients for rearing adult *C. nipponensis* (Hagen et al. 1970, Hagen and Tassan 1972, Gibson and Hunter. 2005), as well as providing a convenient means for mass storage of the adults.

Life table data can be used to predict population growth (Chi 1990) and to plan mass rearing of species for biological control purposes (Chi and Getz 1988). In our studies, it was demonstrated that, green lacewings have a longer developmental time (Table 1 and Fig. 1), an extended life expectancy (Fig. 4), and a prolonged preoviposition period (Table 2, Figs. 2 and 3) during a shortened photoperiod in contrast to those reared under a longer photoperiod. They also showed obvious diapause characteristics such as changes in body colour. Most green lacewings, e.g., *C. nipponensis* adults (Xu et al. 2004) are facultatively multivoltine, with the succession of generations most often regulated by photoperiod-mediated diapause (Canard 2005). A considerable amount of previous research on the induction

and termination of diapause involved a combination of the effects of photoperiod and temperature (Roditakis and Karandinos 2001, Wang et al. 2009). While an abbreviated photoperiod is a primary diapause inducer, and an extended photoperiod is capable of breaking diapause; other factors such as low temperature may also play critical roles in the initiation and cessation of diapause (Irwin et al. 2001, Teixeira and Polavarapu 2005). We studied the effect of long and short photoperiods at a constant temperature (25°C) and found that *C. nipponensis* adults exhibited diapause features under a short photoperiod that were similar to those occurring in adults overwintering in the field, although they were able to successfully oviposit without requiring an increased light period corresponding to a long photoperiod. The prolonged adult longevity and delayed reproduction in this study demonstrate that diapause in *C. nipponensis* may be induced by a short photoperiod alone. Raising the temperature even without altering the light cycle will also accelerate termination of diapause. Being able to take advantage of this phenomenon is very useful in successfully maintaining large colonies of predator species. Natural enemies can readily be induced to enter diapause by simply shortening their photoperiod. The shortened photoperiod alone will induce diapause for storage of adults, while terminating diapause prior to application can be accomplished by raising the temperature at any chosen time. The green lacewings had a higher survival rate (Fig. 1), but lower fecundity (Table 2, Figs. 2 and 3)

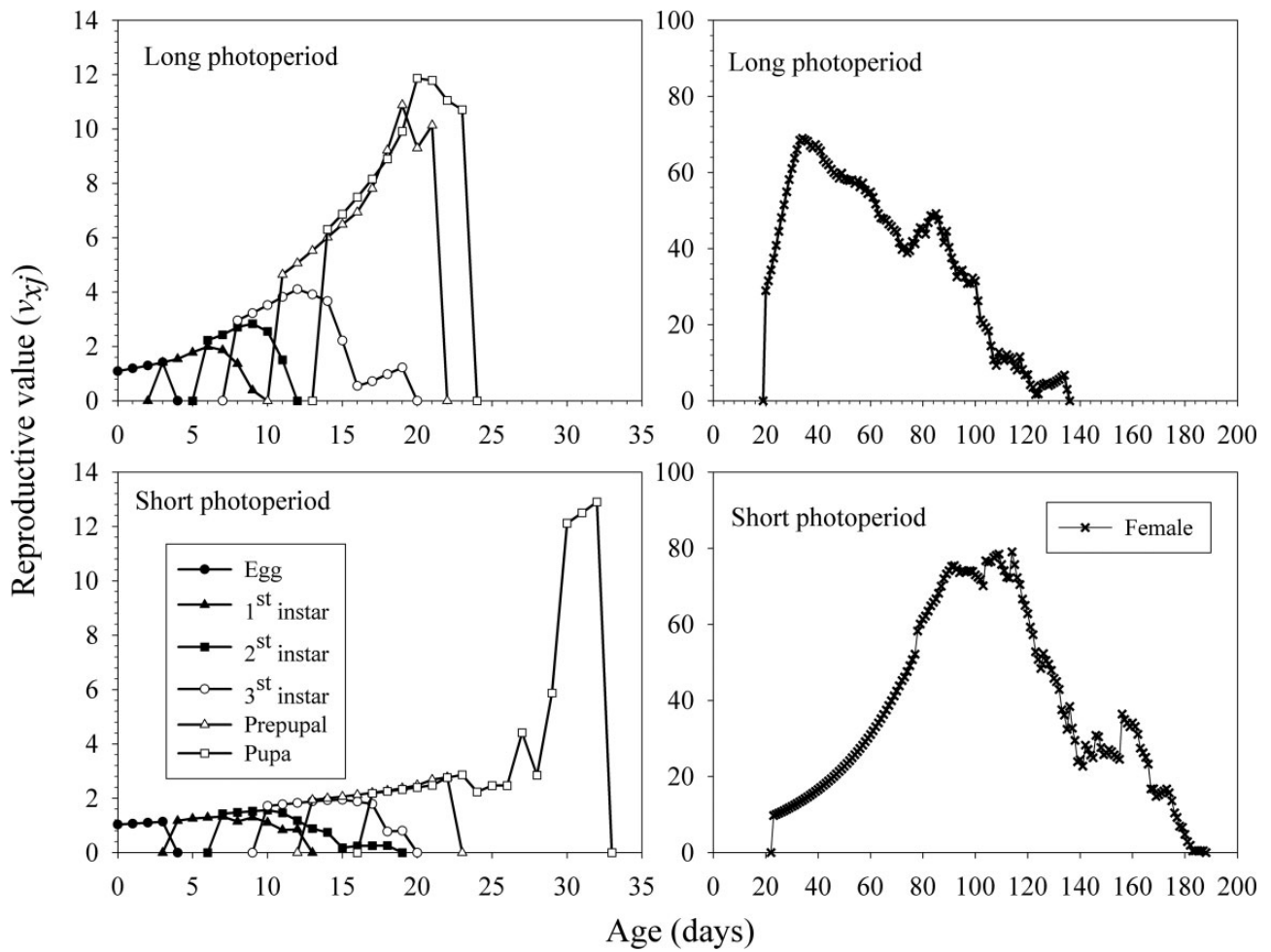


Fig. 5. Reproductive value of each age-stage group of *C. nipponensis* at 25 °C under long (15L: 9D) and short photoperiods (9L: 15D).

Table 3. Population parameters (mean ± SE) at long and short photoperiod

Parameter	Long photoperiod	Short photoperiod	P
Intrinsic rate of increase (r) (d^{-1})	0.0859 ± 0.0050	0.0306 ± 0.0041	<0.0001
Net reproduction rate (R_0)	63.06 ± 11.14	34.60 ± 12.42	0.08807
Mean generation time (T)	48.15 ± 1.77	113.73 ± 5.48	<0.0001
Finite rate of increase (λ) (d^{-1})	1.0897 ± 0.0055	1.0311 ± 0.0042	<0.0001

Standard errors were estimated by using 200,000 resampling. Differences between two treatments were compared by using paired bootstrap test.

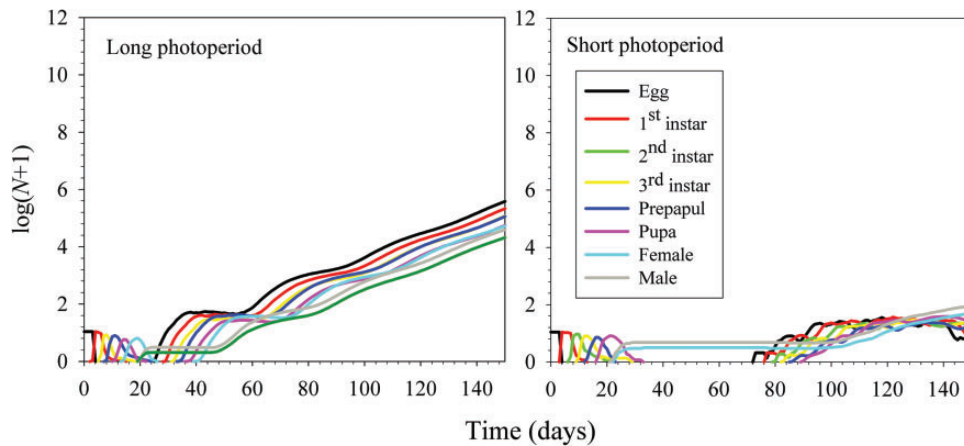


Fig. 6. Population projection of *C. nipponensis* at 25 °C under long (15L: 9D) and short photoperiods (9L: 15D).

during the shortened photoperiod in our study. The decrease in mortality during the short photoperiod, would ultimately favor growth of the population. Previous studies have found that photoperiod is an important environmental factor in optimizing the rate of egg development (Śniegula and Johansson 2010, Śniegula et al. 2016). The decrease in the m_x , R_x (Fig. 2) and $L_x m_x$ values during the short photoperiod (Fig. 3) may be a reflection of the greater male proportion in this photoperiod. The v_{xj} values in Fig. 5 demonstrate that individuals from the short photoperiod made a larger contribution than those in the long photoperiod. The intrinsic rate of increase (r) and finite rate of increase (λ) (Table 3) show that the population trend was increasing. Our study proves that it may be feasible to successfully store natural enemies using a shortened photoperiod to induce diapause. Whether this is suitable for development of offspring requires further study.

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