3. INVESTIGATIONS OF APHID AND BENEFICIAL INSECT ABUNDANCE, DISPERSAL AND SPATIAL DISTRIBUTION ACROSS FIELDS

3.1. INTRODUCTION

It is now well recognised that insects exist as discrete patches of local populations that together constitute a metapopulation and it has been demonstrated that this phenomenon occurs in agricultural landscapes for some predatory groups (reviewed for Carabidae by Thomas et al., 2002) and pests (Winder et al., 1999). The size of these local populations within a metapopulation may differ depending on the species and can extend over several hectares (Holland et al., 1999). However, most studies have been conducted within parts or across whole fields (Holland et al., 1999; Thomas et al., 2002) and the extent to which these metapopulations extend across boundary features (e.g. field boundaries, tracks, watercourses and roads) is not understood. For some species, such non-crop areas form stable habitats that are seasonally essential for aestivation or overwintering (Sotherton, 1984). Recolonisation of the ephemeral cropped areas then occurs when conditions there become more suitable (Wissinger, 1997). Habitats at field margins can also act as refuges from agricultural operations that may impose certain mortality risks to individuals within the field. That part of a population taking refuge within non-crop habitats may then act as an important source population for the rapid re-colonisation of fields following catastrophic disturbances (Holland et al., 2000). However, for species that inhabit the cultivated areas alone, features such as field boundaries and roads may act as barriers to movement and dispersal between fields (Mader et al., 1990; Mauremootoo et al., 1995; Thomas et al., 1998), and consequently may influence epigeal arthropod distribution patterns or impose metapopulation structure on their populations by fragmenting them into local populations. Few studies have investigated how non-crop habitats and their distribution in fragmented farmland affect the spatial dynamics of beneficial insects. Moreover, the extent to which non-crop habitats at field boundaries restrict insect movement between fields has rarely been studied extensively. There is also little definitive evidence to explain why insects are frequently heterogeneously distributed within fields, even though investigating how arthropods are distributed in agricultural landscapes can provide important and useful insights into how best to encourage them for pest control (Thomas et al., 2001). Within fields, abiotic and biotic factors may influence spatial dynamics and, consequently, levels of natural biological control. The most influential abiotic factors are likely to be those related to crop management practices (eg. pesticide inputs, crop rotations and tillage). Biotic factors include suitability and location of overwintering habitats, soil type and moisture, cover by vegetation within fields and food availability. The issues relating to invertebrate spatial dynamics were reviewed by Thomas et al. (2002) for Carabidae but the principles discussed are applicable to a wider ranger of invertebrates.

Funding to establish additional non-crop habitats within farmland is now available through various agri-environment schemes. Some of these habitats will be colonised by beneficial invertebrates and this may increase levels of biocontrol in nearby fields. However, little information is available on where these should

be located to maximise their benefits for biocontrol and biodiversity. Studies of insect spatial pattern in relation to non-crop habitats will provide guidance on the location of non-crop habitats.

Insecticides are known to cause mortality of many non-target species but some are able to re-colonise after spraying from unsprayed refuges such as field margins and adjacent unsprayed fields (Duffield et al.; Holland et al., 2000). The extent and rapidity of this process depends upon the mobility of individual species, the extent and location of unsprayed refuges and to what extent there are barriers to their movement. A better understanding of insect distributions and movement will aid the insecticide risk assessment process by allowing the potential for reinvasion to be estimated. Species or groups of invertebrates at greatest risk may be identified, and mitigation measures developed to reduce the impact on the population.

3.1.1. Generalist Beneficial Invertebrates

The studies of spatial distribution patterns focussed on generalist predatory invertebrates, as other groups such as parasitoids and the specialist aphid predators, hoverflies and ladybirds, are highly mobile, active fliers and so their spatial distribution on farmland needs to be studied at greater spatial scales. The manipulation of parasitoids and hoverflies with respect to field margins was investigated in other parts of the project (section 2). Generalist predators are numerically dominant within agroecosystems and occupy a wide range of niches and so are important members of the natural enemy community attacking pests in arable field crops. Manipulative experiments demonstrated that generalist predators alone can keep cereal aphid populations below damage thresholds (Edwards et al., 1979; Carter et al., 1980; Chambers et al., 1982; Chiverton, 1986; Holland & Thomas, 1997). Moreover, because they are present when aphids first appear they have the potential to slow down or prevent the development of aphid outbreaks (Edwards et al., 1979; Chiverton 1986), especially when aphid numbers increase slowly (Carter et al., 1980; Chambers et al., 1982). They also inhabit the field and the boundaries throughout the year and are consequently influenced by a wide range of agricultural practices, the response varying according to the species ecology and phenology.

Studies of generalist predator spatial dynamics have focussed on quantification of spatial pattern within fields or parts thereof (Ericson, 1978; Hengeveld, 1979; Holland et al., 1999; Thomas et al., 2001), their capacity to penetrate field boundaries (Thomas et al., 1998; 2001), relationship to pests (Warner et al., 2000; Winder et al., 2001), the impact of changes in cropping (Brown, 2000) and response to insecticide applications (Thomas & Jepson, 1997; Holland et al., 2000). The spatial dynamics of generalist predators within the same field over more than one year have only been investigated once (Brown, 2000). Moreover, the majority of these studies were on carabid beetles (Carabidae), although other insects such as rove beetles (Staphylinidae) are known to be important for pest control (Dennis & Wratten, 1991). All studies of generalist predator distribution patterns have used pitfall traps, which measure a combination of activity/density. To what extent these relate to actual density has always been debatable.

3.1.2. Pests

The spatio-temporal dynamics of several pest species has been investigated, including that of cereal aphids (Schotzko & Knudsen, 1992; Winder et al.,1999), slugs (Bohan et al., 2000), pea leaf weevil (Schotzko & Quisinberry, 1999), brassica pod midge (Warner et al., 2000) and cabbage stem weevil, pollen beetle and cabbage seed weevil (Ferguson et al., 2003). Most data exists for cereal aphids, and in the UK their distribution has been examined in detail using a grid based sampling approach within eight cereal fields (Winder et al., 1999 & unpublished data). These have shown that pest species exhibit heterogeneous distribution patterns within fields, but the location of areas of high and low density may vary through time. Redistribution may occur following initial colonisation in response to a range of factors, but predation, environmental conditions and host suitability have all been shown to have an affect (Winder et al., 2001; Ferguson et al., 2003). Knowledge of a pest's spatial dynamics can assist when developing integrated management strategies. Crop scouting can be improved to ensure that spatial pattern is taken into account (Alexander et al., submitted), thereby gaining the most accurate measurement of infestation levels for the minimum cost. Chemical intervention can be targeted at those areas of highest risk, for example for those species invading from the field edges. Finally, the relative importance of abiotic and biotic factors may be determined if appropriate additional sampling is conducted and this can lead to the development of alternative cultural methods of control.

In this project the large-scale, spatio-temporal dynamics and movement of beneficial epigeal insects was investigated along with measurements of some of the most likely influential biotic factors over three years (Section 3.2-3.4). The landscape was also manipulated to increase the proportion of non-crop habitat through the use of set-aside strips. Experimental studies were then conducted to confirm the influence of some biotic factors (Section 3.5-3.7).

3.2. INVESTIGATION OF THE LARGE-SCALE, SPATIO-TEMPORAL DYNAMICS OF PREDATORY EPIGEAL INVERTEBRATES IN ARABLE FARMLAND.

This study formed one of the main components of the overall project and aimed to investigate a number of issues in relation to the population Density, Distribution and Dispersal (hence 3D Farming) of predatory invertebrates in field crops. The primary aims were to investigate:

- The spatial pattern of predatory invertebrate distributions across a contiguous block of fields
- The within and between year stability of predatory invertebrate aggregations
- The scale of these aggregations for different species and groups of invertebrates
- The association with biotic and abiotic factors in the field
- The relative contribution of different field boundary types to invertebrate diversity within the field
- The extent of the influence of field boundaries on invertebrate abundance and diversity within the cropped area.

Beneficial invertebrates were sampled using pitfall traps in conjunction with measurements of plant cover and soil moisture. To investigate within-year spatial changes sampling was conducted four times in 2000 while between-year changes were determined by sampling twice in the following two years. An additional post-harvest sample was taken in some fields in 2001.

3.2.1 Materials and Methods

3.2.1.1. *Field site*

Figure 3.1. Site layout and cropping for the Cranborne site in 2000-02.
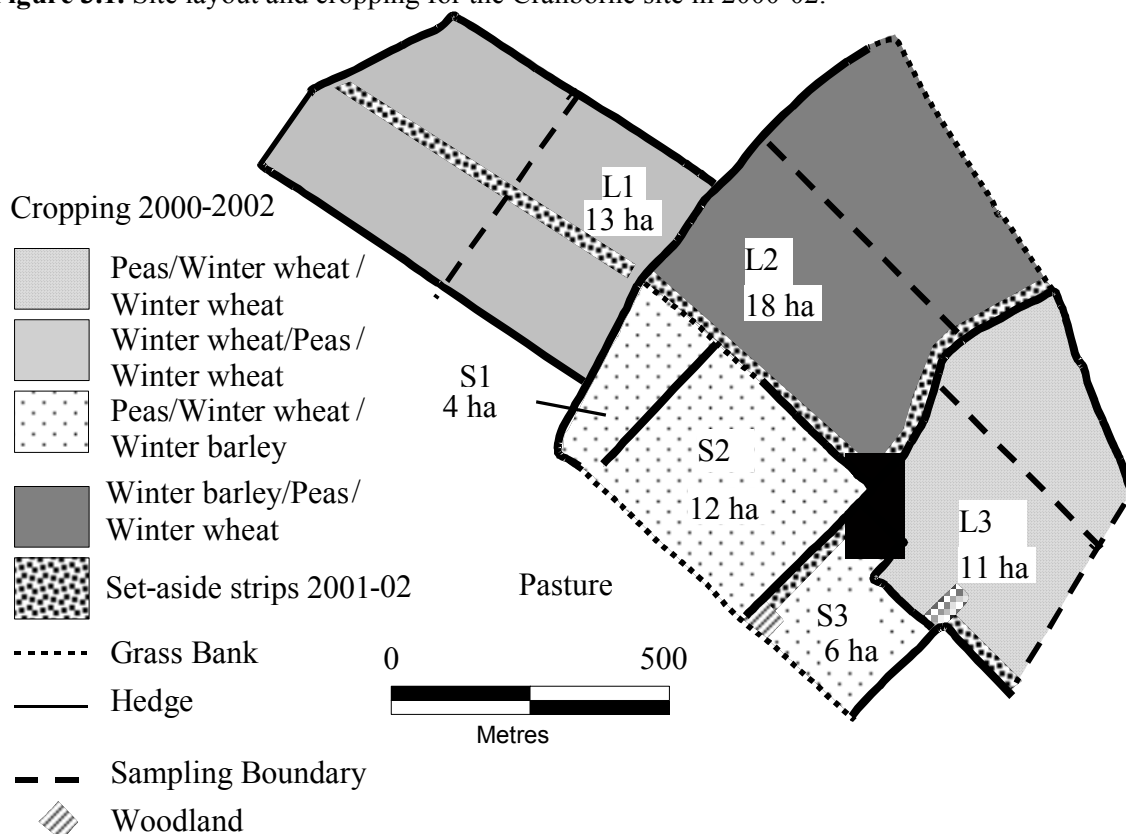
The study area, covering 66 ha in Dorset, comprised six arable fields separated by mature hedgerows or grassy banks (Fig. 3.1). The majority of hedgerows comprised a hedge with an herbaceous/grass bank. In many places the dominant species were barren brome (*Anisantha sterilis*) and stinging nettle (*Urtica dioica*). A beetle bank was established across one of the larger fields and formed a boundary to the sampling area. The crop rotation was of winter wheat, spring-sown forage peas and winter barley. The three smaller fields were all at the same stage of the crop rotation while that of the three large fields differed. After the first year of sampling a number of 24 m wide set-aside strips, sown with a mixture of kale, millet, *Phacelia tanacetifolia*, quinoa, triticale, sunflowers and yellow sweet clover, were established around the edge of four of the fields. The insecticide `pirimicarb' (0.27 kg ha^{-1}) was applied on 17/6/2000 to fields S1-S3 & L3 and to L2 on 24/6/2001.

3.2.1.2. *Insect sampling*

Epigeal invertebrates were sampled simultaneously across the study site using paired pitfall traps arranged in a grid pattern with 973 sampling points (Fig. 3.2). The pitfall traps were arranged in an offset grid pattern with 40 x 20 m spacing within each field. The grid extended across the whole of the three smaller fields, but only half the area of each large field was covered (Fig. 3.2). At each sampling point there were two pitfall traps (6 cm diam.), partly filled with water and detergent, and these were opened for one week on four occasions in 2000 and twice in 2001 and 2002 (Table 3.1). Each sample location was surveyed and located using the national grid reference using a differential Global Positioning System (Geoexplorer 3, Trimble, California, USA). After collection all arthropods were removed and stored in 70% alcohol. The majority of the catch comprised carabid beetles (Coleoptera; Carabidae), rove beetles (Coleoptera; Staphylinidae) and spiders (Arachnida; Araneae). The Carabidae and Staphylinidae were identified to species; other genera or families were also identified in each sample and are listed in Table 3.2 along with their overwintering location. Numbers of 19 species of Carabidae, 10 staphylinid species and 7 families were listed. Many money spiders (Araneae; Linyphiidae) were also caught but pitfall trapping provides an unreliable estimate of their abundance and they were not identified (Topping & Sunderland, 1992).

Table 3.1. Sampling dates for insect distribution studies.

Pitfall trapping		Weed cover	
Cereals	**Peas**	**Cereals**	**Peas**
2-9/5/2000	16-23/5/2000	4/5/2000	18/5/2000
6-13/6/2000	6-13/6/2000	6/6/2000	7/6/2000
28/6-5/7/2000	28/6-5/7/2000		
12-19/7/2000	12-19/7/2000	14/7/2000	18/7/2000
4-11/6/2001	4-11/6/2001	7-12/6/2001	7-8/6/2001
9-16/7/2001	9-16/7/2001	11-13/7/2001	10-11/7/2001
5-12/9/2001	5-12/9/2001		
10-17/6/2002	10-17/6/2002	13/6/2002	13/6/2002
8-15/7/2002	8-15/7/2002		

Figure 3.2. Sampling positions within each field.
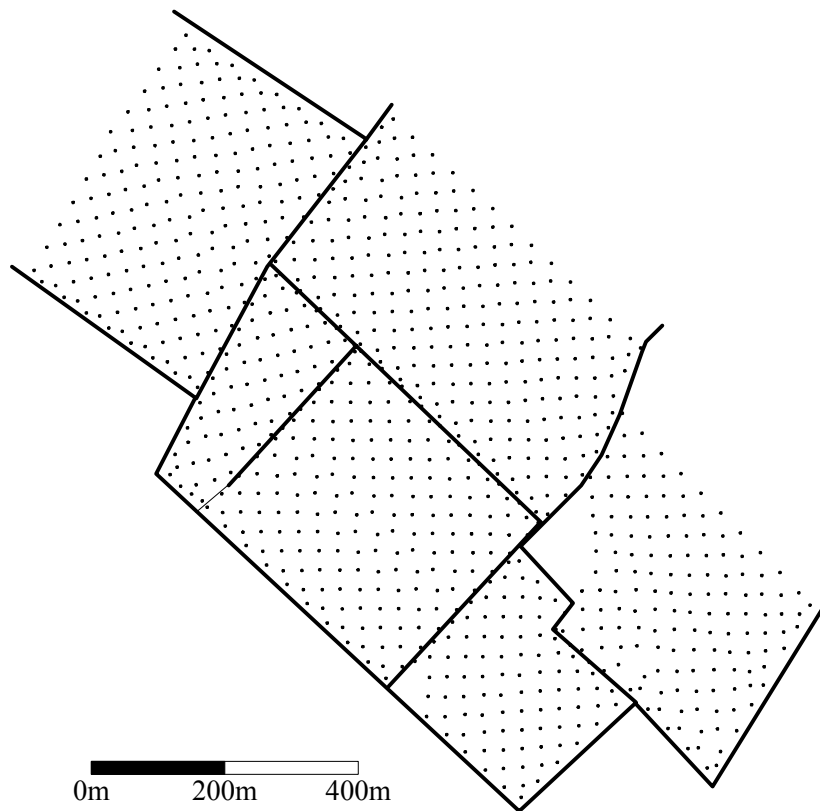
3.2.1.3. *Ground cover*

The proportion of ground covered by vegetation and soil moisture are both factors that are considered to influence the distribution of epigeal invertebrates and therefore measurements of these were made across the study area. The proportion of bare ground and that covered by broad-leaf and grass weeds and the crop was measured each year around each sampling position. Estimates were taken at five points within a 5m area of the pitfall sampling position on three occasions in 2000, twice in 2001 and once in 2002 (Table 3.1).

3.2.1.4. *Soil moisture*

Soil moisture was estimated by measuring electrical conductivity using a soil probe (Theta Probe). Measurements were taken in 2000 (26/6-13/7). Three measurements were taken within 2m of each sampling position in four of the fields. However, owing to equipment failure in the other two fields (L1 and L2) measurements were taken at each sampling position along alternate rows only.

In autumn 2001 the fields were surveyed for electrical conductivity by Magnascan (Turftrax), from which soil moisture was estimated. Soil type was also measured by combining information from Magnascan with soil sampling across the study area. Soil moisture for each sampling position was estimated by entering the data into a GIS system and calculating the mean soil moisture around each sampling position using voronie correction.

Table 3.2. Invertebrates recorded in spatial studies 2000-02 and their overwinter location where known.

Taxa	Overwinter location
Carabidae	
Agonum dorsale	Boundary
Agonum muelleri	Boundary
Amara spp.	Boundary & Field (varies between species)
Asaphidion flavipes	Boundary
Bembidion lampros	Boundary
Bembidion obtusum	Boundary & Field
Calathus fuscipes	Field
Calathus melanocephalus	Field
Carabus spp.	Boundary
Demetrias spp.	Boundary
Harpalus affinis	Field
Harpalus rufipes	Field
Loricera pilicornis	Field
Nebria brevicollis	Boundary
Notiophilus biguttatus	Field
Pterostichus cupreus	Field (larvae) & Boundary (as adults)
Pterostichus madidus	Field (larvae) & Boundary (as adults)
Pterostichus melanarius	Field (larvae) & Boundary (as adults)
Trechus quadristriatus	Field
Carabid larvae	Field & Boundary
Total Carabidae	
Number of carabid species	
Boundary overwintering Carabidae	
Staphylinidae	
Paederus spp.	Boundary
Philonthus cognatus	Field
Philonthus spp.	
Stenus spp.	Boundary
Tachinus spp.	Boundary
Tachyporus chrysomelinus	Boundary
Tachyporus hypnorum	Boundary
Tachyporus nitidulus	Boundary
Tachyporus obtusum	Boundary
Xantholinus spp.	Boundary
Staphylinid larvae	Field & Boundary
Total Staphylinidae	
Number of Staphylinid species	
Elateridae	Field
Elaterid larvae	Field
Curculionidae	Boundary
Coccinelidae	Boundary
Gastrophysa polygoni (Chrysomelidae)	Boundary
Other Chrysomelidae	Boundary
Other Coleopteran larvae	
Lycosidae	Boundary & Field
Total predatory invertebrates	
Number of carabid & staphylinid species	
Boundary overwintering invertebrates	Boundary

Both the above techniques identify relative changes in soil moisture but cannot be used to determine actual soil moisture levels. In addition, the soil moisture levels determined in the autumn may not reflect those that occur in the preceding or following summer because soil moisture can be transitory, the soil type having a strong influence.

3.2.1.5. *Data analysis*

To determine whether the distribution of insects or the environmental parameters were spatially aggregated into patches of higher than average numbers or gaps of lower than average numbers their distribution was analysed using SADIE analysis (Spatial Analysis by Distance IndicEs) (Perry et al. 1999), termed "red/blue" analysis. This calculates the degree of clustering in the form of (i) 'patches' of large counts, using the overall index $\bar{v}_i$ and its associated probability P_i, or (ii) 'gaps' of small counts, using the overall index $\bar{v}_j$ and its associated probability P_j (Perry et al., 1999). For a particular set, if all of these indices have values around unity, conformation of the data to the null hypothesis of spatial randomness is indicated; a value of at least one index well above unity indicates spatial non-randomness of some form. Distribution data are presented as two-dimensional contour maps from counts, drawn using the package Surfer for Windows Version 6.04 (Golden Software Inc, Colorado, USA). Analyses were conducted for data from across the whole study area and in some cases for each field.

To test whether two data sets were spatially correlated, the correlation coefficient, X, between the clustering indices of each set was calculated according to the method described by Perry & Dixon (2002). Hence, if the indices of set one are denoted z_{i1}, with mean q_1 and those of set two z_{i2}, with mean q_2, then a measure of local spatial association for position i is given by:

$$\chi_i = n(z_{i1} - q_1)(z_{i2} - q_2) / [\Sigma_i(z_{i1} - q_1)^2 \Sigma_i(z_{i2} - q_2)^2]^{1/2}$$

The overall spatial association is the mean of these local values, $X = \Sigma_i \chi_i / n$. The significance of X was tested against values X_{rand} from a randomisation test that included a Dutilleul (1993) adjustment procedure to provide a probability value P_D.

There may also be differences in the invertebrate community composition between crops and between years. To test for crop differences, multivariate analyses were conducted on the pitfall data using routines in PRIMER (PRIMER 5.2.9, PRIMER-E Ltd). These analyses are relatively robust as they are non-parametric and make very little assumption about the nature of the data (Clarke & Warwick, 2001). A two way crossed ANOSIM was used to test for significant differences (inferred from similarities) between the invertebrate community composition of the samples according to crop, removing any year differences. Data was averaged across fields so that 'field' was the basic unit of analysis; June and July data were analysed separately. ANOSIM is based on a similarity matrix, which in this case was calculated using fourth root transformed data and the Bray-Curtis similarity co-efficient. The R statistic (global or pair-wise) that is generated reflects

the observed differences between the groups (in this case crops), contrasted with differences among replicates within them. The test is based on rank similarities between samples in the similarity matrix. R falls between 0 and 1 giving an absolute measure of how separated the groups are; 0 indicates that they are virtually indistinguishable and 1 indicates that all similarities within groups are less than any similarity between groups (i.e. groups are very different). The R statistic itself is a useful comparative measure of the degree of separation of sites, and its value is at least as important as its statistical significance, if not more so (Clarke & Warwick, 2001). As with standard univariate tests, it is possible for R to be significantly different from zero yet inconsequentially small if there are many replicates at each site. (Clarke & Warwick, 2001). Where a significant difference was found, SIMPER was used to characterise that difference. This identified which species discriminated the invertebrate communities between crops, based on rank abundance. The limitation is that the routine compares two groups at a time and this can complicate interpretation of the analysis.

3.2.2 Results

Spatial distribution data were collected for 29 species from seven invertebrate families over three years. In total 501,963 individual invertebrates were identified over the three years. Some invertebrate groupings were also compiled and these included: boundary overwintering Carabidae, total boundary overwintering invertebrates, number of carabid species, number of staphylinid species, number of carabid and staphylinid species, total number of predatory invertebrates and total species richness. Data from across the six fields for all of these species/families/groupings was analysed to determine the extent to which spatial patterning existed and the extent of spatial association between and within years. Association with the key environmental parameters of soil moisture and vegetation cover was also examined for many of these invertebrate groups. In addition, data for individual fields was analysed for some groups. Owing to the enormity of the data output, only a selection of the data can be presented here. These were selected as being either typical for an invertebrate family or being highly relevant to the overall aims of the project.

3.2.2.1. *Abundance and distribution patterns in 2000*

The abundance of carabid beetles increased from May through to July but the species richness declined (Table 3.3). In contrast, numbers and species richness of staphylinid beetles peaked in June. Thus in June the pitfall catch comprised Carabidae (44%) and Staphylinidae (42%), but in July the fauna comprised primarily Carabidae (94%). Two species, *Pterostichus madidus* and *P. melanarius*, which are large generalist predatory species, formed 91% of the pitfall trap catch at this time. The fauna was more diverse earlier in the summer with a more even species composition. The species that overwinter as adults in the field boundaries were most abundant early in the year (May and June). In contrast, those that overwinter as larvae within fields and emerge as adults were most abundant in July. The latter group were most abundant overall and, as a consequence, the total number of invertebrates was highest in July.

Table 3.3. Mean and 1 standard error (SE) for each predatory arthropod group across the six fields in 2000.

	May		June		early July		mid-July	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Agonum dorsale	0.73	0.04	1.41	0.07	0.30	0.02	0.26	0.02
Bembidion lampros	5.94	0.27	2.14	0.12	0.19	0.02	0.26	0.03
Bembidion obtusum	0.87	0.05	0.48	0.04	0.03	0.01	0.03	0.01
Nebria brevicollis	2.79	0.17	2.00	0.10	0.06	0.01	0.08	0.01
Poecillus cupreus	0.70	0.08	1.50	0.18	0.21	0.03	0.07	0.02
Pterostichus madidus	1.17	0.05	4.35	0.36	113.70	4.25	89.99	2.87
Pterostichus melanarius	0.14	0.01	12.46	1.20	10.96	0.92	9.91	0.83
Total Carabidae	17.30	0.46	26.95	1.49	127.53	4.44	103.02	3.16
No. carabid species	5.35	0.06	5.44	0.07	3.21	0.05	3.48	0.06
Boundary overwintering Carabidae	10.37	0.36	6.54	0.22	0.62	0.04	0.70	0.04
Philonthus cognatus	10.22	0.54	21.20	0.54	8.59	0.28	3.27	0.09
Total Staphylinidae	16.87	0.50	25.55	0.53	9.20	0.28	3.68	0.10
No. Staphylinid species	1.79	0.03	2.35	0.03	1.31	0.03	1.20	0.02
Lycosidae	1.40	0.08	3.33	0.22	0.54	0.04	0.48	0.04
No. carabid & staphylinid species	7.14	0.07	7.14	0.07	4.52	0.06	4.68	0.06
Total predatory invertebrates	36.09	0.66	60.72	1.71	139.62	4.49	109.08	3.16
Boundary overwintering	16.88	0.44	10.19	0.27	1.09	0.06	1.00	0.05

The red/blue SADIE analysis was used to test whether the distribution of invertebrate species or groupings was clustered into patches or whether gaps existed where few were present. There was evidence of significant clustering across the study area into patches, with gaps between these, for all the species and groups analysed, with a few exceptions on each date in 2000 (Table 3.4), as was also the case in 2001 (Table 3.5) and 2002 (Table 3.6). The strength of clustering varied between species and groups. Most species were also heterogeneously distributed within fields (data not presented here).In 2000, the boundary overwintering Carabidae and total invertebrates showed strong clustering on all four sampling occasions, but there were some differences in their distribution patterns. The boundary overwintering Carabidae remained largely associated with the field boundaries throughout the summer and only spread across the whole field in field S1 and to some extent in field S2 (Fig. 3.3). Patches of the group that included all boundary overwintering species were similarly distributed.

Figure 3.3. Spatial clustering for boundary overwintering Carabidae in a) June 2000 and b) early July 2000. The maps indicate clusters of relatively high counts ($v_i>1.5$) and small counts ($v_j<-1.5$).
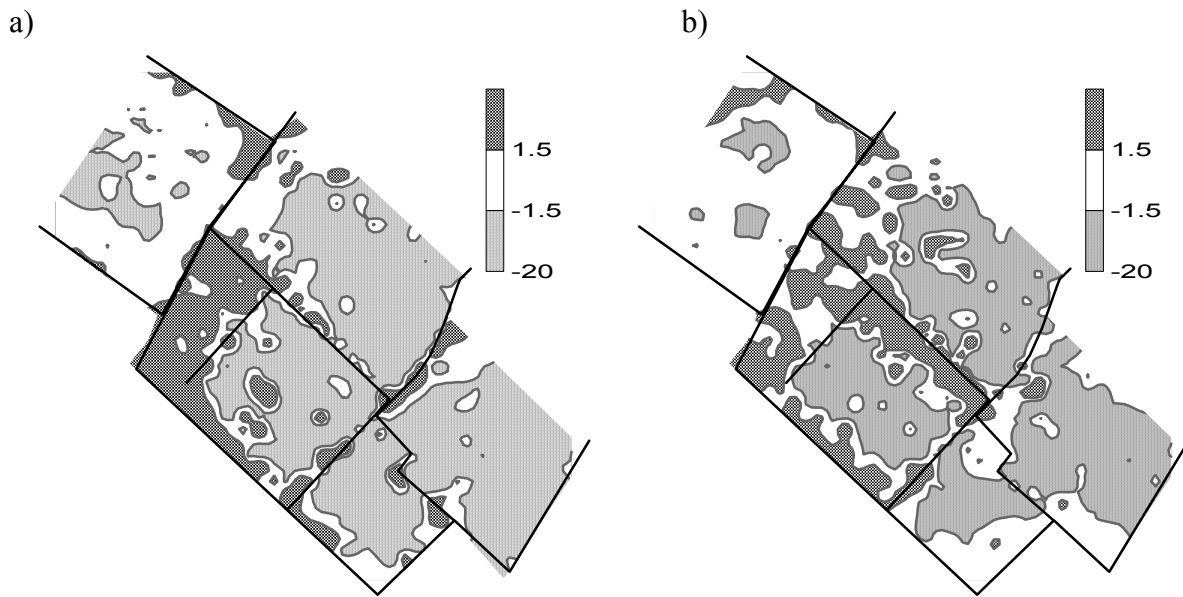
a)

b)

Figure 3.4. Spatial clustering in early July 2000 for a) *P. madidus* and b) *P. melanarius*. The maps indicate clusters of relatively high counts ($v_i>1.5$) and small counts ($v_j<-1.5$).
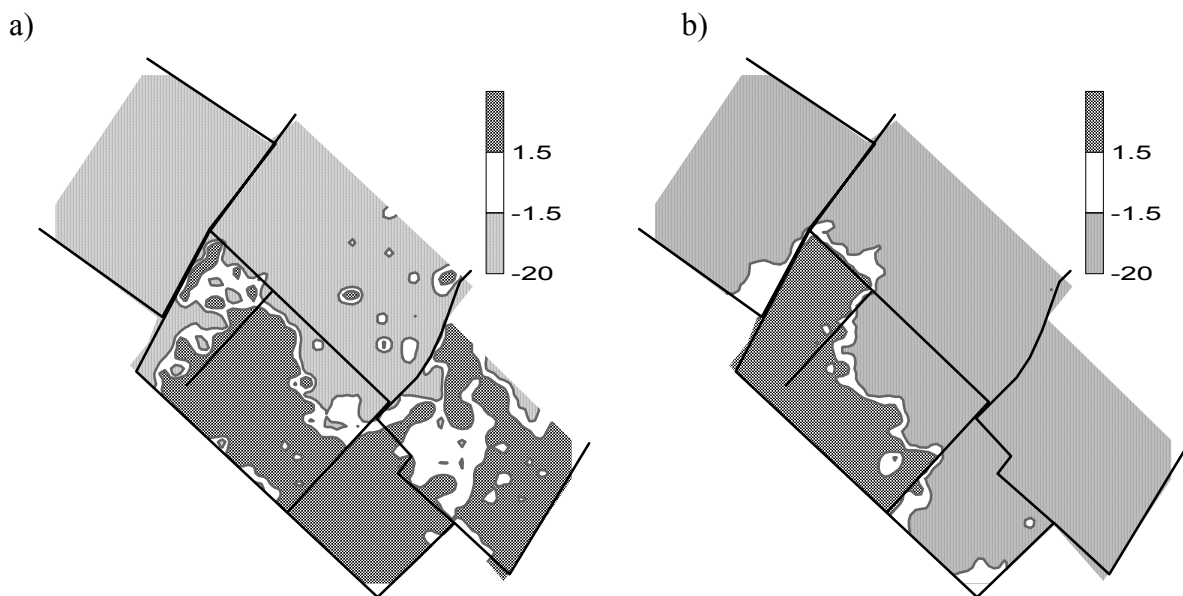
a)

b)

Table 3.4. Degree of clustering into 'patches' using overall index $\bar{v}_i$ and associated probability P_i, or of 'gaps' using overall index $\bar{v}_j$ and associated probability P_j for each predatory arthropod group across the six fields in 2000. (***=P<0.001, **= P<0.01, **= P<0.05).

	May				June				early July				mid-July			
	$\bar{v}_j$	P_i	$\bar{v}_i$	P_j	$\bar{v}_j$	P_i	$\bar{v}_i$	P_j	$\bar{v}_j$	P_i	$\bar{v}_i$	P_j	$\bar{v}_j$	P_i	$\bar{v}_i$	P_j
Agonum dorsale	-4.1	***	3.8	***	-4.9	***	5.6	***	-2.4	***	2.6	***	-2.9	***	3.0	***
Bembidion lampros	-3.0	***	3.2	***	-2.4	***	2.4	***	-2.0	***	2.0	***	-1.7	**	1.7	**
Bembidion obtusum	-1.4	*	1.3		-2.3	***	2.2	***	-1.1		1.2		-5.6	***	5.6	***
Nebria brevicollis	-3.4	***	3.9	***	-2.3	***	1.4	***	-1.4	*	1.4	*	-1.2		1.3	
Poecillus cupreus	-3.2	***	2.9	***	-3.3	***	3.3	***	-3.3	***	3.3	***	-2.3	***	2.4	***
Pterostichus madidus	-2.8	***	2.8	***	-3.9	***	3.8	***	-5.2	***	5.0	***	-6.3	***	6.4	***
Pterostichus melanarius	-2.6	***	2.5	***	-4.2	***	4.7	***	-4.3	***	4.6	***	-4.4	***	4.9	***
Total Carabidae	-2.3	***	2.2	***	-3.8	***	3.3	***	-4.8	***	4.6	***	-5.7	***	5.8	***
No. carabid species	-2.6	***	2.6	***	-4.9	***	5.1	***	-4.5	***	5.3	***	-5.0	***	5.3	***
Boundary overwintering Carabidae	-2.2	***	2.1	***	-3.3	***	3.6	***	-2.9	***	2.8	***	-2.6	***	2.3	***
Philonthus cognatus	-8.6	***	9.2	***	-7.4	***	8.0	***	-2.6	***	2.5	***	-2.5	***	2.7	***
Total Staphylinidae	-6.8	***	7.5	***	-6.8	***	7.5	***	-2.5	***	2.5	***	-3.1	***	3.4	***
No. Staphylinid species	-1.6	**	1.6	**	-1.6	**	1.6	**	-1.8	**	2.2	***	-4.3	***	4.6	***
Lycosidae	-1.6	***	1.6	**	-1.5	*	1.5	*	-1.6	*	1.5	*	-2.3	***	2.2	***
No. carabid & staphylinid species	-3.5	***	3.5	***	-3.5	***	3.5	***	-5.0	***	5.5	***	-5.9	***	6.2	***
Total predatory invertebrates	-5.9	***	6.3	***	-3.8	***	3.1	***	-4.7	***	4.5	***	-3.8	***	3.1	***
Boundary overwintering invertebrates	-3.1	***	3.2	***	-2.8	***	2.6	***	-2.5	***	2.9	***	-3.2	***	2.8	***

Table 3.5. Degree of clustering into 'patches' using overall index $\bar{v}_i$ and associated probability P_i, or of 'gaps' using overall index $\bar{v}_j$ and associated probability P_j for each predatory arthropod group across the six fields in 2001. (***=P<0.001, **= P<0.01, **= P<0.05).

|	June				July			
	$\bar{v}_j$	P_i	$\bar{v}_i$	P_j	$\bar{v}_j$	P_i	$\bar{v}_i$	P_j
Agonum dorsale	-3.8	***	3.5	***	-1.8	***	1.8	**
Bembidion lampros	-2.1	***	2.1	***	-1.8	***	1.8	**
Bembidion obtusum	-3.4	***	3.6	***	-0.8		0.9	
Nebria brevicollis	-5.4	***	5.1	***	-1.9	**	1.9	**
Poecillus cupreus	-3.0	***	3.1	***	-1.6	*	1.6	*
Pterostichus madidus	-6.5	***	5.3	***	-3.7	***	3.5	***
Pterostichus melanarius	-3.5	***	3.3	***	-4.4	***	4.7	***
Total Carabidae	-4.1	***	4.3	***	-3.0	***	2.8	***
No. carabid species	-1.9	***	2.1	***	-3.5	***	3.5	***
Boundary overwintering Carabidae	-5.3	***	5.1	***	-2.5	***	2.6	***
Philonthus cognatus	-3.3	***	3.0	***	-3.5	***	3.0	***
Total Staphylinidae	-5.6	***	5.5	***	-2.4	***	2.2	***
No. Staphylinid species	-4.6	***	5.1	***	-2.4	***	2.5	***
Lycosidae	-1.9	***	2.0	***	-1.4	*	1.4	*
No. carabid & staphylinid species	-4.3	***	4.5	***	-2.4	***	2.7	***
Total predatory invertebrates	-5.3	***	5.2	***	-2.6	***	2.4	***
Boundary overwintering invertebrates	-5.8	***	5.4	***	-1.8	**	1.9	**

Table 3.6. Degree of clustering into 'patches' using overall index $\bar{v}_i$ and associated probability P_i, or of 'gaps' using overall index $\bar{v}_j$ and associated probability P_j for each predatory arthropod group across the six fields in 2002. (***=P<0.001, **= P<0.01, **= P<0.05).

	June				July			
	$\bar{v}_j$	P_i	$\bar{v}_i$	P_j	$\bar{v}_j$	P_i	$\bar{v}_i$	P_j
Agonum dorsale	-3.4	***	3.1	***	-3.0	***	3.4	***
Bembidion lampros	-3.0	***	3.1	***	-1.6	**	1.7	**
Bembidion obtusum	-3.0	***	3.2	***	-1.5	*	1.5	*
Nebria brevicollis	-2.3	***	2.2	***	Insufficient data			
Poecillus cupreus	-1.2		1.2		-1.6	*	1.6	*
Pterostichus madidus	-6.3	***	5.8	***	-4.4	***	3.9	***
Pterostichus melanarius	-4.1	***	4.4	***	-3.6	***	3.6	***
Total Carabidae	-5.6	***	4.6	***	-4.0	***	3.5	***
No. carabid species	-3.9	***	4.1	***	-6.4	***	6.0	***
Boundary overwintering Carabidae	-3.6	***	3.5	***	-3.7	***	3.7	***
Philonthus cognatus	-3.3	***	3.0	***	-2.7	***	2.7	***
Total Staphylinidae	-3.5	***	3.5	***	-2.5	***	2.5	***
No. Staphylinid species	-4.1	***	3.7	***	-2.3	***	2.3	***
Lycosidae	Insufficient data				-1.5	*	1.5	*
No. carabid & staphylinid species	-4.8	***	5.0	***	-5.6	***	6.1	***
Total predatory invertebrates	-5.1	***	3.9	***	-3.9	***	3.5	***
Boundary overwintering invertebrates	-3.4	***	3.5	***	-3.3	***	3.8	***

Those beetle species that overwintered as larvae within fields and emerged as adults, for example the carabids *P. madidus*, *P. melanarius* and the staphylinid *Philonthus cognatus*, showed the strongest evidence of clustering into patches and gaps when they were most abundant (Tables 3.4, 3.5 & 3.6). The distribution patterns of the two *Pterostichus* species were quite different; *P. madidus* occurred throughout the study area whereas *P. melanarius* was confined to two fields (Fig. 3.4). The distribution and movement of these two species are more fully described in Holland *et al*. (2002; 2004).

The number of predatory invertebrates peaked in early July then started to decline. Numbers were highest in fields L1 (winter wheat), S2 (peas) and S3 (peas) during May and June but in July were highest in the pea fields S2, S3 and L3 (Fig. 3.5).

Figure 3.5. Spatial clustering for total predators in 2000. a) May, b) June, c) early July and d) late July. The maps indicate clusters of relatively high counts (v_i>1.5) and small counts (v_j<-1.5).

a)

b)

c)

d)
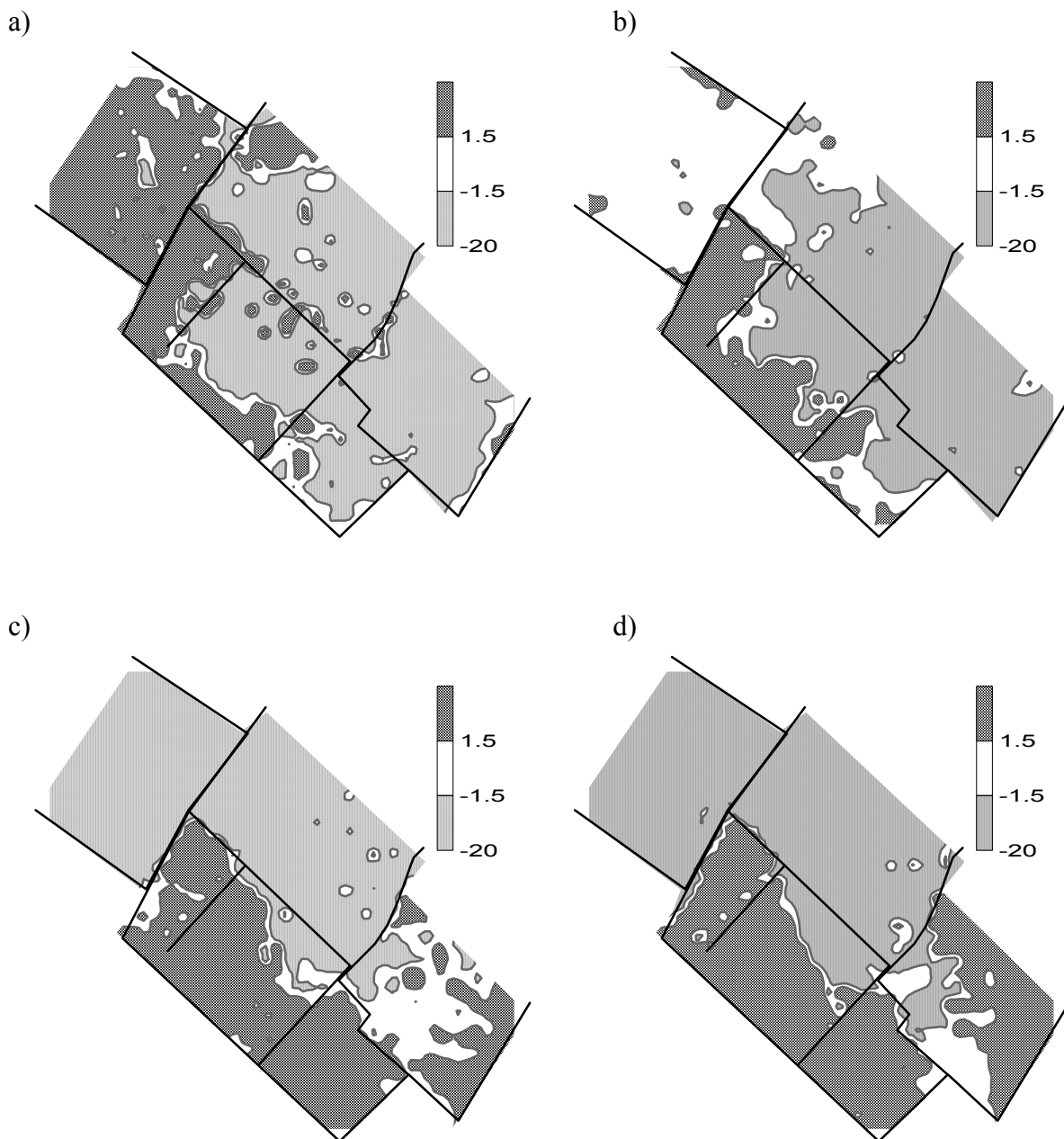
3.2.2.2. *Abundance and distribution patterns in 2001 and 2002*

In 2001, fewer predatory arthropods were caught compared to the previous year (Tables 3.3 & 3.7). In June, the pitfall catch comprised Carabidae (49%) and Staphylinidae (40%), by July the Carabidae (74%) were the most numerous compared to Staphylinidae (21%). *P. melanarius* and *P. madidus* were not as abundant as in the previous year but still formed 60% of the catch.

Table 3.7. Mean and 1 standard error (SE) for each predatory arthropod group across the six fields in 2001.

	June		July	
	Mean	SE	Mean	SE
Agonum dorsale	0.73	0.05	0.74	0.05
Bembidion lampros	0.62	0.04	0.77	0.08
Bembidion obtusum	0.09	0.01	0.01	0.00
Nebria brevicollis	4.89	0.25	0.03	0.01
Poecillus cupreus	0.76	0.09	0.40	0.07
Pterostichus madidus	0.84	0.04	18.90	0.73
Pterostichus melanarius	0.45	0.06	1.75	0.14
Total Carabidae	9.80	0.32	25.14	0.72
No. carabid species	3.35	0.06	4.99	0.08
Boundary overwintering Carabidae	6.38	0.26	1.72	0.10
Philonthus cognatus	8.44	0.52	5.86	0.23
Total Staphylinidae	11.38	0.56	9.74	0.33
No. Staphylinid species	4.37	0.12	3.71	0.06
Lycosidae	2.49	0.16	0.41	0.05
No. carabid & staphylinid species	7.72	0.14	8.71	0.11
Total predatory invertebrates	24.73	0.79	34.19	0.82
Boundary overwintering	7.72	0.29	2.64	0.13

The number of predators caught in 2002 was higher than in 2001 but lower than in 2000 (Table 3.8 compared with 3.3 & 3.7). In June, the predators comprised Carabidae (68%) and Staphylinidae (29%), but by July the Carabidae were again the most prolific group, comprising 94% of the catch. Again the two *Pterostichus* species comprised a large proportion of the catch (51% in June, 82% in July).

The location of some species and groups changed between 2000 and 2001. In 2001 and 2002, the patches of boundary overwintering Carabidae and of total invertebrates were found around and within the larger fields (Figs. 3.6 & 3.7) and were less evident in the smaller fields. In 2002, boundary overwintering Carabidae were found throughout most of fields L1 and L2 (Fig. 3.7). The total number of boundary overwintering invertebrates showed considerable changes in the location of patches in June from the smaller fields in 2000, to L3 in 2001 and to L1 and S1 in 2002. For July, the change was predominantly from the smaller fields in 2000 to L1 and L2 in 2001 and 2002 (Figs. 3.5, 3.6 & 3.7).

In 2001, patches of *P. madidus* were found in the three largest fields (two growing peas and one winter wheat) and in 2002 in L2 and L3 (Fig. 3.8). The patches of *P. melanarius* persisted in the same fields over the three years. *P. madidus* formed a large proportion of the total number of predators and consequently their distribution showed the same pattern, as described more fully in Holland *et al.* (2003).