Covariance analysis of fluctuations in local populations of pear psyllids and anthocorid bugs

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Cross-correlation analysis of fluctuations in local populations of pear psyllids and anthocorid bugs

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Abstract. 1. To test whether predatory anthocorids migrate into pear orchards when populations of pear psyllids are building up, a cross-correlation analysis was carried out on their population numbers. Predator and prey population sizes were assessed weekly in 3 consecutive years (1991–93) by sampling pear leaves for eggs and nymphs of psyllids and pear tree branches for adult psyllids, as well as adults and nymphs of predatory anthocorids. The time-series consisted of numbers (per leaf or branch) averaged over preselected pear trees in an orchard and, in addition, over other trees selected along the hedgerows flanking the orchard.

2. The fluctuations in populations of adult and juvenile anthocorids showed strong cross-correlations with those of the eggs and nymphs of pear psyllids, but less correlation with adults of pear psyllids, as expected based on their increased ability to escape from predation. The psyllids always appeared first on the pear trees, resulting in positive phase shifts. The first peak of adult anthocorids on pear trees was always later than the first peak in the hedgerows, and the first peak of nymphal anthocorids on pear trees was always later than the first peak of adults on these pear trees. In each of the 3 years, anthocorids were rarely observed in the pear orchard during the first part of the growing season (April–June), but during the second half of the growing season (July–August) there was a strong numerical response of the anthocorid populations to increasing population densities of pear psyllids.

3. These results provide support for the hypothesis that the numerical response of the predators to prey density is caused initially by migration of anthocorids into the pear orchard and then by a reproductive response. The migrants originate from the hedgerows and other trees elsewhere, where they feed on aphids during the first part of the growing season.

Key words. *Anthocoris*, covariance analysis, cross-correlation, local dynamics, predator–prey interactions, *Psylla*.

Introduction

Pear psyllids, such as *Psylla pyricola* Foerster*, P. pyry* L., and occasionally *P. pyrisuga* Foerster, cause severe outbreaks in pear orchards in western Europe, especially when broad-spectrum insecticides are applied. From February onwards, the overwintered female starts laying eggs on buds and then on pear leaves where ultimately all nymphs acquire their food.

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During a typical growing season in The Netherlands, pear psyllids complete two to three overlapping generations.

The anthocorid predatory bugs *Anthocoris nemoralis* (F.), *A. nemorum* (L.), *Orius majusculus* Reuter, *O. minutus* (L.), and *O. vicinus* (Ribaut) play a major role in suppressing pear psyllid populations (Fuog, 1983; van der Blom *et al.*, 1985; Solomon *et al.*, 1989; Booij, 1990; Drukker *et al.*, 1995). Early in the growing season, however, the anthocorids feed on psyllids and other homopterans on trees flanking the pear orchard or elsewhere (Scutareanu *et al.*, 1993). Hence, to feed on psyllids they have to migrate into the pear orchard.

Table 1. The number and mean percentage of psyllid adults on pear trees and of anthocorid adults on pear trees (1991, 1992, 1993) and in hedgerows (1993) over the season. (1) *Psylla pyricola*, (2) *P. pyri*, (3) *P. pyrisuga*, (4) *Anthocoris nemoralis*, (5) *A. nemorum*, (6) *Orius* spp.

	Psyllid adults				Anthocorid adults							
	On pear trees				On pear trees				In hedgerows			
	Percentage			Total number	Percentage			Total number	Percentage			Total number
Year	(1)	(2)	(3)		(4)	(5)	(6)		(4)	(5)	(6)	
1991	87.4	12.4	0.2	2468	75.1	3.0	21.9	165	46.1	38.5	15.4	13*
1992	94.3	5.7	0.0	373	71.9	1.8	26.3	57	43.1	22.4	34.5	58†
1993	99.6	0.1	0.3	931	83.7	11.6	4.7	43	41.5	57.1	1.4	101‡

*One sample (week 29).
†Five samples (weeks 77, 81, 83, 84, 86).
‡Twelve samples (weeks 118, 120, 121, 123, 125, 127, 129, 130, 132, 135, 137, 138).

Table 2. Total number and mean frequency (%) of anthocorid adults in samples collected from different tree species in hedgerows over the season in 1993.

| | *Crataegus monogyna* | | *Alnus glutinosa* | | *Populus nigra* | |
Anthocorids	Total number	Percentage	Total number	Percentage	Total number	Percentage
A. nemoralis	62	86.1	10	38.5	0	0
A. nemorum	7	9.7	16	61.5	3	100
Orius spp.	3	4.2	0	0	0	0

Anthocorid bugs increase in numbers in pear orchards when the density of pear psyllids increases, and this numerical response of the predators increases with prey density (Balkhoven & Jansen, 1988; Stäubli *et al.*, 1992). As anthocorid bugs are scarce or virtually absent in the orchards from April to June, the aggregative response is thought to arise mainly from immigration. Laboratory and field experiments have shown that adult anthocorid bugs are attracted to, and arrested on and around, *Psylla*-infested pear trees and this aggregative response increases with the density of psyllids on these pear trees (Drukker *et al.*, 1995). These bugs use olfaction to locate *Psylla*-infested trees, and are guided by herbivore-induced volatiles emanating from pear trees under attack by psyllids (Scutareanu *et al.*, 1996, 1997). It was hypothesised, therefore, that the aggregative response of the predators to prey density in the orchard arises initially from synomone-mediated immigration, followed by a reproductive response.

To test this hypothesis by observations at the population level, an analysis was made of the fluctuations in numbers of pear psyllids and predatory bugs in an orchard located in De Watergraafsmeer near Amsterdam (The Netherlands) in three consecutive years (1991–93). This was achieved by weekly sampling of the predator and prey populations on pear trees in the orchard and on trees in the hedgerows flanking the orchard, and by applying a cross-correlation analysis on these time-series data (e.g. Lingeman & van de

Klashorst, 1992). The results presented here provide strong support for the hypothesis that anthocorid bugs move into pear orchards in response to the density of pear suckers on pear trees.

Materials and methods

Observation site

A group of eight pear trees (four in each of two rows), variety *Conference*, was chosen as an observation site inside an apple orchard (≈ 0.72 ha) located in Watergraafsmeer, Amsterdam. The orchard is bordered on the east (60 m from the group of selected pear trees), south (48 m), and north (58 m) sides by alder (*Alnus glutinosa* L.) hedgerows, and on the west side (10 m) by a mixed windbreak of poplar (*Populus nigra* L.) and alder. On the south side (58–60 m away from the group of selected pear trees), two hawthorn trees (*Crataegus monogyna* Jack.) were located over a ditch, ≈ 10 m away from the southern alder hedgerow.

Sampling procedure

Each year from April to October, leaf samples (30 leaves) were collected, two to four times per month, from
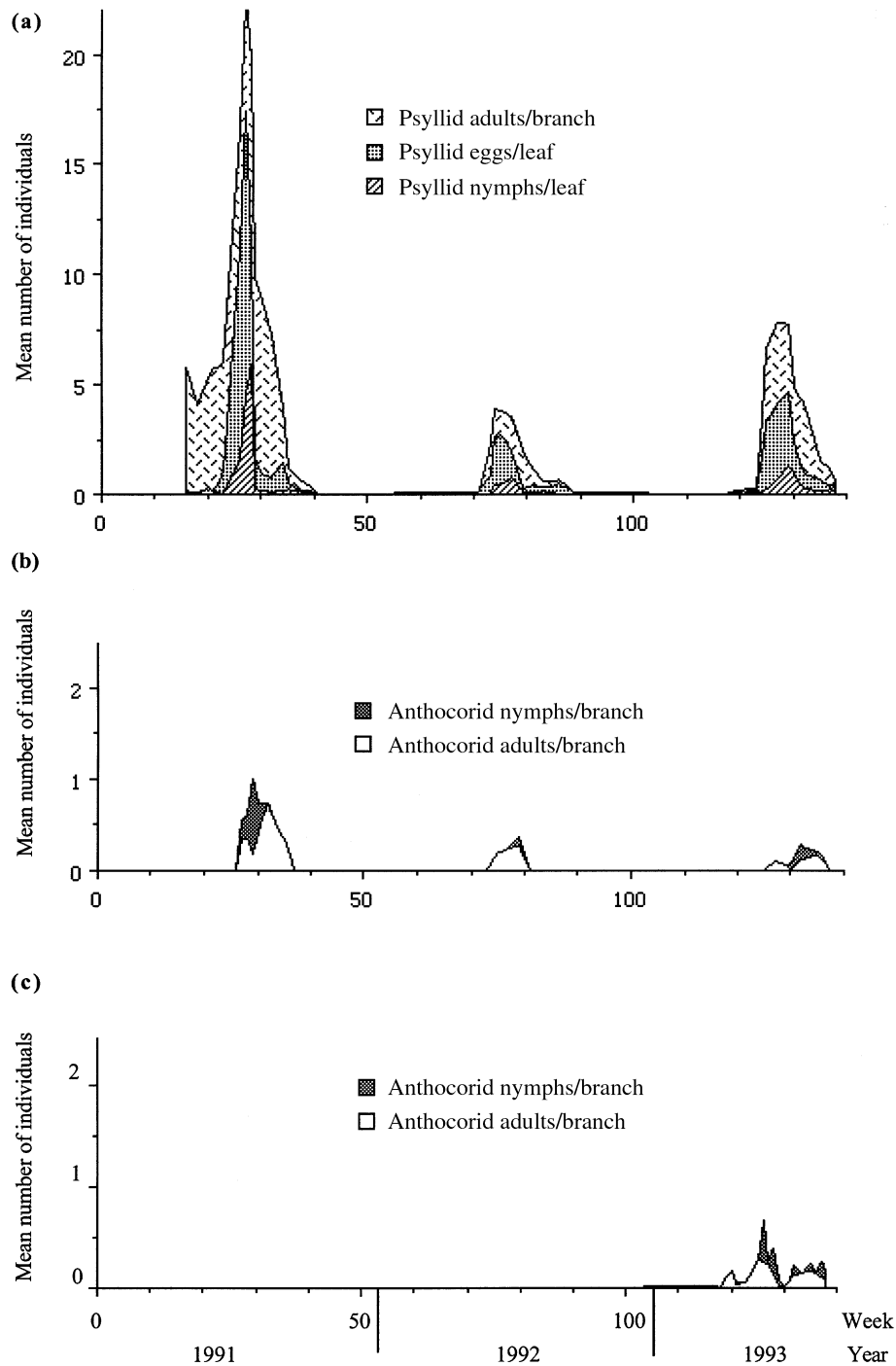
Fig. 1. The abundance (mean number of individuals) of (a) psyllid prey and (b) anthocorid predators (scale 5×) on pear trees over the season in 1991, 1992, and 1993, and of (c) anthocorids in hedgerows (scale 5×) in 1993. The weeks were numbered successively from January 1991 to December 1993.

six of the eight selected pear trees to assess the density of *Psylla* eggs and nymphs. Beating net samples were collected from the remaining two selected trees (30 branches per sample), and from the hedgerows (60 branches per sample) each time from 8–15 alder and poplar and from the two hawthorn trees, in order to assess *Psylla* adult and anthocorid adult and nymph populations, respectively. Fewer samples were collected from hedgerows in 1991 and 1992 (see Results and Table 1). All samples were examined under a binocular microscope.
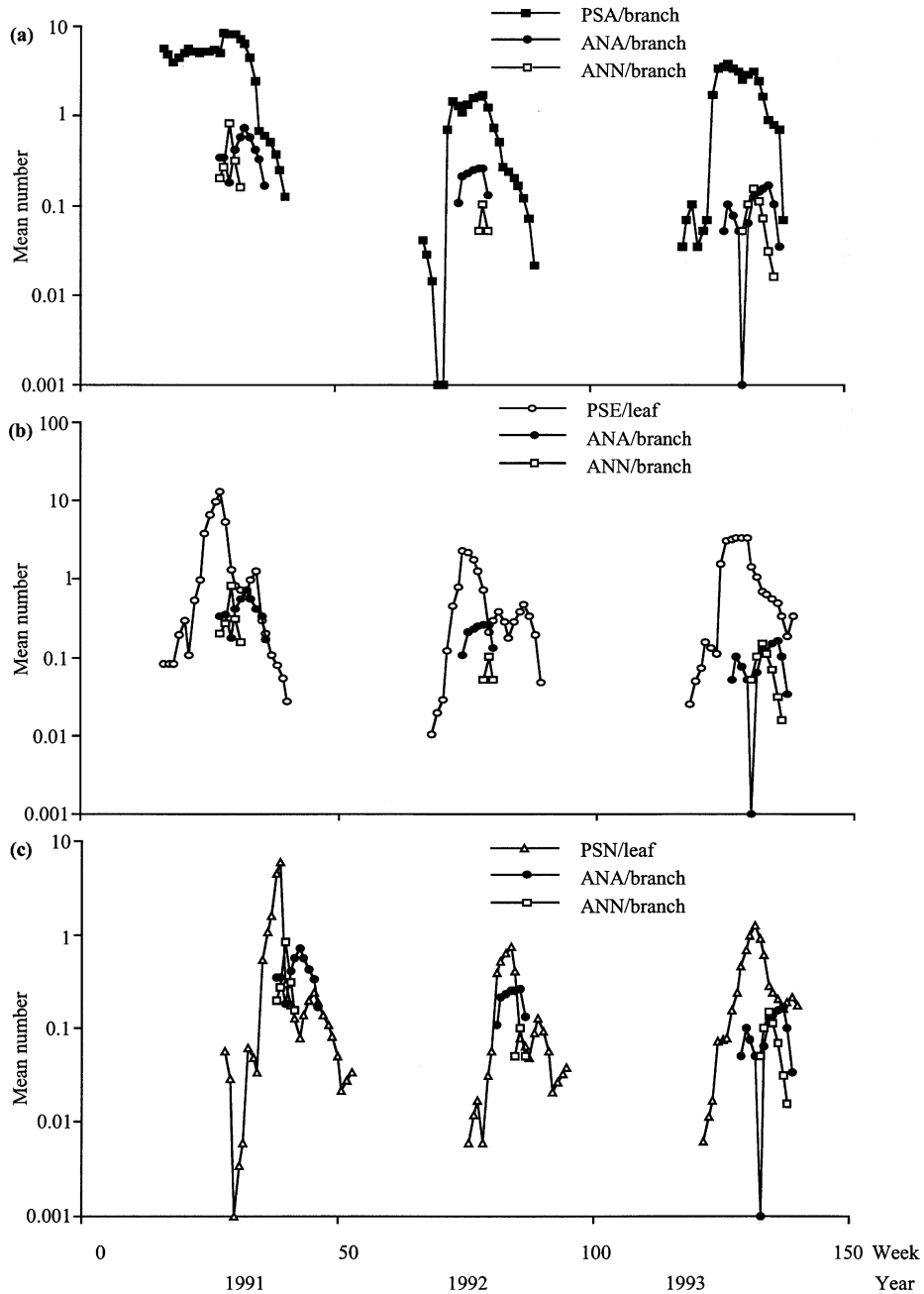
Fig. 2. Log data-series showing the fluctuation of the density (a) of psyllid adult, (b) egg, (c) nymphs and of anthocorid adults and nymphs (a, b, c) on pear trees over the season in 1991, 1992, and 1993. PSA, psyllid adults; PSE, psyllid eggs; PSN, psyllid nymphs; ANA anthrocorid adults; ANN, anthrocorid nymphs. The weeks were numbered successively from January 1991 to December 1993.

Cross-correlation analysis technique

The interdependence of the dynamics of the prey and its predator populations was analysed by the estimation of the cross-covariance and cross-correlation (Lingeman & van de Klashorst, 1992).

Consider two discrete time-series $\{X_t\} = X_1, \ldots X_n$ and $\{Y_t\} = Y_1, \ldots Y_n$, respectively. Define $x_t = X_t - \overline{X}$ and $y_t = Y_t - \overline{Y}$, then the estimators of the cross-covariance are defined as follows:

$$C_{xy}[k] = \frac{1}{N - K - 1} \sum_{t=1}^{N-k} x_t y_{t+k}$$

Table 3. Total time period of the observed stage and overlap period of the psyllid prey and anthocorid predator populations on pear trees over the season in 1991–93 run on psyllid adults/branch (PSA), psyllid eggs/leaf (PSE), psyllid nymphs/leaf (PSN), anthocorid adults/branch (ANA), and anthocorid nymphs/branch (ANN).

Psyllids/ Anthocorids	1991		1992		1993	
	Time period (dates)	Overlap (days)	Time period (dates)	Overlap (days)	Time period (dates)	Overlap (days)
PSA	24/4 to 5/10		13/4 to 17/9		6/4 to 27/8	
PSE	24/4 to 5/10		20/4 to 17/9		6/4 to 27/8	
PSN	24/4 to 28/10		20/4 to 17/9		6/4 to 27/8	
ANA	5/7 to 11/9	69	1/6 to 14/7	43	1/6 to 16/8	76
ANN	5/7 to 7/8	33	29/6 to 14/7	15	30/6 to 9/8	40

$$C_{xy}[-k] = C_{yx}[k] = \frac{1}{N-k-1} \sum_{t=1}^{N-k} y_t x_{t+k}$$

Consequently, the cross-correlation is:

$$R_{xy}[\pm k] = \frac{C_{xy}[\pm k]}{\sqrt{C_{xx}[0] C_{yy}[0]}}$$

where $C_{xx}[0]$ and $C_{yy}[0]$ are the estimated variances of $\{X_t\}$ and $\{Y_t\}$.

If periodic components of the same frequency are present in both series, this will lead to high values of the cross-correlation at the corresponding lags. The height of the peaks and the phase shifts were determined and plotted. The place of the cross-correlation peak determines the phase shift between the prey (x) and predator (y) populations in every season. The height of the peaks can be considered to be a relative measure of connectivity between prey and predator. The phase shift between these periodic segments is equal to the lag value of the first maximum of the cross-correlation function. The amplitude spectrum shows the degree of correlation between the prey and predator populations and the phase spectrum shows the corresponding phase shifts between the two populations.

This method of time-series analysis is applied to a predator and prey population at a local spatial scale to study the interactions between psyllid prey (x), which appears first on the host plant (pear trees), and the anthocorid predators (y), which arrive later in the season (i.e. a positive phase shift between predator and prey populations). It was hypothesised that the anthocorids forage between April and June on other prey species outside pear orchards (i.e. in surrounding hedgerows), and, when psyllids increase in numbers, from the end of June to September, migrate into pear orchards to find psyllid prey.

The data represent a week-by-week time-series of mean numbers of individuals per leaf (eggs and nymphs of psyllids) or per branch (adult psyllids and adult and nymphal anthocorids) in the group of selected pear trees, as well as hedgerow trees. Where samples for certain weeks were missing, values were estimated by linear interpolation between sample means before and after. The original data represented 64.5% (47 weeks) of the total time-series, the values for the remaining 26 weeks being obtained by interpolation. For prey (x) and predator (y) in each stage of development, the time-series involved 28 weeks in 1991, 23 weeks in 1992, and 22 weeks in 1993, giving a total of 73 weeks. The cross-correlations were calculated and plotted using a procedure described by Lingeman and van de Klashorst (1992). The apparently high number of interpolated points in the series hardly affected the results of the cross-correlation analyses.

Results

Local abundance of pear psyllids and anthocorid bugs

Densities of psyllids on pear trees were highest in 1991, intermediate in 1993, and lowest in 1992 (Table 1, Fig. 1a). This pattern was also found for anthocorid adults and nymphs on pear trees, but their densities were much lower than those of psyllids (Table 1, Fig. 1b) and in 1993 slightly lower than those of anthocorids in hedgerows (Table 1, Fig. 1c). Every year, *P. pyricola* was the dominant species of pear sucker in the orchard whereas *A. nemoralis* was the most frequent among the anthocorids on pear (Table 1) and hawthorn (Table 2). On alder trees, *A. nemorum* was the most numerous, whereas on poplar it was the only species present (Table 2). To all other trees in the hedgerows together, hawthorn represented the most important source of *A. nemoralis* for migration to *Psylla*-infested trees.

Temporal variation of prey and predator populations

Fluctuations of psyllid adults, eggs, and nymphs, and of anthocorid adults and nymphs on pear trees followed a similar pattern in all 3 years (Fig. 2). The psyllid population began to develop early in spring (April) whereas the anthocorids did not appear until after mid June, by which time pear psyllids had passed the egg and nymph peaks of their second generation (Fig. 2b,c). Anthocorids and psyllids on pear trees occurred
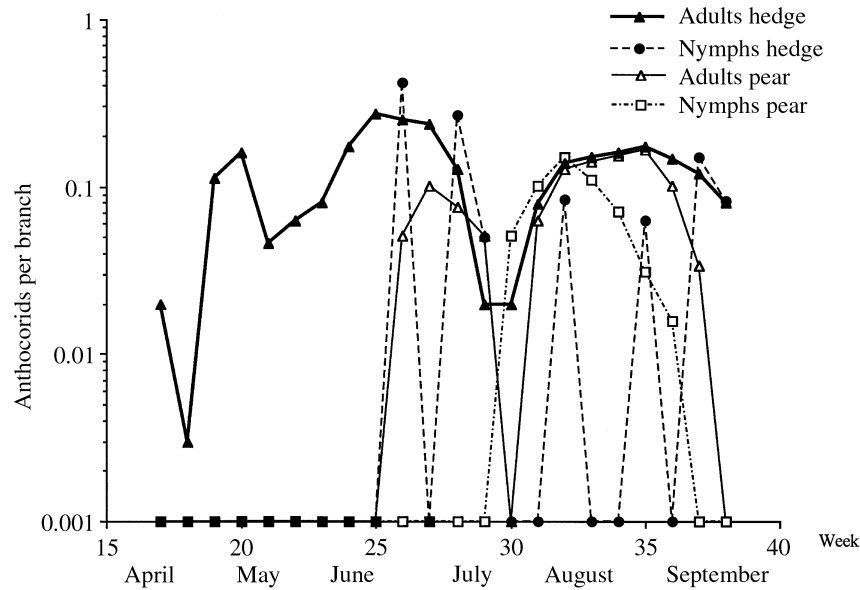
Fig. 3. The presence of anthocorid adults and nymphs in hedgerows (hedge), and adults and nymphs on pear trees (pear) over the season in 1993.

Table 4. Highest peak value and phase shift from lag zero of cross-correlation of the psyllid prey and anthocorid predator populations over the season in 1991 to 1993 run on psyllid adults/branch (PSA), psyllid eggs/leaf (PSE), psyllid nymphs/leaf (PSN), anthocorid adults/branch (ANA), and anthocorid nymphs/branch (ANN).

Psyllid/ Anthocorids	Highest peak value of cross-correlation			Phase shift of highest peak (weeks)		
	1991	1992	1993	1991	1992	1993
PSA/ANA	0.80	0.88	0.83	3	0	2
PSA/ANN	0.57	0.65	0.80	0	1	5
PSE/ANA	0.87	0.73	0.88	5	2	7
PSE/ANN	0.92	0.85	0.92	2	4	5
PSN/ANA	0.77	0.98	0.90	5	1	5
PSN/ANN	0.89	0.83	0.94	1	2	3

together in the orchard from June to the end of August or beginning of September (Table 3).

Anthocorid predator populations in hedgerows vs. pear orchard

Anthocorids were present in hedgerows long before they appeared in the pear orchard (Fig. 3). In hedgerows they produced a first generation on hawthorn, alder, poplar, or other trees and shrub species using psyllid, aphid, and other homopteran species as prey. Sampling of hedgerows showed that the anthocorid nymphs appeared in the second part of June (Fig. 3). Strikingly, in the pear orchard, the sharp increase of adults at the end of June was always several weeks before the nymphs started to increase in July. The anthocorid nymphs also appeared earlier in the hedgerow than in the pear orchard.

Cross-correlation analysis of psyllid and anthocorid populations

The peak values of cross-correlations of psyllid populations (adults, eggs, and nymphs) with anthocorid populations (adults and nymphs) on pear trees, and the phase shift of those peaks at corresponding lags are presented in Table 4 and graphically in Fig. 4 (1992 only). Given that the vulnerability of psyllids to predation decreases with the stage of development of the psyllids and increases with the stage of development of the anthocorid, it is interesting to note that the weakest cross-correlations (0.57–0.80) are found between psyllid adults and anthocorid nymphs. Thus, cross-correlations were lowest when predator and prey were of approximately the same size. In all other cases, cross-correlations were on average equally high. The highest peak value (0.98) was between anthocorid adults and psyllid nymphs in 1992, despite the fact that psyllid and
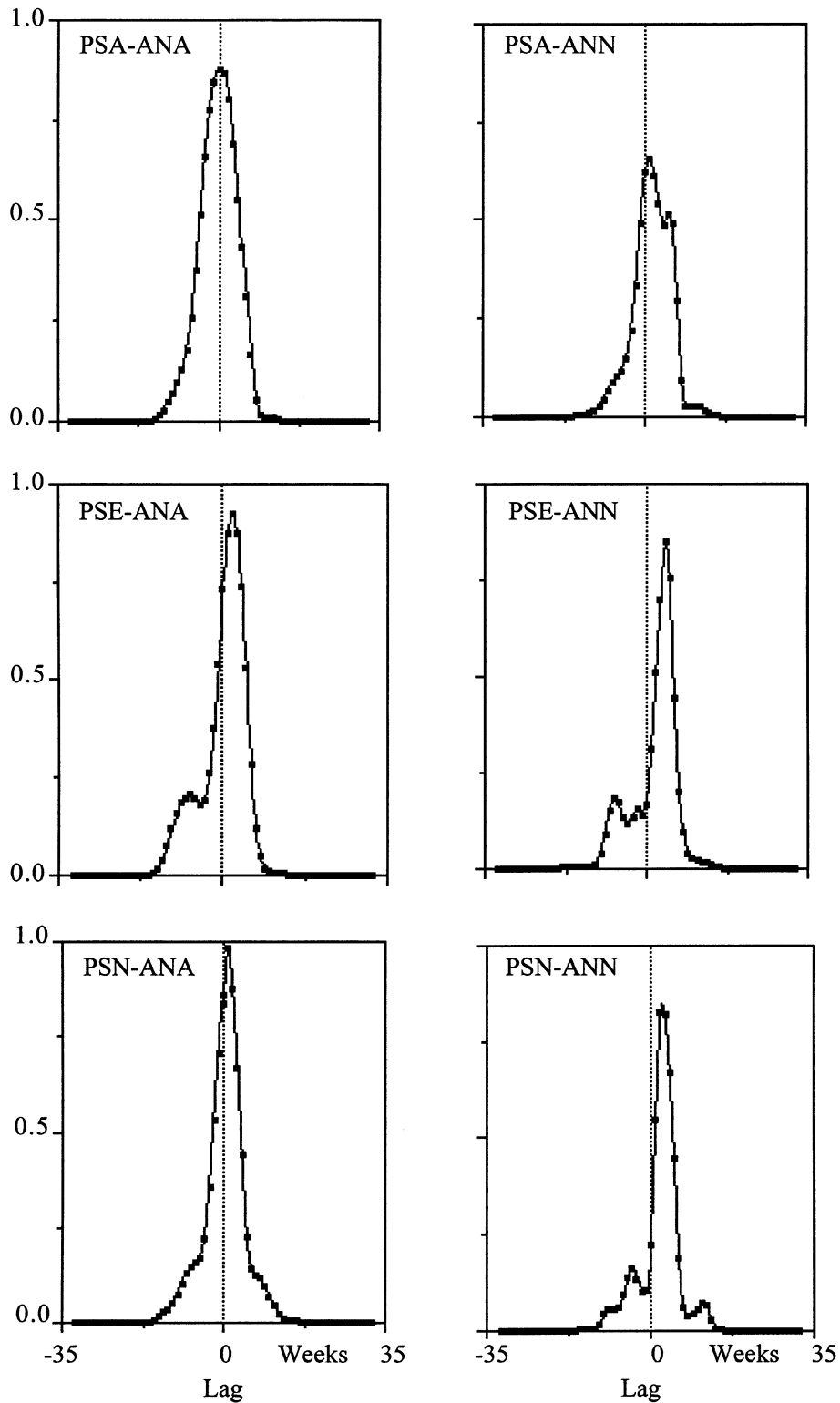
Fig. 4. Cross-correlations of psyllid adults, eggs, and nymphs with anthocorid adults and nymphs in 1992. *x*-axis = phase shift from lag 0, in weeks; *y*-axis = peak height. PSA, psyllid adults/branch; PSE, psyllid eggs/leaf; PSN, psyllid nymphs/leaf; ANA, anthrocorid adult/branch; ANN, anthocorid nymphs/branch.

anthocorid densities were low. Alternatively, this high correlation may be caused by the fact that feeding by psyllid nymphs induces the pear tree to produce volatiles, which in turn attract anthocorid adults.

Except for two cases, highest cross-correlation peaks of predator and prey coincided and all phase shifts between prey and predators had positive values. Phase shifts were largest relative to prey eggs and smallest relative to adult prey, with the nymphs in between these extremes. The phase shifts, however, show considerable between-year variation, which can probably be attributed to differences in climate.

Discussion

Analysis of population fluctuations of pear psyllids and anthocorids in a pear orchard and surrounding hedgerows provides support for the hypothesis that anthocorids move into the orchard from surrounding shrubs and trees (hawthorn, alder) starting in mid June when psyllid populations start to grow. This is because adult anthocorids decrease in numbers in hedgerow trees and simultaneously increase in the pear orchard, and because the increase in adult anthocorids at the end of June consistently appears several weeks before the nymphal anthocorids start to increase in July. Because (1) the olfactory attraction to *Psylla*-infested pear trees has been demonstrated in the laboratory (Drukker & Sabelis, 1990) and in pear orchards (Drukker *et al.*, 1995), (2) the volatile chemicals induced in pear trees after attack by psyllids have been identified (Scutareanu *et al.*, 1996, 1997), and (3) the olfactory response of anthocorids in the pear orchard has been found to be (prey) density dependent (Drukker *et al.*, 1995), there is now increasing evidence for synomone-induced aggregative response of anthocorids to *Psylla* density via migration into the orchard.

There is also a strong numerical response of anthocorid predators to the density of psyllids in the pear orchard. This follows from the high cross-correlations of immature psyllids (nymphs and eggs) with mobile stages of anthocorids (adults and nymphs), and the fact that the phase shifts between peak values of prey and predator are always positive. Moreover, the phase shifts relative to psyllid eggs have values that are close to the time needed for the psyllids to complete a generation, those relative to nymphs are clearly less than a generation, and those relative to adults are the shortest, sometimes even zero. These results were interpreted as an indication for higher attack success on the nymphal stages of the prey. The rationale here is as follows. First, anthocorid nymphs and adults have great difficulty in capturing the winged psyllid adults, which jump immediately upon disturbance. Hence, a short phase shift probably implies that they are feeding on the eggs produced by the adult psyllids rather than on the adults themselves. Second, the long phase shift relative to the eggs of the psyllids coincides with the time needed for the anthocorids to develop into nymphs and adults. Third, the intermediate phase shift relative to the nymphs of the psyllids coincides with the time needed for the anthocorids to develop from nymph to adult. Finally, it should be noted that in all samples the anthocorids consisted of several species (Table 1) and that these species may differ in their prey stage preference. For example, the *Orius* spp. seem to prefer psyllid eggs, whereas the *Anthocoris* spp. seem to prefer the nymphs (Fuog, 1983). Moreover, these species may differ in their response to herbivore-induced plant synomones.

The combination of aggregative and numerical response of anthocorids to the density of psyllids in pear trees will ultimately determine the degree to which the trees will be damaged by herbivory. There is evidence that the aggregative response increases with the density of psyllids (Drukker *et al.*, 1995). Here, it was shown that there are strong cross-correlations between the densities of psyllids and anthocorids. Thus, it may well be that anthocorids represent an important mortality factor in the dynamics of pear psyllids. Because the amount (and number) of plant volatiles produced increases concomitant with increases in the density of psyllids (Scutareanu *et al.*, 1997), it was hypothesised that these herbivore-induced volatiles play a role in the aggregative and numerical responses of the anthocorids to the density of psyllids. The larger the number of psyllids attacking a tree, the larger the amounts of volatiles produced, the more anthocorid predators are attracted and, once attracted, the more strongly these predators are arrested in the leaf area under attack by the psyllids. There is a need to test this hypothesis critically in all its aspects, taking into account that the responses may depend on pear cultivar (work in progress), constitutive direct and indirect defence, tree condition (fertilisation, induced direct and indirect defence), species of *Psylla* and anthocorids.

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