

## POPULATION DYNAMICS OF AN HERBIVOROUS LADY BEETLE, *HENOSEPILOACHNA NIPONICA*, IN A SEASONAL ENVIRONMENT

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### SUMMARY

(1) A population study of the thistle-feeding lady beetle, *Henosepilachna niponica*, was conducted from 1976 to 1980 at two sites along the River Ado in central Japan. Life tables were constructed for five generations at the two sites.

(2) Two basic population processes were operative: a density-independent survival process causing population fluctuations, and a density-dependent reproductive process generating marked population stability relative to the availability of food resources.

(3) Predatory arthropods were the most important cause of mortality of eggs and larvae. A high level of predation was responsible for the low adult density of one of the populations. The predation was restricted to early in the reproductive season.

(4) Seasonal adversity (heat stress in midsummer, and autumn flood) decreased the survival of newly-emerged adults but from then on adult survival up to the reproductive stage was more likely to be size- and sex-dependent.

(5) Foliage damage of thistle plants by beetle-feeding and leaf senescence was particularly clear after summer. Leaf amino acid and water contents declined from the beginning of the growing season.

(6) Seasonal change in the causes of the major mortality factors coupled with deteriorating food resources profoundly affected the demographic features and individual success from egg to the reproductive stage of the lady beetle.

### INTRODUCTION

Environmental variability and unpredictable resources are of paramount importance in insect population dynamics (Wilbur, Tinkle & Collins 1974; Southwood *et al.*, 1974; Roff 1974; Levin 1976; Southwood 1977; May 1979; Hassell 1980). The most significant and widespread aspect of habitat heterogeneity is seasonality (Fretwell 1972). Such seasonal habitat changes have also been recognized as important selective pressures producing definite sets of life history patterns of organisms (Boyce 1979; Taylor 1981; Tauber & Tauber 1981; Roff 1983).

Nevertheless, very few field studies have explored the consequences of seasonal heterogeneity of habitats for insect population dynamics throughout the whole lifetime. Many authors have used key-factor analyses and associated techniques for analysing natural populations (Varley & Gradwell 1960, 1970; Varley, Gradwell & Hassell 1973; Podoler & Rogers 1975), in which overall mortality caused by a particular factor is usually divided and examined separately for different developmental stages. However, individuals in the same stage are unrealistically assumed to be exposed to identical mortality levels and

resource conditions. Thus, it is difficult to interpret the precise roles of environmental seasonality on population dynamics using conventional techniques.

Since 1976 I have compared several local populations of a thistle-feeding lady beetle, *Henosepilachna niponica* (Lewis) living in different habitats (Ohgushi & Sawada 1981, 1984, 1985a, b; Ohgushi 1983). Nakamura & Ohgushi (1981) suggested the importance of inter-patch dispersal and density-dependent reduction in fecundity as possible regulatory mechanisms of the lady beetle population in a temperate climax forest. Furthermore, Ohgushi & Sawada (1985a) revealed that the behavioural response of ovipositing females to the availability and condition of food resources is a causal mechanism responsible for population persistence in dynamic equilibrium with the available food supply. However, impacts of seasonally changing mortality factors and available food resources on the herbivore population dynamics have still remained unsolved.

The main purposes of this paper are (i) to determine the basic population processes affecting change and stability; (ii) to evaluate seasonal changes in major mortality factors and available food supply; and (iii) to clarify how the seasonally changing habitat variables determine demographic parameters and individual fitness.

## STUDY AREA

Ohgushi & Sawada (1981) studied this lady beetle at six sites (A–F) in five valleys along the River Aso and its tributary, the River Aso, in north-western part of Shiga Prefecture in central Japan. I report here on the results of a 5-year investigation at site A and site F which are representative of downstream and upstream habitats, respectively. Each study site is described fully in Ohgushi & Sawada (1985a).

## MATERIALS AND METHODS

*Henosepilachna niponica* is usually univoltine. It feeds exclusively on leaves of the thistle, *Cirsium kagamontanum* (Nakai), in the study area. Seasonal occurrences of immature and adult populations are given in Ohgushi & Sawada (1981, 1984).

The census was performed at intervals of 1–3 days from early May to early November during 1976–80, as described in Ohgushi & Sawada (1985a).

### *Estimation of population size*

#### *Egg*

The number of eggs that hatched from labelled egg batches was evaluated by counting the empty egg shells that still remained on the leaves after hatching. Eggs cannibalized by adults or larvae were recognizable by the basal remains of egg shells on the leaves. Egg predation by the earwig, *Anechura harmandi* (Burr), was recognized by the characteristic remains of egg shells on the leaves. Some eggs failed to hatch and remained blackened and shrivelled: this was referred to as 'miscellaneous' mortality.

#### *Larva and pupa*

Only fourth instar larvae could be counted. The total numbers reaching the medial age of fourth instar larval and pupal stages were estimated using the method of Southwood & Jepson (1962). Larvae parasitized by the parasitic wasps, *Watanabeia afissae* (Watanabe)

(Eulophidae) or *Pediobius foveolatus* (Crowford) (Proctotrupidae) were easily recognized by the characteristic larval corpses that remained on the leaves.

#### *Adult*

Adult populations were studied by mark–release–recapture experiments. Sex, body length, and capture history at each time and place were recorded for individual beetles, and newly-marked adults were immediately released on the thistle plants where they were captured. On following censuses, each adult was usually identified without being recaptured. Total recruits of reproductive (overwintering) and newly-emerged adults were calculated using the Jolly–Seber stochastic model (Jolly 1965; Seber 1973).

#### *Seasonal changes in leaf quality*

Seasonal changes in leaf water content and leaf amino acid levels were estimated by sampling at monthly intervals from May to November in 1982. One thistle plant was selected randomly for sampling during the season at each study site, (A1 and F1 at the respective plots). On every sampling date, two leaves from each of the lower, middle, and upper parts of the plant were bagged with ice and returned to the laboratory for analysis. Rosette leaves were added to the sampling scheme when they appeared in autumn. When plants were destroyed after a large flood on 2 August, another plant (A2 and F2) at each site, next to the test plant, was substituted. One thistle leaf at each position was weighed, oven-dried for 24 h and weighed again to give leaf water content. Another leaf was used to identify levels of leaf amino acids (mg per g dry weight) using an automatic amino acid analyser K-101 AS equipped with a column of Kyowa gel 62210-S. Total amino acid levels were determined by accumulating amounts of five dominant amino acids detected in thistle leaves: aspartic acid, threonine, serine, glutamic acid, and alanine.

### ANNUAL CHANGES IN POPULATION DENSITY

Life tables for *H. niponica* over the five generations at study sites A and F are given in Appendices 1 and 2, respectively. Before analysing the major habitat components affecting the population, it is useful to summarize how the population fluctuated relative to food abundance.

The annual changes in population density in each life stage together with their variances (as an index of the magnitude of population fluctuations) are shown in Fig. 1. By comparing observed year-to-year density fluctuations among different stages, two main points can be made. First, despite the fact that reproductive adults showed a larger population fluctuation over the five generations, egg density remained remarkably stable at both of the study sites. Second, the density fluctuations became more apparent as the life stages advanced. Ohgushi & Sawada (1985a) showed that a marked density-dependent reduction in oviposition rate was the main cause of the stabilization of egg density with respect to resource abundance. In contrast, no density-dependent mortality was detected during the period from egg to reproductive adult stage (Table 1). As a result, population density in the later stages could no longer be stabilized. This implies that two distinct processes occur in the population fluctuations of the lady beetle: one stabilizing and one disturbing. That is, on the one hand the population density was repeatedly disturbed during the egg to adult period, while on the other hand, population stability was attained in the reproductive season.

Egg densities were almost equivalent in the two local populations. However, the new

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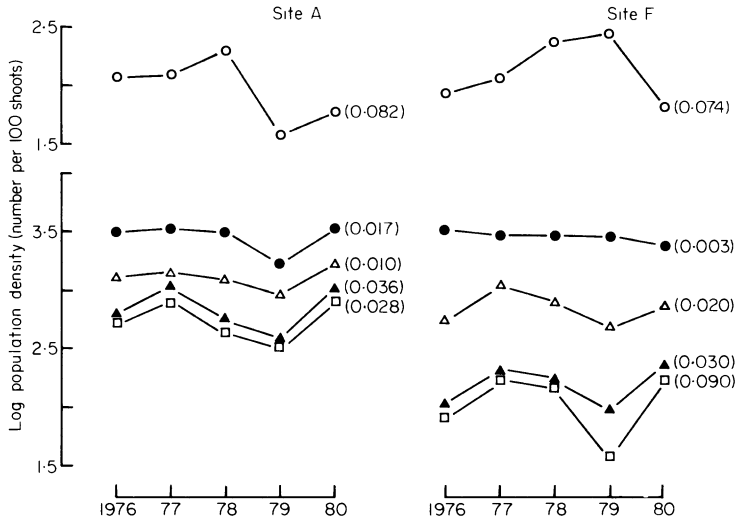


FIG. 1. Annual changes in population density (number per 100 shoots) at the downstream site A and the upstream site F for 1976–80. (○) Reproductive adults; (●) eggs; (△) newly-hatched larvae; (▲) fourth instar larvae; (□) newly-emerged adults. Variance of population densities for the 5 years is in each parenthesis.

TABLE 1. Results of linear regression analysis of submortality ( $k$ -value) on population density (log number per 100 shoots). Correlation coefficient ( $r$ ) and values of slope ( $b$ )

Stage	Site	$b$	$r$	$t$	$P$
Egg	A	0.30	0.66	1.51	N.S.
	F	1.55	0.50	1.00	N.S.
1st–3rd instar larva	A	–0.74	–0.75	1.99	N.S.
	F	–0.03	–0.05	0.08	N.S.
4th instar larva–new adult	A	0.14	0.64	1.44	N.S.
	F	–0.64	–0.75	1.93	N.S.
New adult–reproductive adult	A	–0.32	–0.35	0.64	N.S.
	F	–0.59	–0.61	1.32	N.S.

adult density of the downstream population A was significantly higher than that of the upstream population F over the study period ( $t = 4.52$ ,  $P < 0.005$  for transformed log density).

## MORTALITY FACTORS AND THEIR SEASONAL PATTERNS

*Immature stages*

Overall egg mortality at site A ranging from 46.2 to 61.2% (mean, 54.4%) was significantly lower than that at site F, ranging from 62.5 to 83.2% (mean, 74.1%) ( $t = 3.47$ ,  $P < 0.01$  for transformed log mortality). Mortality during the early larval period (1st–3rd instar) at site A was estimated as 26.5–57.0% (mean, 45.7%) compared with significantly higher mortality ranging from 68.8 to 81.6% (mean, 78.0%) at site F ( $t = 6.44$ ,  $P < 0.001$  for transformed log mortality). Mortality during the late larval and pupal stages was low and no significant difference existed between the two populations.

*Natural enemies*

Seasonal occurrences of eggs hatched and those killed by the main mortality factors at sites A and F are given in Fig. 2a,b, respectively. Most egg losses at site F were due to arthropod predation, which was responsible for a higher egg mortality of population F than of population A. Field experiments showed that arthropod predation was the most important factor causing the high mortality during the egg and early larval period at the

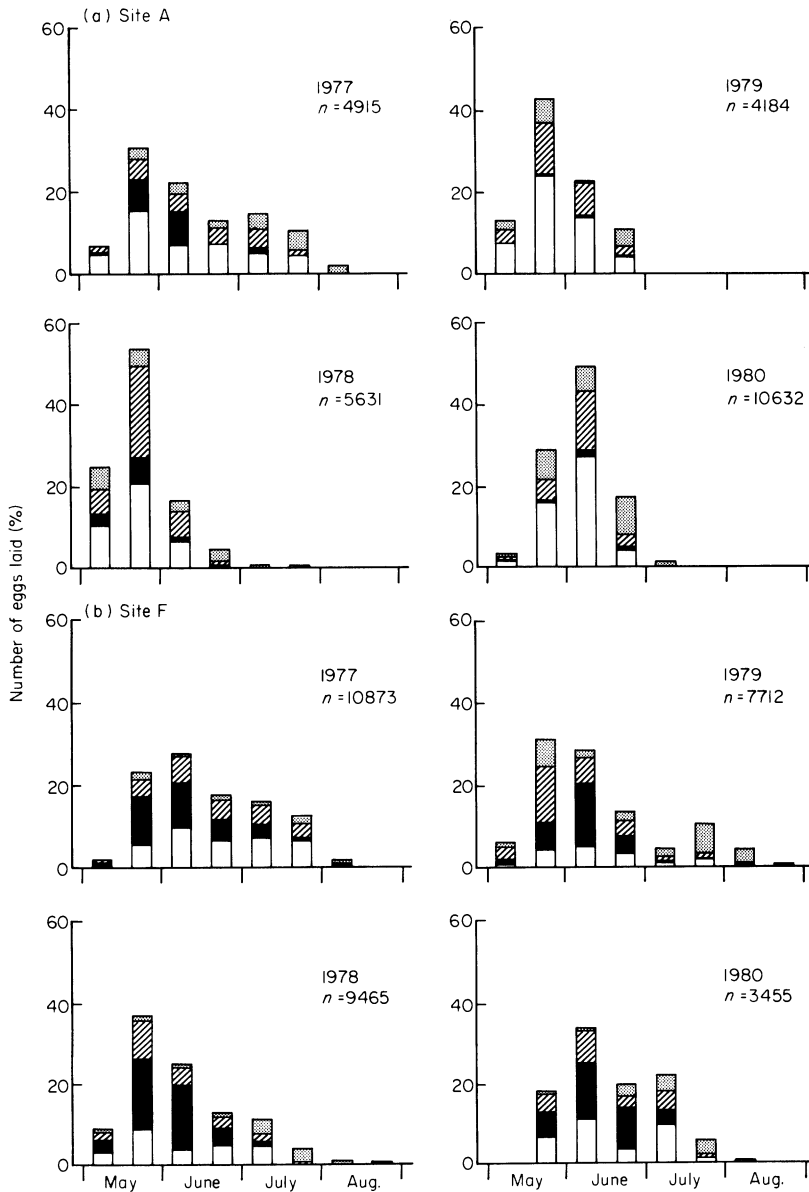


FIG. 2. Seasonal changes in numbers of eggs hatched and those killed by major mortality factors at (a) site A and (b) site F: (□), eggs hatched; (■) eggs eaten by arthropod predators; (▨) eggs cannibalized by adults or larvae; (▩) eggs shrivelled and blackened.

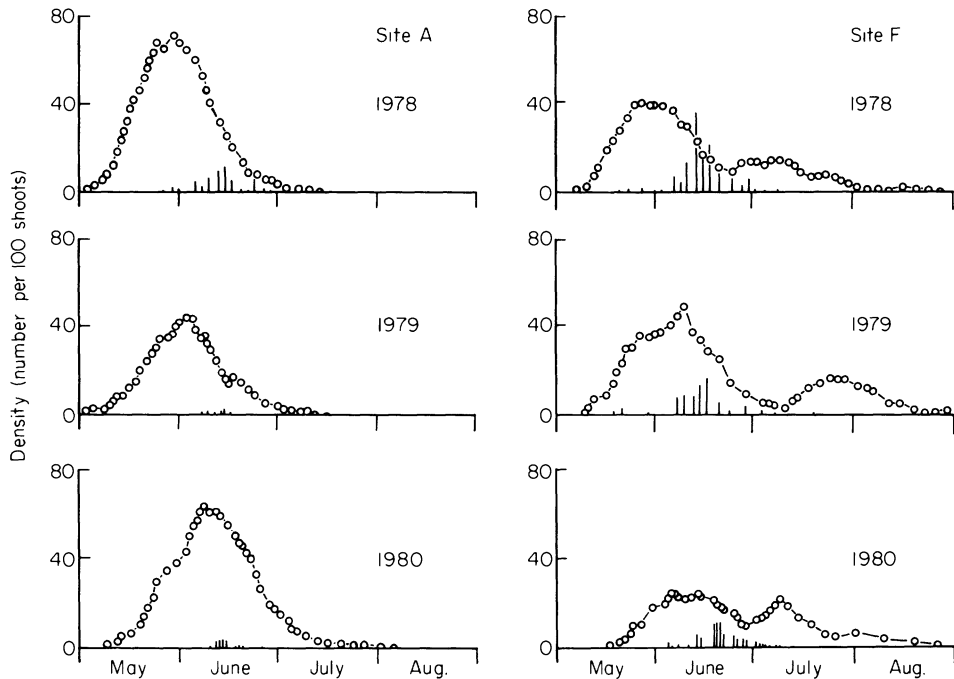


FIG. 3. Seasonal changes in density (number per 100 shoots) of egg batches (○) and earwigs (vertical bars) found on thistle plants at sites A and F.

upstream site (Ohgushi & Sawada 1985b). Earwigs, predatory bugs, and ground-beetles were identified as predators of eggs and young larvae (Appendix 3). Of these, the earwig, *Anechura harmandi* (Burr) was the most important and numerous predator here; its density on thistle plants reached a peak around mid-June (Fig. 3), corresponding with the hatching period of the lady beetle, when the earwigs were frequently observed attacking eggs and/or young larvae. The earwig density in June at site F (mean, 7.2 per 100 shoots) was significantly higher than that at site A (mean, 2.0 per 100 shoots) throughout the study period ( $t = 4.08$ ,  $P < 0.01$  for transformed log density). Meanwhile, as larvae grow, they become immune from predation by the earwig, although a few old larvae were attacked by predatory bugs (Appendix 3). Arthropod predators usually occurred early in the reproductive season, so individuals emerging late successfully escaped intense predation (Fig. 2a,b).

The percentage of larvae killed by the parasitic wasps, *W. afissae* or *P. foveolatus*, was small and independent of density, varying from 0.5 to 4.4% (mean, 2.6%) at site A and from 1.8 to 11.5% (mean, 5.6%) at site F for 1976–80.

#### Cannibalism

Adult female beetles were observed feeding on their eggs in the field on fifty-two occasions; males were not observed cannibalizing the eggs, which supports the report of Nakamura & Ohgushi (1981). Young larvae also exhibited cannibalism, frequently feeding on eggs which remained unhatched in their own egg batches. Since seasonal occurrence of egg cannibalism was synchronized with predation, egg cannibalism was more important at site A where predation was low (Fig. 2a).

*Summer stress and flood*

The percentage of egg mortality from other causes (miscellaneous) in the first half of the reproductive season was low; but became important in the later period (Fig. 2a,b). Most miscellaneous mortality was probably a consequence of unfavourable weather in midsummer, since laboratory experiments showed that most eggs died at temperatures above 30 °C (H. Sawada & T. Ohgushi, unpublished).

A large June flood in 1979 caused a great destruction of larval populations, especially at site F (Fig. 1); however, eggs and pupae were seldom washed away by the flood due to their firm attachment to the leaves.

*Adult stage*

Most adult beetles that survived up to the reproductive stage were recaptured after mid-September (Fig. 4a,b). In other words, only adults remaining alive after that point will

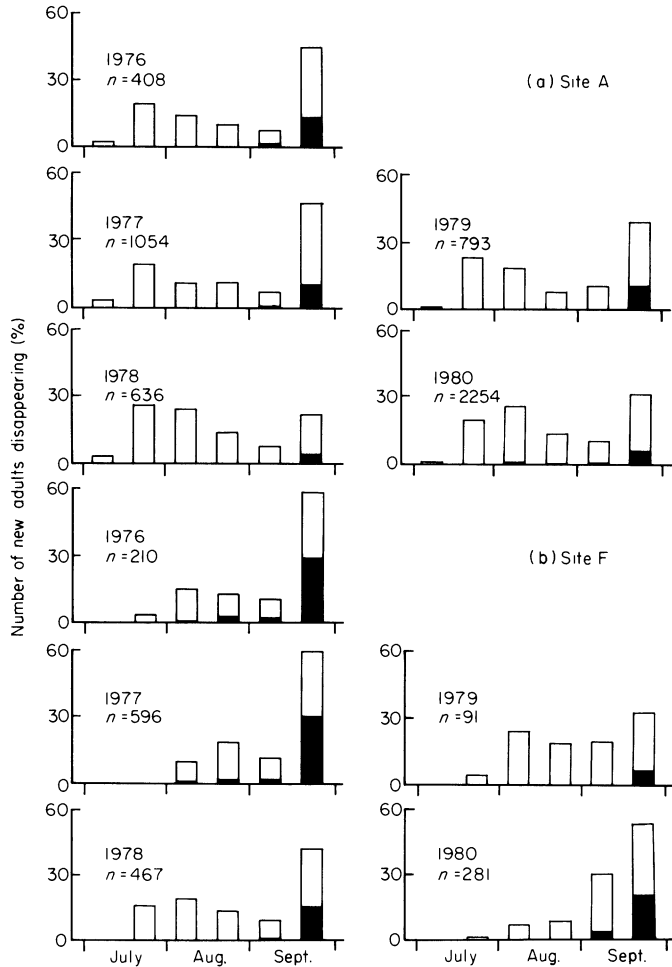


FIG. 4. The numbers of new adults disappearing (vertical bars) in each half-monthly period during the pre-hibernation stage and those surviving up to the reproductive stage in the following spring (filled bars) at (a) the downstream site A and (b) the upstream site F. The number of adult beetles in late September includes all adults which disappeared thereafter.

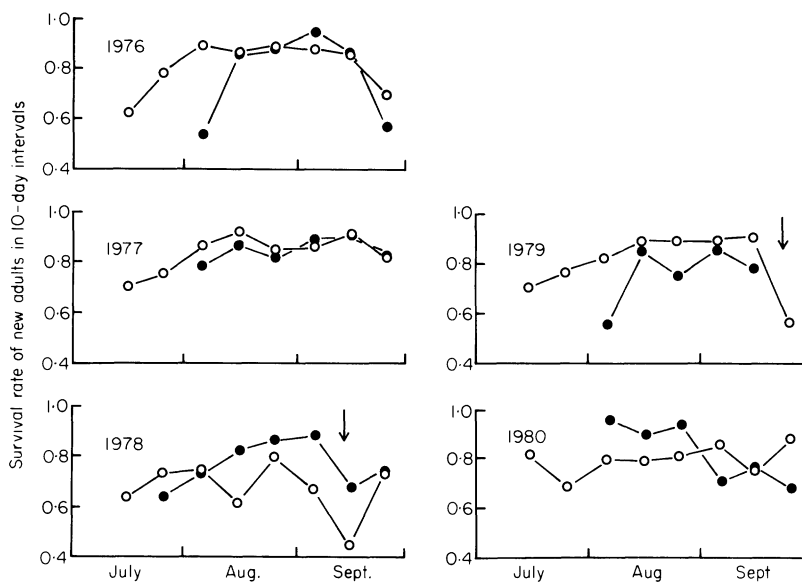


FIG. 5. Seasonal changes in adult survival in 10-day intervals during the pre-hibernating period at site A (○) and site F (●) for 1976–80. Estimates were calculated from daily survival on each census obtained by the Jolly–Seber method. Vertical arrows indicate the occurrence of flood.

reproduce. Since new adults seldom disperse during the pre-hibernating period (Ohgushi 1983), most of the adult losses occurring before mid-September are probably due to death. On the assumption that all adults surviving at mid-September enter hibernation, the maximum survival until hibernation is equal to the number of adults at that point divided by the total number of adults emerged. The estimate ranged from 22.5 to 45.7% (mean, 37.1%) at site A, and from 36.3 to 59.6% (mean, 49.7%) at site F. The higher adult survival of population F compared with population A was not statistically significant ( $t = 2.08$ ,  $0.05 < P < 0.1$  for transformed log survival). The minimum survival during hibernation was obtained on the same assumption and ranged from 31.6 to 50.6% (mean, 40.0%) at site A, and from 26.2 to 84.3% (mean, 60.0%) at site F. An exceptionally low estimate at site F (26.2%) was also a reflection of the great adult losses in a large flood in later September 1979 (see Fig. 5). Winter survival at site F was significantly higher than that at site A ( $t = 2.67$ ,  $P < 0.05$  for transformed log survival) when the 1979 data were omitted.

Adult survival was lowest at the beginning of adult emergence, from mid-July to early August (Fig. 5). The poor survival was particularly clear in the hottest summer (1978); but it was obscure in the unusually cool summer of 1980. Presumably the observed low survival was due to the effects of heat in midsummer. Autumn floods in 1978 and 1979 evidently reduced adult survival.

Overwintering adults were, on average, larger than newly-emerged adults (Fig. 6). In females, a statistically significant difference was detected in 3 out of 5 years at site A and in 4 years at site F. This suggests that smaller adults suffer a higher mortality during the period from adult emergence to the reproductive season in the next year. The sex ratio (expressed as a proportion of females) increased from newly-emerged to overwintering populations (Fig. 7). Consequently, the size- and sex-dependent mortality resulted in larger adults and a higher proportion of females in the reproductive season.



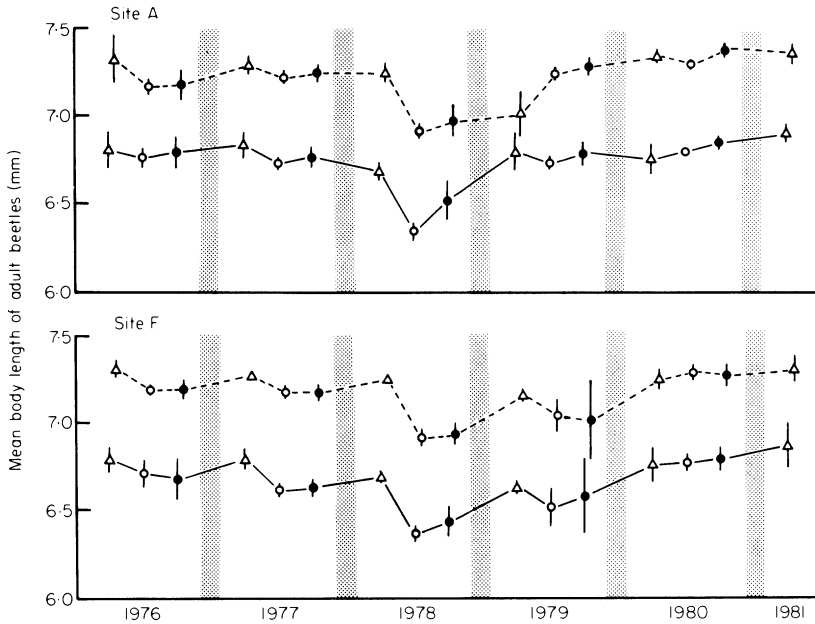


FIG. 6. Annual changes in mean body length of adult beetles at site A and site F for 1976–81. (○), newly-emerged adults; (●), adults just before hibernation (those still alive in mid-September); (△), adults overwintering. Solid and dashed lines show male and female, respectively. Vertical bars indicate 95% confidence limits. Shaded areas show the hibernating period.

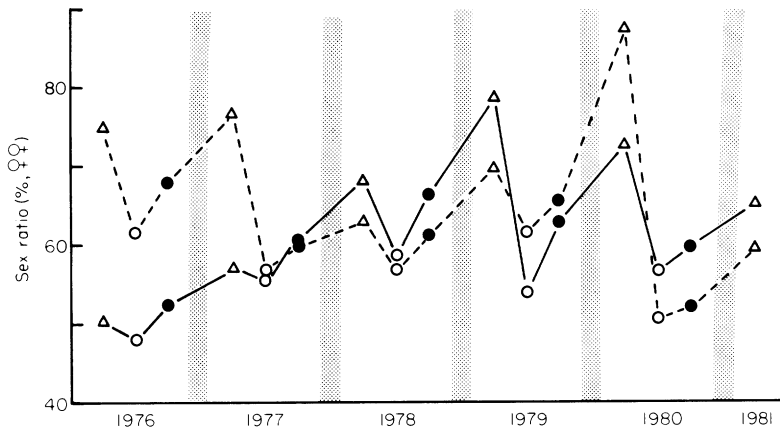


FIG. 7. Annual changes in sex ratio (% ♀♀) of adult populations at site A (solid line) and site F (dashed line) for 1976–81. (○), newly-emerged adults; (●), adults just before hibernation (those still alive in mid-September); (△), adults overwintering. Shaded areas show the hibernating period.

## SEASONALITY OF FOOD RESOURCES

### *Seasonal changes in food resource abundance*

Thistle plants grow rapidly from sprouting (in late April) to late June, becoming full-sized, i.e. 1.5–1.8 m in height, by late August (Fig. 8). They flower over 2 months from mid-August. Old leaves mature and eventually wither after summer.

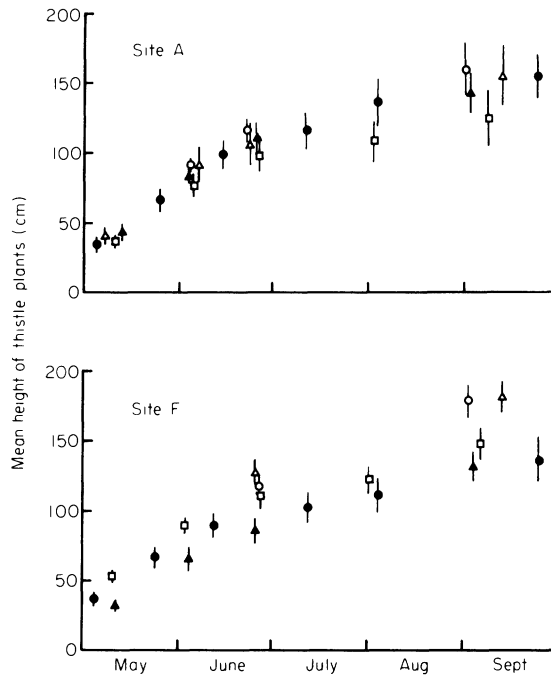
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FIG. 8. Seasonal changes in mean height of thistle plants at site A and site F. Vertical bars show 95% confidence limits. (○), 1976; (△), 1977; (□), 1978; (●), 1979; (▲), 1980.

Most thistle leaves in late June showed little damage, but there were some severely damaged plants in 1978 at site A (Fig. 9). As the season advanced, a number of thistle plants received considerable leaf damage, especially at site A with a higher larval density (Fig. 9). Besides the herbivore load, physiological senescence of matured leaves was particularly enhanced after August; the extent of leaf-withering tended to be accelerated by beetle-feeding.

*Seasonal changes in food resource quality*

The percentage moisture of thistle leaves was high (about 90%) in fresh leaves in May (Table 2). It then declined as the season progressed, although there was a large inter-plant difference in water content. Newly-emerged rosette leaves had a high water content (mean, 94.2%), compared with old leaves at any positions (ranging from 84.3 to 86.1%). Total

TABLE 2. Seasonal changes in leaf water content (% fresh wt.) of the thistle, *C. kagamontanum*, during 1982

Study site	Leaf location	A1 or F1				A2 or F2		
		17 May	15 June	15 July	16 Aug.	17 Sept.	20 Oct.	18 Nov.
A	Lower	90.3	88.3	61.0	86.6	80.5	82.4	—
	Middle	90.3	85.0	77.1	89.1	85.6	86.7	88.1
	Upper	90.6	88.7	87.4	88.0	79.5	84.7	—
	Rosette	—	—	—	—	94.7	95.3	95.6
F	Lower	92.6	86.9	84.3	85.2	87.2	86.2	—
	Middle	89.5	86.6	81.9	90.6	86.3	84.4	—
	Upper	85.3	83.3	83.0	87.7	85.3	85.4	—
	Rosette	—	—	—	—	—	93.8	91.6

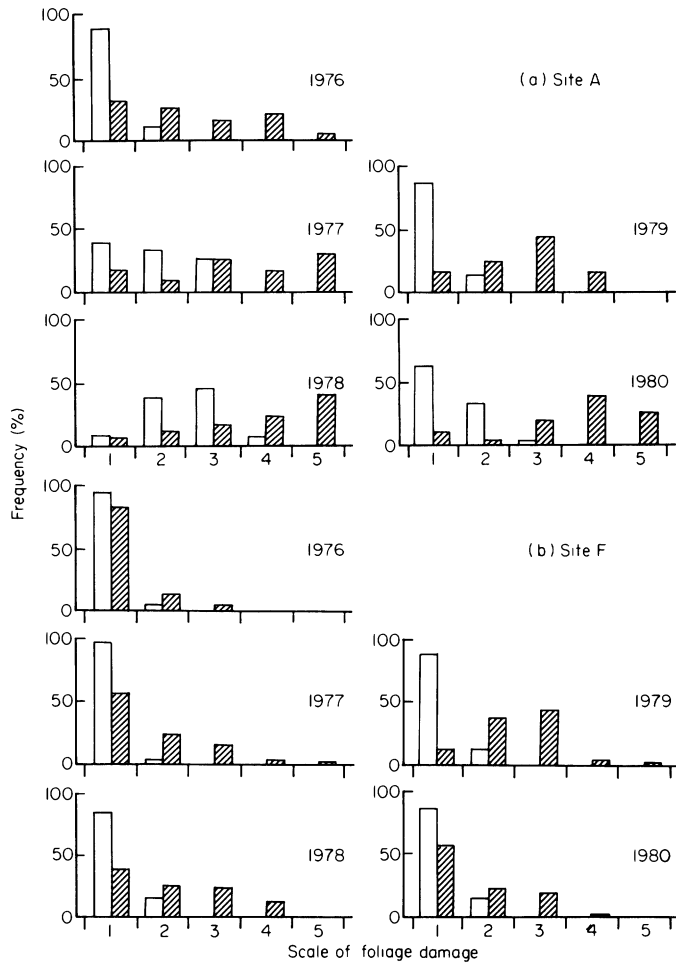


FIG. 9. Frequency distributions of foliage damage of thistle plants due to beetle-feeding at (a) site A, and (b) site F, for 1976-80. (□), late June; (▨), early September. Each thistle plant was put into one of five categories: 1 (0-20%), 2 (20-40%), 3 (40-60%), 4 (60-80%) and 5 (80-100% of foliage damage).

TABLE 3. Seasonal changes in total leaf amino acid levels (mg per g dry wt. of leaf) of the thistle, *C. kagamontanum*, during 1982

Study site	Leaf location	A1 or F1				A2 or F2		
		17 May	15 June	15 July	16 Aug.	17 Sept.	20 Oct.	18 Nov.
A	Lower	3.99	3.20	0.62	3.85	2.58	2.76	—
	Middle	4.62	2.05	1.47	5.35	6.16	4.19	2.58
	Upper	4.08	4.08	2.39	4.72	3.28	2.72	—
	Rosette	—	—	—	—	13.06	14.33	9.55
F	Lower	4.49	2.25	1.41	0.93	3.51	1.11	—
	Middle	4.98	3.80	3.05	4.22	2.83	1.93	—
	Upper	2.82	2.45	1.98	2.59	1.97	3.64	—
	Rosette	—	—	—	—	—	14.31	7.27

Total amino acids include aspartic acid, threonine, serine, glutamic acid and alanine.

amino acid contents at every leaf location tended to decrease seasonally, although the level varied considerably among individual plants (Table 3). Newly-emerged rosettes had remarkably high amino acid contents. However, the proportion of highly nutritious rosette leaves remained at a comparatively low level compared with old senescent leaves in autumn. Consequently, as the season progresses, food resources for larvae or newly-emerged adults become less favourable in terms of quantity and quality.

*Effects of seasonally deteriorating resources*

Newly-emerged adults were smaller, the later the timing of emergence (Fig. 10). This was more apparent at site A perhaps because of depleted food supplies. Body size of these

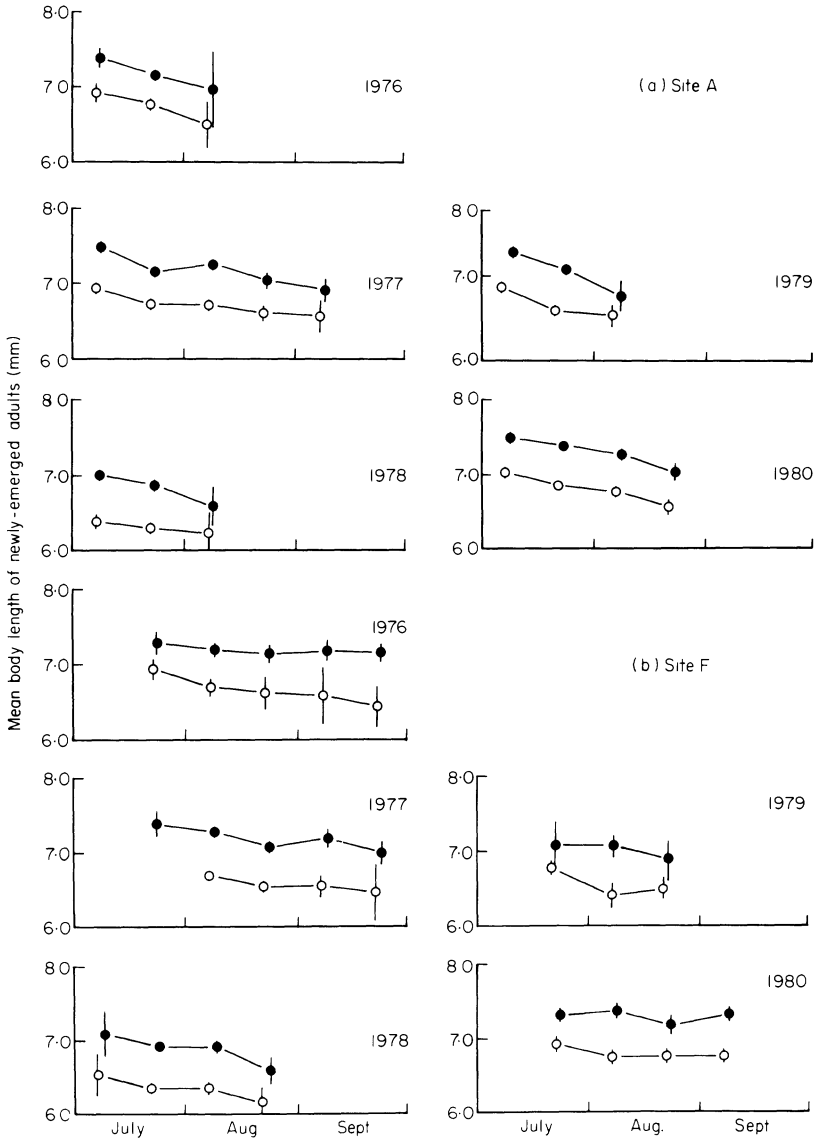


FIG. 10. Seasonal changes in mean body length of new adults at emergence in male (O) and female (●) beetles at (a) the downstream site A, and (b) the upstream site F, for 1976-80. Vertical bars show 95% confidence limits.

beetles has a significantly negative correlation with leaf damage of thistles at the site where they emerged (T. Ohgushi, unpublished). Thus, the decreased size late in the season is probably related to deteriorating food resources. Indeed, a number of small adults emerged in 1978 when high exploitation of thistle plants was observed (Fig. 9a,b). The reduction in adult size brought about by food deficiency was also found in an artificially introduced population of the lady beetle at the campus of Kyoto University, where severe food depletion occurs every year (Sawada 1984). As already mentioned, small adults are unlikely to survive to the reproductive stage in the following spring. Moreover, in the year of high larval density, larval death from starvation occurred locally at site A where some thistle plants were highly depleted at adult emergence. Therefore, food deficiency during summer and autumn considerably affects adult survival and thus reproductive contribution, particularly that of individuals emerging late.

### DISCUSSION

The results from the present study demonstrated that *H. niponica* has two basic population processes with regard to population change and stability through time. External mortality agents usually operate as density-independent disturbing factors generating year-to-year population fluctuations. On the other hand, the lady beetle has a remarkable density-dependent regulatory process based on the characteristic oviposition behaviour in response to feeding conditions (Ohgushi & Sawada 1985a). As a result, the egg density stayed within an extremely narrow range; the ratio of the maximum to the minimum densities was only 2.0 (site A) and 1.4 (site F) over the five generations, thus providing an excellent example of a stable natural insect population (Wolda 1978).

The basic population processes revealed here emphasize the consequence of the timing of disturbing factors for population stability. Habitat perturbations, such as floods, will greatly distort population stabilization if they occur in the reproductive season when population regulation occurs (Ohgushi & Sawada 1985a). The large June flood in 1979 washed away most reproductive adults at site A; as a result, the egg density remained at an unusually low level (see Fig. 1). In contrast, external catastrophes occurring in the non-reproductive season rarely influence population stability. Despite the marked reduction in adult populations by large autumn floods in 1978 and 1979, the egg populations of the next generation almost recovered to the previous level of density (see Fig. 1). The significant effects of flood on population dynamics were also shown in a chrysomelid beetle, *Gastrophysa viridula*, living in a river bank and an island in the river (Whittaker, Ellistone & Patrick 1979).

A major factor determining the new adult density in each habitat in my study was arthropod predation causing differential mortalities during the immature stages. This is also supported by the fact that reduced predation led to a remarkably high adult density and thus to severe food depletion in the introduced population of *H. niponica* (Sawada 1984). The results thus agree with the view that natural enemies play a key role in reducing the population levels of herbivorous insects (DeBach 1974; McClure 1977; Eickwort 1977; Lawton & McNeill 1979).

Adult survival to the reproductive stage largely depends on the length of the period of exposure to various mortality factors, and on the availability of resources. Because there is no clear difference in the daily survival between the two populations (Ohgushi & Sawada 1981), the upstream population with a shorter pre-hibernating period (mean, 47.8 days) had, as expected, higher survival until hibernation than the downstream one with a longer period (mean, 69.3 days). The shorter period at site F was a result of the delayed adult

emergence, due to the prolonged oviposition period in conjunction with heavy predation eliminating individuals emerging early (see Fig. 2b). Since poor nutrition results in weakened individuals being more vulnerable to external factors (McNeill 1973), it is also likely that greater food stress at site A contributes to the lower adult survival there. Seasonal decline in feeding conditions is responsible for reduced adult size, which in turn leads to lower survival to the reproductive stage. Winter survival is presumably linked to physiological conditions of individuals, such as fat body reserves, which depend on the favourableness of the food supply. Unfavourable food can not provide enough inositol, which the hibernating adults need to protect them from freezing (Hoshikawa 1981).

Mortality factors showed definite seasonal changes during the comparatively long reproductive season (Fig. 2a,b). So I now turn to the problem of individual success from the egg to the reproductive age throughout the season. Individual success is generally determined by a combination of three main components mentioned above: (i) time-restricted arthropod predation; (ii) seasonally deteriorating food resources; and (iii) length of the period from egg to hibernation. Individuals which are born at the beginning of the reproductive season suffer heavy predation and a prolonged period exposed to various mortality sources; on the other hand, favourable feeding conditions are guaranteed during their development. As the season progresses, the costs of predation and a long pre-hibernation period continuously decrease. Nevertheless, much improvement of individual success is unlikely, because an alternative cost of resource stress appears. Individuals which are born at the end of the season have low success, due to a more severe resource deterioration resulting in reduced body size and eventual larval starvation. In addition, heat stress causes high egg mortality in this period (see Fig. 2a,b).

This scenario also suggests that the relative success of individuals is strongly affected by the larval density enhancing resource deterioration. If the density is considerably depressed by heavy predation in the early season, as at site F, and thus resource stress remains less critical throughout the season, the relative success is higher in later cohorts with a shorter pre-hibernation period. In contrast, the reverse is expected in the habitat where reduced predation allows high larval density, as at site A, and thus severe food exploitation occurs. In this case, later cohorts will no longer be advantageous because of intensified competition and little energy storage for overwintering.

The results illustrate how the temporal heterogeneity within a generation profoundly affects not only population dynamics but also individual success of the lady beetle. Since most insect populations persist in seasonally changing environments, we need to pay more attention to the seasonality of various components of the habitat to understand insect population dynamics in the real world.

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## APPENDIX 1

Life tables for the lady beetle, *Henosepilachna niponica*, during 1976–80 at the downstream site A.  $lx$  = numbers surviving;  $dx$  = numbers dying;  $100 qx$  = % mortality

Age class	1976		1977		1978		1979		1980	
	$lx$	$dx$	$lx$	$dx$	$lx$	$dx$	$lx$	$dx$	$lx$	$dx$
Overwintering adults plus immigrants	105		183		362		93		200	
Eggs										
Sex ratio	50.4		51.1		58.0		66.7		62.2	
	2868		4994		5713		4246		10 868	
Predation	770	26.8	892	17.9	588	10.3		29	0.7	254
Cannibalism	194	6.8	1034	20.7	2035	35.6		1135	26.7	2468
Miscellaneous	744	25.9	817	16.4	876	15.3		798	18.8	2738
Total	1708	59.6	2743	54.9	3499	61.2		1962	46.2	5460
Newly-hatched larvae	1160		2251		2214		2284		5408	
Predation + unknown	618	53.3	596	26.5	1161	52.4		1301	57.0	2129
Fourth instar larvae	542		1655		1053		983		3279	
Parasitism	22	4.1	72	4.4	28	2.7		12	1.2	17
Predation + unknown	45	8.3	402	24.3	248	23.6		115	11.7	650
Total	67	12.4	474	28.6	276	26.2		127	12.9	667
Newly-emerged adults	475		1181		777		856		2612	
Sex ratio	47.5		55.7		61.1		53.1		55.9	
Overwintering adults	108		203		68		110		344	

## APPENDIX 2

Life tables for the lady beetle, *Henosepilachna niponica*, during 1976-80 at the upstream site F.  $lx$  = numbers surviving;  $dx$  = numbers dying;  $100 qx$  = % mortality

Age class	1976		1977		1978		1979		1980	
	$lx$	$100 qx$	$lx$	$100 qx$	$lx$	$100 qx$	$lx$	$100 qx$	$lx$	$100 qx$
Overwintering adults plus immigrants	269		434		812		789		114	
Eggs	75.0 10 423		70.0 11 264		63.2 9815		64.7 8114		67.1 3916	
Sex ratio										
Predation	6290	60.3	3580	31.8	4102	41.8	2358	29.1	1505	38.4
Cannibalism	647	6.2	2651	23.5	2029	20.7	2297	28.3	731	18.7
Miscellaneous	1738	16.7	806	7.2	1058	10.8	2099	25.9	452	11.5
Total	8675	83.2	7037	62.5	7189	73.2	6754	83.2	2688	68.6
Newly-hatched larvae	1748		4227		2626		1360		1228	
Predation + unknown	1408	80.5	3451	81.6	2055	78.3	1096	80.6	845	68.8
Fourth instar larvae	340		776		571		264		383	
Parasitism	39	11.5	34	4.4	27	4.7	15	5.7	7	1.8
Predation + unknown	40	11.8	71	9.1	19	3.3	144	54.5	57	14.9
Total	79	23.2	105	13.5	46	8.1	159	60.2	64	16.7
Newly-emerged adults	261		671		525		105		319	
Sex-ratio	58.3		59.0		57.8		62.4		51.7	
Overwintering adults	129		328		134		10		75	

## APPENDIX 3

Arthropod predators on each stage identified in the field (\*\*\*) and suspected predators confirmed by laboratory feeding experiments (\*)

Arthropod predators	Developmental stages of the lady beetle			
	Egg	Larva and pupa	Newly-emerged adult	Reproductive adult
<b>Araneida</b>				
<i>Theridion kompirense</i> (Bös. et Str.)		**		**
<i>T. yunohamense</i> (Bös. et Str.)			**	
<i>Enoplognatha japonica</i> (Bös. et Str.)				**
<i>E. transversifoveata</i> (Bös. et Str.)				**
<i>Neoscona scylla</i> (Karsck)			**	
<i>Xysticus croceus</i> (Fox)		*	**	**
<b>Coleoptera</b>				
<i>Amara congrua</i> (Morawitz)	*	*		
<i>Agonum ehikoense</i> (Habu)		*		
<i>A. sylphis sylphis</i> (Jedlička)		*		
<i>A. lampros</i> (Bates)		*		
<i>Chlaenius naeviger</i> (Morawitz)		*		
<i>Dicranoncus femoralis</i> (Chaudoir)		*		
<i>Harmonia axyridis</i> (Pallas)	**	**		
<i>Athemus suturellus</i> (Motschulsky)	**	*		
<i>Cantharis lewisi</i> (Pic)	*	*		
<i>Themus episcopalis</i> (Kiesenwetter)	*			
<i>Megalopaederus wadai</i> (Scheerpelitz)		*		
<b>Dermaptera</b>				
<i>Anechura harmandi</i> (Burr)	**	**		
<b>Heteroptera</b>				
<i>Picromerus lewisi</i> (Scott)		**		
<i>Adelphocoris triannulatus</i> (Stål)		**		
<i>Piocoris varius</i> (Uhler)		**		
<i>Nabis apicalis</i> (Matsumura)		*		
<b>Neuroptera</b>				
<i>Dendroleon jezoensis</i> (Okamoto)		**		