FACTORS AFFECTING THE MORTALITY OF WINTER MOTH IN THE LOWER MAINLAND OF BRITISH COLUMBIA.

by

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ABSTRACT

Populations of winter moth, *Operophtera brumata* (L.), were monitored at four sites in Richmond, British Columbia, between 1989 and 1992. Populations peaked in 1990 on both blueberry and birch and declined with an eventual population crash in 1992. Parasitism by *Cyzenis albicans* (Fall.) fluctuated between years at each site. Parasitism reached its highest levels on both birch (ca. 55%) and blueberry (ca. 35%) in 1991. Pupal predation was the most important stage specific mortality factor throughout the four years. In 1992, the year of population crash, larval mortality was high. Trends in "death of pupae due to unknown causes" were linked to larval mortality and are suggested to result mainly from poor foliage quality. An unusually early spring in 1992, may have led to the observed increases in these two mortality factors. The incidence of viral or other diseases among the populations are low.

Generally, pupal predation peaked in 1990 (ca. 90%) and then declined. *Pterostichus* spp., *Amara* spp., *Harpalus affinus* and subsoil beetle larvae are implicated as important predators. The levels and trends in predation were similar at sites with very different assemblages and abundances of beetles. There were no differences in the abundances of beetles at each site between 1991 and 1992. However, many of the important predatory species declined in 1992. An examination of the possible interactions between *C. albicans* and generalist predators is made. The increased range of pupal sizes in the soil, due to the presence of *C. albicans* may be a mechanism for inducing a numerical response among generalist predators. However, simultaneous population declines at sites with low levels of *C. albicans* indicate that winter moth outbreak and decline in North America may be induced by a number of different factors.

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street kids of Bogotá.

CHAPTER 1
GENERAL INTRODUCTION

One of the most frequently cited examples for the success of classical biological control is that of the winter moth, *Operophtera brumata* (L.), in Canada, controlled by its parasitoid, *Cyzenis albicans* (Fall.) (Embree 1971, DeBach 1974, Hassell 1978, Embree and Otvos 1984, Murdoch *et al.* 1986). There has been extensive monitoring of both the moth and parasitoid populations in eastern Canada in the 1950's and 1960's (Cuming 1961, Embree 1965b, 1966), and in western Canada in the 1980's (Roland 1986a, 1986b, 1988, 1992). Long-term population studies have also been carried out on endemic populations in Britain (Hassell 1969a, 1969b, Varley *et al.* 1973). Because of this, these two species have formed a basis for much of the development of modern ideas in population dynamics theory (Varley and Gradwell 1968, 1970, 1973, Varley *et al.* 1973) and host-parasitoid interactions (Hassell 1968, 1980, 1987, Hassell and May 1974, May 1978). In this study, examination of the mortality factors acting on a new post-introduction outbreaking population of winter moth in Richmond, British Columbia, will be made in the light of the above information. In particular, I address the question of why *C. albicans* has been necessary to bring about winter moth population decline in Canada.

This first chapter offers a brief introduction to the winter moth and its parasitoid and presents a background for understanding winter moth population dynamics.

1.1 Winter moth

Distribution: The winter moth, *O. brumata,* is one of five old world *Operophtera* species. It is distributed throughout central Europe, east to the Volga and the Caspian Sea and in the south to the Caucus and the Black Sea. The species also occurs on Iceland, the

Faroe Islands, Great Britain and Ireland. It ranges from Northern Scandinavia (though absent from the extreme north) to the Mediterranean. Winter moth also occurs around the Amur, in Ussuri in southeastern Siberia, and on Hondo in Japan (Fig. 1) (Tenow 1972, Skou 1986). The main areas of mass occurrence of winter moth include regions bordering the North Sea and the Baltic, southern England, northern France, Holland, Belgium, northern Germany, Poland, the Baltic states, Denmark and Sweden (Tenow 1972).

Winter moth was recently introduced to the Faroe Islands, either from the British Isles or northern Europe (there is no phytosanitary control of material brought from Denmark, Scotland, Norway and Iceland). Interestingly, the moth does not exist on some of the larger southern islands of the Faroes (i.e. Sandoy and Suduroy) which are opposite prevailing winds (Koponen 1985). Winter moth has also recently become established in North America on both the east and west coasts (Hawboldt and Cuming 1950, Smith 1950, Ferguson 1978, Gillespie *et al.* 1978); this will be addressed in more detail in Chapter 2.

The life cycle: *Operophtera brumata* is one of a small number of geometrids whose adults are adapted for winter existence. The male has a wingspan of about 23 - 31mm. The wings are grayish brown, the forewing having numerous dark, wavy, transverse lines. The hind wings have one or two indistinct transverse lines though these may sometimes be lacking. There may be colouration differences between populations (pers. obs.). Females are brachypterous with very short wing remnants of about 2mm in length. The body is grayish, brownish or grayish black. The wings are steel gray with a black transverse band near the termen.

The adults usually emerge in October and November, though they may emerge earlier, (i.e. September) in more northerly regions and later, (i.e. December) during mild winters or in southern regions (see Wylie, 1960a). Alma (1969) describes male flight

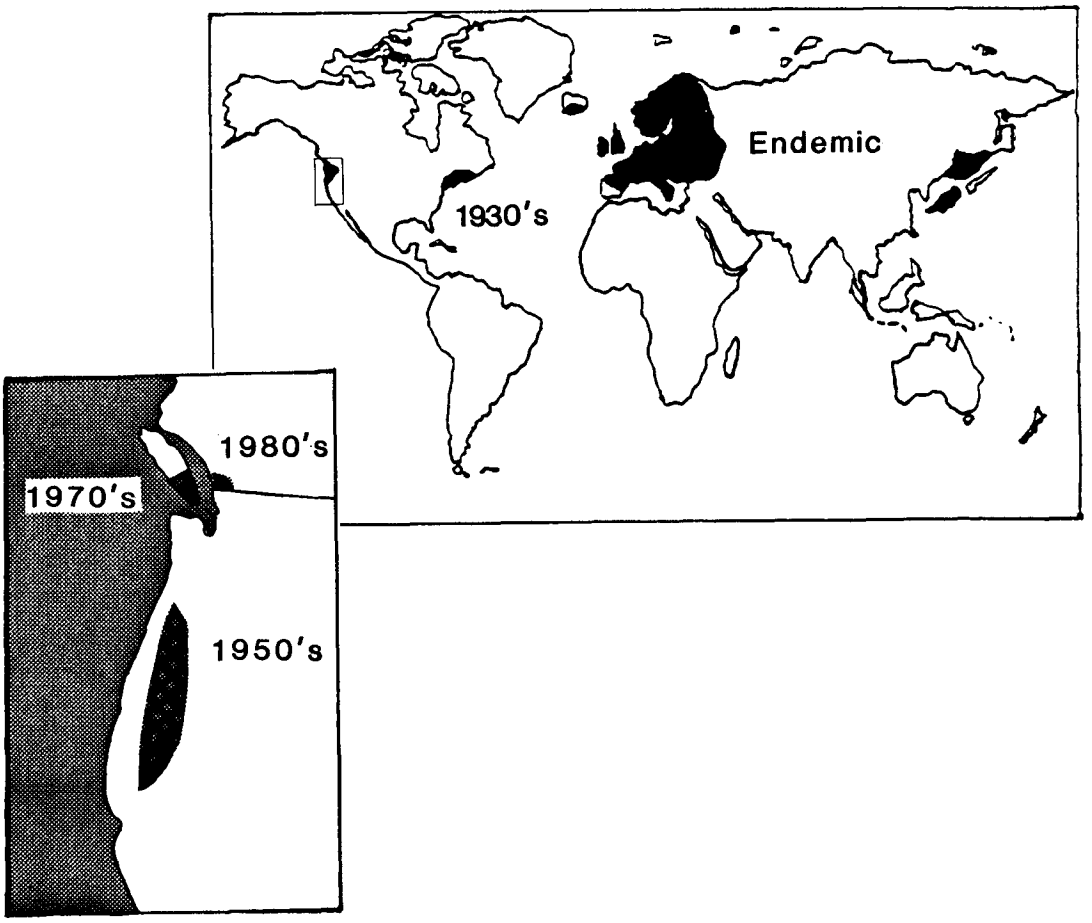

Figure 1. World wide distribution of the winter moth, *Operophtera brumata* (L.). Dates indicate probable introduction events into North America; to Nova Scotia in the 1930's and inset, to the western United States in the 1950's, Vancouver Island in the 1970's and the Lower Fraser Valley in the 1980's (see also Chapter 2).

activity in Britain and suggests a temperature threshold for flight at between 5 and 5.5°C. Females usually emerge about a week after the males. After the females emerge, they climb adjacent trees and mate during this ascent, usually at about 1 - 2 meters from the ground. Female sex pheromone attracts males and operates at unusually low temperatures (4 - 15°C), exhibiting an upper response limit which coincides with the lower response limit of other reported moth sex pheromone systems (usually 15 - 17°C) (Roelof *et al.* 1982).

Females lay up to 300 eggs (but generally 70 - 200 eggs) in cracks on the bark, and under lichens and mosses. The eggs are laid singly or in small groups and are ovoid, but somewhat flat, 0.7 - 0.8mm long and 0.5mm wide. The surface of the egg is reticulated by minute ridges separated by shallow pits. Newly laid eggs are light green in colour, later changing to orange and finally deep brown or black before larval eclosion. Eggs overwinter with a suggested developmental threshold of about 3.9 - 4°C (Embree 1970, Kimberling and Miller 1988). The time for egg development depends on the region. In southern Italy the egg stage lasts only about two months whereas in northern Europe it lasts about eight months. These differences can be partially attributed to temperature differences between regions, but there are also intrinsic differences between the populations (Wylie 1960a, Holliday 1985). Authors disagree on whether there is a diapause, but there again appear to be differences between regions (Wylie 1960a, Bonnemaison 1971, Holliday 1985). Kimberling and Miller (1988) suggest that responses to chilling of winter moth eggs indicate that there is a diapause even where other authors had discounted it (see also Tauber and Tauber 1976). The eggs are extremely cold tolerant with supercooling points estimated to be between -31°C (Macphee 1967, Hale 1989) and -37°C (Hale 1989).

In British Columbia larval eclosion is from mid-March till April. There are five larval instars. The first instar is the main dispersal stage (some second instars may also disperse). Dispersal is by means of parachuting on a silk thread. The degree and distance of

dispersion depends on temperature and climatic conditions as well as the condition of the host plant foliage on larval eclosion (Edland 1971, Holliday 1977). The larval stage lasts from March till May or June and the larvae then spin to the ground to pupate.

Pupation occurs about 1 - 2 cm below the soil surface where a cocoon is spun. The length of pupation varies between regions. In Italy, for example, pupation can last for eight months while in northern Europe it lasts for about three months, so there are intrinsic population differences (Wylie 1960a, Holliday 1983). In British Columbia, pupation is from early to mid-May with adult emergence in mid November, a period of about six months.

Host plants and damage: Although the larvae are largely monophagous, the species is polyphagous primarily on deciduous but also on coniferous trees (Wint 1983). Mrkva (in Wint 1983) indicated that winter moth feeds on about 160 species of deciduous trees and shrubs. Wint (1983) indicates that the species is known to feed on plants from 14 different plant families.

It is generally accepted that oak (*Quercus* spp.) is the primary host (Varley and Gradwell 1958, Feeny 1970, Hunter 1990). Other important hosts include: apple, (*Malus* spp.), pears (*Pyrus* spp.), plums and blackthorn (*prunus* spp.), hazel (*Corylus avellanae* L.), beech (*Fagus sylvatica* L.), hawthorn (*Crataegus monogyna* Jacq.), etc. (Wint 1983). In southern Europe beech trees are an important host, while in central Europe, willows (*Salix* spp.) are more important (Topp and Kirsten 1991). In North America, important hosts include: oak, apple, birch (*Betula* spp.), highbush blueberries (*Vaccinium corymbosum* L.), raspberries (*Rubus* spp.) and commercial filberts (*Corylus* spp.) (Embree 1965b, Gillespie *et al.* 1978, AliNiazee 1986, Fitzpatrick *et al.* 1991a).

In Scotland, considerable attention has recently been directed to winter moth as a pest of Sitka spruce, (*Picea sitchensis* (Bong) Carr) (Stoakley 1985, Hunter *et al.* 1991). Previously populations built up on birch or on heather (*Calluna vulgaris* L.) and then switched to the Sitka spruce. Now however, it appears that the outbreaks build up directly on the spruce. The larvae cause substantial damage and distorted growth of the spruce trees (Watt and Macfarlane 1991).

1.2 Winter moth parasitoids

A number of parasitoids have been recorded from the eggs, larvae and pupae of winter moth in Europe (see Sechser 1970a, 1970b, Wylie 1960b). On the two occasions when winter moth was introduced to Canada it went into post-introductory outbreak (Embree 1965b, Gillespie *et al.* 1978). This implicated natural enemies as responsible for maintaining population equilibrium in Europe, and so parasitoids were introduced from Europe to Canada in an attempt at biological control. Only two of the introduced parasitoids, *Cyzenis albicans* (Fall.) and *Agrypon flaveolatum* (Grav.), became established (Cuming 1961, Roland 1988).

The extent of native parasitoids attacking winter moth in Nova Scotia, before introduced parasitoids became established, is unknown. However, in British Columbia, a number of native parasitoids, normally parasitic on Bruce's spanworm, *Operophtera bruceata* (Hulst), were recorded from winter moth. The most important was an unnamed *Phobocampe* sp. (Ichneumonidae) (Gillespie and Finlayson 1981, Humble 1984). Three further species, *Trichistus crassus* Tow. and Tow., *Agrypon provancheri* (Dalla Torre) and *Cyzenis pullala* (Tsnd.), also parasitised winter moth. By 1981, there was ca. 1.5% parasitism of winter moth larvae, mainly attributed to these native parasitoids, although *C. albicans* was already present in the population at that time (Humble 1985b).

A number of native pupal parasitoids have also been recorded from winter moth in British Columbia. *Coccugomimus hesperus* Tow. and Tow. and *Buathra dorsicarinata* (Pratt) were found to parasitise 4% of the winter moth-spanworm pupal complex in Victoria in 1981, and 10% in 1982. These species most commonly attacked winter moth. A further species, *Cratichneumon* sp., preferred Bruce's spanworm (Humble 1985a).

Adults of *C. pullala* and *C. albicans* are almost morphologically indistinguishable. Furthermore, *A. provancheri* is morphologically very similar to *A. flaveolatum*. These were once regarded as synonymous species (Gillespie and Finlayson 1981, Barron 1989). These species similarities may cause some difficulty in assessing the success of the biological control. However, it is apparent that the native parasitoids were not capable of preventing winter moth outbreak, or of causing outbreak decline, since it was not until *C. albicans* and *A. flaveolatum* became established that outbreak decline occurred and population stability was reached.

1.2.1 *Cyzenis albicans*

Cyzenis albicans has largely been implicated in the successful biological control of winter moth in Canada (Hassell 1980, Embree 1991). This Tachinid fly is widely distributed over the range of the winter moth. It is found from central Sweden to central Switzerland but probably does not occur in the more southern regions of winter moth distribution (i.e. Sicily) (Wylie 1960b). The distribution of *C. albicans* in Japan and eastern Asia has not been discribed.

The life cycle: The life cycle of *C. albicans* is synchronized with that of the winter moth. Intrinsic differences between regions in the timing of adult emergence correspond

with winter moth larval hatch in those regions (Wylie 1960b). Adult females emerge approximately seven days after males. Mating occurs during daylight. Following mating, the adult females feed on flowers, sap fluxes and honey due for about four weeks (Embree and Sisojevic 1965). By the end of that time the winter moth are in their fifth instar and the parasitoid females have their full complement of eggs, about 1000-2000 (Hassell 1980). Laying occurs over a period of 8 - 16 days. In the field, maximum egg populations occur 7 - 14 days after the beginning of oviposition.

Shiny black microtype eggs of approximately 0.17mm in length are laid on foliage near caterpillar feeding damage. Eggs are concentrated on the lower portions of the trees (Embree and Sisojevic 1965). Embree and Sisojevic (1965) found ca. 80% of eggs are laid immediately beside caterpillar feeding damage and predominantly on the underside of leaves (see also Wylie 1960b). Because of the mode of oviposition there is a significantly clumped distribution of eggs. Parasitism is correlated with host density, where host densities are high (Embree and Sisojevic 1965, Hassell 1980). *Cyzenis albicans* responds to damage from a number of defoliators on different host plants. Parasitism may be more efficient on oak (Embree 1966, Roland 1986a, 1986b, 1990a), but Hassell (1980) found no difference between the levels of parasitism on oak and those on hawthorn, *Crataegus oxyacanthoides* Thuill., blackthorn, *Prunus spinosa* (L.), or hazel, *Corylus avellana* (L.). However, *C. albicans* is more successful in parasitizing winter moth on oak than on apple (*Malus* spp.) (Embree 1966, Holliday 1977, Roland 1986a, 1986b, 1990a).

Wylie (1960b) and Hassell (1980) have described the mode of parasitism in detail. The eggs are viable for about eight weeks. Each egg contains a fully formed first instar larva. The larva is ingested and hatches in the mesenteron of the host, penetrates the gut wall and lodges in the salivary gland causing a swelling of the surrounding tissue. This first instar lasts as long as it takes the host to pupate. There is no molting until after host

pupation. After host pupation, the first instar larva makes a respiratory funnel that opens to the exterior on the ventral side of the pupa near the thoracic-abdominal junction. It feeds with its posterior spiracles inserted in the funnel until only the empty pupal case remains. When mature the parasite larva withdraws its spiracles from the funnel, reverses itself and forms a puparium inside the empty host pupa. The pupa goes into diapause and adults emerge the following spring.

Cyzenis albicans is known to develop to maturity from *Triphosa dubitata* (L.) and *Eupithecia pimpinellota* (Hbn.) in the wild, and has been reared to maturity from *Operophtera fagata* (Scharf.), *Rhyacionia buoliana* (Schiff) (Olethreutidae) and *Galleria mellonella* (L.) (Pyralidae) in laboratory studies (Wylie 1960a, Embree and Sisojevic 1965). Embree (1965a) estimated that 27% of Bruce's spanworm in Nova Scotia were parasitized by *C. albicans*. However, a number of common defoliators will not support *C. albicans* to maturity, i.e. *Cosmia trapezina* (L.), *Erannis defoliana* (Clerk.), *Alsophila pometoria* (Harr.), *Malacosoma americanum* (F.), and *Pseudexentera cressoniana* Clem.(Embree and Sisojevic 1965, Hassell 1969a).

Mortality: Mortality of adult *C. albicans* has not been studied in detail. Adults are probably eaten by a number of bird species. The parasite *Perilampus ruficornis* (Fab.) and a fungus *Entomophthora muscae* (F.) Fris. also attack adults but the extent of this in nature is unknown (Wylie 1960b). Hassell (1969a) indicated that the key factor in *C. albicans* population dynamics was total egg mortality. This results from the high reproductive potential of the adults with resultant low levels of host parasitization. Synchronization with the host is important in determining the extent of this mortality. To survive, an egg must be swallowed by a winter moth larva or other suitable host, each of which supports only a single parasitoid to pupation. Eggs laid after host pupation will not survive. Likewise, eggs consumed by second or third instars generally rupture and do not survive. Furthermore,

consumption of the eggs by defoliators, other than suitable hosts, represents a considerable source of mortality. Of the total number of parasitoid eggs found on foliage at Oak Hill, Nova Scotia in 1962, 16% occurred beside feeding damage caused by *P. crossonionia.* This resulted in a reduced effectiveness of *C. albicans* (Embree and Sisojevic 1965).

Pupal death is also an important source of mortality. In general soil mortality of *C. albicans* at Whytham Wood, was greater than the corresponding soil mortality of winter moth. Hyperparasitism is a significant source of soil mortality for *C. albicans.* In Britain, *Phygadeuom dumetorum* (Grav.) has been implicated in causing significant mortality of *C. albicans* in some years (Hassell 1969a). In Victoria, two native hyperparasites, *Phygadeuon* sp. and *Villa (Hemipenthes) catulinia* Coq., were parasitizing up to 12% of *C. albicans* in 1981 (Humble 1985b). However, the main cause of soil mortality is pupal predation (Hassell 1969a); this will be discussed in more detail in subsequent chapters.

1.3 Population dynamics of winter moth

The most extensive documentation of winter moth population dynamics has been compiled by Tenow (1972). He collected records from various sources dating back to the 1890's and indicated that winter moth in the Scandes go through outbreaks of approximately 9 - 10 year periodicity. These outbreaks were associated with outbreaks of another Geometrid species, the autumnal moth *Oporinia autumnata* Bkh..

In the 1960's Varley and Gradwell (1968, 1970) compiled life tables of a winter moth population at Whytham Wood near Oxford, England. Analysis of these life tables indicated two important mortality factors. The first was termed 'winter mortality' and was found to be the key factor controlling the population. This factor included all mortality incurred from egg laying through to pupation and thus consisted of mortalities from larval

predation, starvation, dispersal losses and viral or microsporidian diseases. However, they attributed most of the winter mortality to asynchronies between bud burst and egg hatch. The second mortality factor of importance was 'soil mortality'. This factor was attributed mainly to pupal predation and was found to be density dependent thus representing a mechanism of population regulation[1] (Varley and Gradwell 1960, 1963a, 1963b, 1968, 1971, 1973, Varley *et al.* 1973).

When winter moth was first discovered in eastern Canada, a number of parasitoids were introduced to control it. The Tachinid parasitoid, *Cyzenis albicans* (Fall.) was found to be highly efficient at parasitizing larvae at high populations while an introduced Ichneumonid species, *Agrypon flaveolatum* (Grav.) was more efficient at low winter moth populations (Embree 1965b, 1966, 1971). This result was surprising, since in Nova Scotia, *C. albicans* was parasitizing up to 80% of the winter moth larvae on oaks, while in England parasitism was more usually at about 2% (see Roland 1988). Pupal predation received little consideration in Nova Scotia. Small mammals were suggested as being responsible for about 30% of predation (Embree 1965b).

When winter moth was discovered in western Canada, the two parasitoids were quickly released (Williamson 1981a, 1981b, 1981c, 1984, 1986, and see details in Chapter 2). As in Nova Scotia, parasitism increased to high levels, about 70%, after which the winter moth population began to decline. However, Roland (1986a, 1988, 1990b) suggested that it was not *C. albicans* that was actually responsible for the decline, but that increased death of pupae in the soil initially caused the population reduction. On reanalysing Embree's data from Nova Scotia, Roland (1986a, 1988) found that Embree

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[1] Recently there has been much debate concerning the regulatory role of pupal predation. Den Boer (1986, 1988) maintains that density dependence is not a prerequisite of population regulation and therefore, that mortality of winter moth pupae is not regulatory. Others e.g. Latto and Hassell (1987) and Poethke and Kirchberg (1987) have argued against den Boer. In this thesis I will regard pupal mortality as regulatory.

had overestimated mortality due to *C. albicans* by including in his mortality estimates, death due to nematodes and other parasites. When these other parasites were excluded from analyses, it appears that mortality due to parasitism by *C. albicans* did not increase proportionately to the total mortality. Furthermore, Roland (1988) highlighted the fact that decreases in defoliation had been similar in areas with very different incidences of parasitism. He therefore suggested that soil mortality had, in fact, been more important than parasitism due to *C. albicans* in bringing about winter moth population decline in Nova Scotia.

Roland (1986a, 1988, 1990b) has suggested that the parasitoid may have been important in instigating the decline of winter moth by inducing soil mortality in both Nova Scotia and British Columbia. In Nova Scotia, winter moth populations were high for about 25 - 26 years before the parasitoids were introduced. About four years after the introduction parasites increased and spread, and the decline in winter moth commenced. In Victoria a similar pattern emerged. Winter moth was present at high levels, for only about 6 years before being identified (it was initially mistaken for the native Bruce's spanworm, *Operophtera bruceata* (Hulst)) and soon after its parasitoids were released. Four years later, population reduction began to be noticed. Could *C. albicans* have caused these declines through interactions with generalist predators?

Larvae in Nova Scotia were found to be free of viruses before the introduction of the parasitoid, but a virus was found soon after and spread throughout the population (Embree 1966). In Victoria, in 1978, virus was used in experiments to control winter moth and in the hope of starting an epizootic. The virus was found to control the moth to a small extent, but an epizootic did not occur (Cunningham *et al.* 1981). This may have been due to a lack of parasitoids to transmit the virus. Perhaps if the experiment were tried again in the presence of parasitoids the results would be different.

Roland (1986a, 1988) proposed three mechanisms by which parasitoids could increase soil mortality, two of which refer directly to pupal predation. The first mechanism would cause a numerical response in predators. Since parasitoid pupae are in the ground from early summer through to the following spring while healthy winter moth pupae emerge in winter. Therefore, pupae are available in the soil for an extended period enabling predator populations to build up over winter. A second mechanism suggests that predators preferentially take winter moth pupae over parasitoid pupae, and thus as the population of available healthy pupae in the soil diminishes due to parasitism, the remaining healthy pupae become increasingly susceptible to predation. A third suggested mechanism is that parasitoids increase the transmission of virus or disease causing spores (fungal or microsporidian) among larvae. The larvae pupate, but die as pupae thus increasing soil mortality. These mechanisms are not necessarily exclusive.

Interestingly, in Canada, a similar *Operophtera* species, Bruce's spanworm, often occurs at the same sites as winter moth (spanworm is described in Chapter 4). Spanworm has not received as much attention as winter moth. However, examination of reports from the Forest Insect and Disease Survey indicate that population outbreaks do occur. These outbreaks last for similar periods of time to those of the winter moth. Generally, outbreak decline in spanworm has been attributed to viruses or ground predators (Canadian Department of Forestry 1964, 1974, Embree 1966). If spanworm outbreaks are generally controlled by generalist ground predators, it is surprising that these are not able to suppress winter moth outbreaks as well. There may be differences in the interactions between predators in the soil depending on whether or not the prey pupae have parasitoids and viruses. Without these additional mortality agents, soil predators may be insufficient to suppress outbreaks.

1.4 Objectives

Winter moth was first identified in the lower mainland of British Columbia in 1985. Severe defoliation began to be noticed in 1988 along Highway 99 and at Richmond Nature Park (Wood and van Sickle 1985, 1990, 1991). Losses of blueberries began to occur in the lower mainland due to winter moth infestations (Fitzpatrick *et al.* 1991a). Although the moth probably arrived from Vancouver Island, I regard this as a second introduction into western Canada because of the occurrence of a post-introductory outbreak. However, there are a few important differences with this introduction. Firstly, the main host plants are different, with birch and blueberry being the major available hosts in the Fraser Valley. Secondly, although it is unknown how the moth arrived here, it is likely that transportation of pupae occurred, since the parasitoid *C. albicans* is present, with no record of release.

The objective of this research was to investigate the mortalities influencing winter moth populations in the lower mainland. Winter moth populations at two birch sites and two blueberry sites have been monitored since 1989 so that winter moth population densities, levels of predation and parasitism at these sites is available for four years. In this thesis, I will therefore;

I) Determine the relative importance of parasitoids, disease and pupal predators for winter moth populations in Richmond (Chapter 2).

II) Compare mortality on blueberry and birch, and in particular examine the success of *C. albicans* in parasitizing winter moth on these two hosts (Chapter 2).

III) Investigate predation of winter moth pupae and identify the possible predators of the pupae in birch and blueberry sites in the Lower Fraser Valley (Chapter 3).

IV) Investigate the possibility of a link between parasitism by *C. albicans* and pupal predation (Chapter 3).

CHAPTER 2
MORTALITY OF WINTER MOTH IN BIRCH STANDS AND BLUEBERRY PLOTS IN THE LOWER FRASER VALLEY OF BRITISH COLUMBIA.

2.1 Introduction

Control of winter moth, *Operophtera brumata* (L.), by its parasitoid, *Cyzenis albicans* (Fall.), is commonly cited as one of the most important examples for the success of classical biological control (Embree 1971, DeBach 1974, Hassell 1978, Embree and Otvos 1984, Murdoch *et al.* 1985). Winter moth, native to central and eastern Europe, has only recently become established in North America. The moth was first introduced to eastern Canada around the 1930's (Cuming 1961, Embree 1965b, 1966), but it was only correctly identified in 1950 having been mistaken for the native spring cankerworm, *Paleacrita vernata* Peck (Hawboldt and Cuming 1950, Smith 1950). From 1954 to 1961, a program of biological control was carried out in eastern Canada with the introduction of six parasitoids from Europe. Only two of the parasitoids, *C. albicans* and *Agrypon flaveolatum* (Grav.), became established. The subsequent decline of winter moth populations from 1961 to 1963, was attributed to these two introduced parasitoids (Embree 1966).

The first records of winter moth in western North America are from collections made in 1958. The moth was probably introduced around the 1950's (Ferguson 1978). It is not known whether this was a completely new introduction or whether individuals had been transported from eastern Canada. There appears to have been at least three separate introductions into the west. (1) In Washington and Oregon the winter moth has been present since the 1950's (Ferguson 1978). (2) In British Columbia it appears to have been

first introduced to Vancouver Island (Gillespie *et al.* 1978) with (3) a second, later introduction to the lower mainland (Wood and Van Sickle 1985). Winter moth was correctly identified on Vancouver Island in 1978, having been apparent at high densities only since the early 1970's (Gillespie *et al.* 1978). The moth has now spread on Vancouver Island from Sooke to Nanaimo and Mill Bay (Wood and Van Sickle 1985, 1986, Pivnick 1988).

The main host plants of winter moth on Southern Vancouver Island are Garry Oak (*Quercus garryana* Douglas) and apple (*Malus* spp.). Defoliation was particularly severe in the late 1970's to early 1980's (Gillespie *et al* 1978, Roland 1986a). The two parasitoids, *A. flaveolatum* and *C. albicans*, (from Europe and eastern Canada), were released in Victoria between 1979 and 1982 to control the winter moth (for details on introductions and recoveries see Williamson 1981a, 1981b, 1981c, 1984, 1986). As in eastern Canada, *C. albicans* proved to be effective in parasitizing the moth and has been attributed (though indirectly) to the decline of the moth on Vancouver Island (Roland 1986a, 1988).

In Nova Scotia, although *A. flaveolatum* was suggested to be important in controlling low density populations of winter moth (Embree 1966, 1991) it has been suggested that this species was not crucial to the success of *C. albicans* (Hassell 1980). Levels of parasitism by *A. flaveolatum* are low in Victoria and Vancouver (Roland 1986a, 1992, and pers. obs.) and will not be discussed.

One of the most fascinating paradoxes to arise from these two examples of biological control is that of the discrepancies between the role of *C. albicans* in Britain and its role in both eastern and western Canada. In Britain, winter moth populations are largely governed by the destabilizing effects of 'winter disappearance' (largely dependent on asynchronies in the timing of bud burst and egg hatch) and the stabilizing effects of density

dependent soil mortality (mainly attributed to pupal predation) (Varley *et al.* 1973). Furthermore, *C. albicans* plays only a minor role in winter moth population dynamics since the levels of parasitism are normally low (about 5%) (Hassell 1969a). However, in Canada, on the two occasions where *C. albicans* was introduced, the parasitoid appeared to initiate dramatic crashes in winter moth populations. Parasitism in Nova Scotia had reached levels of 70% on oak six years after its introduction, with levels as high as 80% at some sites. On apple, levels of parasitism as high as 50% were recorded in the early 1960's (Embree 1965b). Hassell (1980) has suggested that lower pupal mortality observed in Nova Scotia may be the key to understanding the differences in the dynamics and interactions of the two species on the two continents. In Britain, winter moth pupal predation is high, and predation of *C. albicans* is expected to be higher due to the extended availability of *C. albicans* pupae in the soil (Hassell 1969a, 1969b, 1980). Therefore, in Britain, *C. albicans* is limited to densities that cause insignificant host mortality. A lower pupal mortality in Canada may have enabled the winter moth population to reach high levels and when *C. albicans* was introduced, low soil mortality allowed it to increase rapidly until it caused winter moth populations to collapse (Hassell 1980).

After the introduction of *C. albicans* to Victoria in 1979, winter moth populations also went into decline. Parasitism reached levels as high as 84% on oak and 50% on apple (Roland 1986a, 1986b). Roland (1986a), investigating the success of *C. albicans*, indicated that some years after its initial introduction, winter moth soil mortality began to increase from levels as low as 10% in 1981 to levels of 96% in 1987 (Roland 1992). A similar observation had been made in Nova Scotia with soil mortality increasing after the introduction of *C. albicans* from 37% in 1954 - 1959 to 94% in 1961 and 1962 (Embree 1965b, Hassell 1969a). Roland's (1986b, 1988) analysis indicated that soil mortality was actually more important than parasitism in bringing about regulation of the winter moth population in Victoria. Roland reanalysed the Nova Scotia data and suggested that

procedures used by Embree may have masked a similar occurrence there. At the time of outbreak collapse in Nova Scotia, soil mortality had also been the most important mortality factor in causing winter moth population reduction. Roland (1988) has suggested that by some unknown mechanism(s), *C. albicans* may have led to the observed increases in soil mortality and thus, indirectly, to population decline.

The introduction of *C. albicans* to Nova Scotia may have aided in the transmission of disease among the population. Viral disease, particularly baculoviral disease, has been reported from a number of declining populations of forest Lepidoptera including Bruce's spanworm in Canada and winter moth in Europe (Wellington 1962, Stairs 1966, Tenow 1972, Cunningham 1982, and see Myers 1988). Winter moth has been shown to be susceptible to all three genera of occluded insect viruses; cytoplasmic polyhedrous viruses, poxviruses and baculoviruses (Wigley 1976). Wigley (1976) identified nuclear polyhedral virus (NPV) of the genus *Baculovirus*, subgroup A, polyhedrosis among an outbreaking winter moth population at Wistman's Wood in England. The virus was responsible for as much as 23% of the observed larval mortality. Feeny (1966 in Wigley 1976) also found NPV in winter moth at Wytham Wood in England, and NPV has been found in populations of winter moth on Scots pine (*Pinus sylvestris* L.) and Sitka spruce (*Picea sitchensis* (Bong) Carr) in Scotland and England (Wigley 1976).

In Nova Scotia, no disease was found to infect winter moth between 1954 and 1961. In 1961 a single individual was found with NPV and by 1964 NPV was found to be 'generally present' throughout the winter moth distribution (in Embree 1966). Therefore, the appearance of NPV coincides with the introduction of the parasitoids and the decline of the winter moth population. Embree (1966) suggests that the origin of the virus in Canada may be from the related Bruce's spanworm, since the occurrence of the virus coincided with that of a very similar virus (*Borelinavirus bruceata,* in Canadian Department of

Forestry 1964, 1974) causing outbreak collapse in spanworm. Cunningham *et al.* (1981) investigated the incidence of infection among field populations of winter moth near Victoria and found no evidence of virus. NPV introduced before the introduction of the parasitoids in 1979 did not become established. Roland (1986a, 1988) found low levels of virus among winter moth populations on Vancouver Island after the introduction of *C. albicans*. It may be that, in the absence of parasitoids there is inefficient viral transmission.

Winter moth was probably introduced into the lower mainland of B.C. in the early 1980's. In 1985 pheromone traps picked up winter moth on fruit trees at Richmond and Tsawwassen (Wood and Van Sickle 1985) and by 1989 moderate to severe defoliation of birch was being attributed to winter moth in Richmond and from Ladner to Surrey (Wood and Van Sickle 1990, 1991). Pheromone trapping has indicated that winter moth has spread throughout the lower mainland and now occurs as far east as Mission. The highest population densities have been recorded at Richmond, Delta and Surrey (Fitzpatrick *et al.* 1991a). The moth is also spreading into Vancouver (pers. obs.). On the mainland, birch *Betula* spp. and blueberry,*Vaccinium corymbosum* (L.), are the main hosts with raspberries, *Rubus* spp., in Ladner also being damaged (Fitzpatrick *et al.* 1991a).

Parasitoids were never released in the lower mainland, but they are present among winter moth populations, presumably having been introduced at the same time or shortly after the winter moth. This recent introduction offers an opportunity to look at a post-introductory outbreaking population of winter moth, with a co-occurring *C. albicans* population, in the light of the recent ideas put forward on the mechanisms of control. I set out to observe the population trends of winter moth, at every life stage, on the lower mainland of British Columbia. I compared blueberry and birch as plant hosts and examined the mortalities affecting populations on these two hosts. I also investigated the prominence

of disease among the Richmond population. A discussion of the possibility for the success of *C. albicans* on the two different hosts will be presented.

2.2. Procedures

Study sites

Four field sites in Richmond, B.C., were chosen for detailed life table analysis of winter moth. These sites are indicated by solid squares in Figure 2.1. Two of the sites were blueberry plots on agricultural land. The other two were predominantly birch woodland. For further details of these sites see Chapter 3.

Blueberry I (BBI, no. 15 in Figure 2.1)

This blueberry plot is 50m x 20m and is not commercially harvested. It contains a number of different varieties of highbush blueberry (*Vaccinium corymbosum* (L.)) and there is considerable variation in size among the bushes. The sparse density of bushes allow an undergrowth mainly of grasses and ferns. There are some young birch (*Betula papyrifera* var. *communata* Marsh) interspersed with the blueberry bushes.

Blueberry II (BBII, no. 16 in Figure 2.1)

This site has an area of about 50m x 20m of highbush blueberries (*V. corymbosum*). The blueberries are not commercially harvested and therefore, have become overgrown and so block light from the undergrowth. The north side of the site adjoins a commercial blueberry plot, where winter moth are controlled by insecticides. The western edge of the plot receives more light which allows some undergrowth. Undergrowth at the

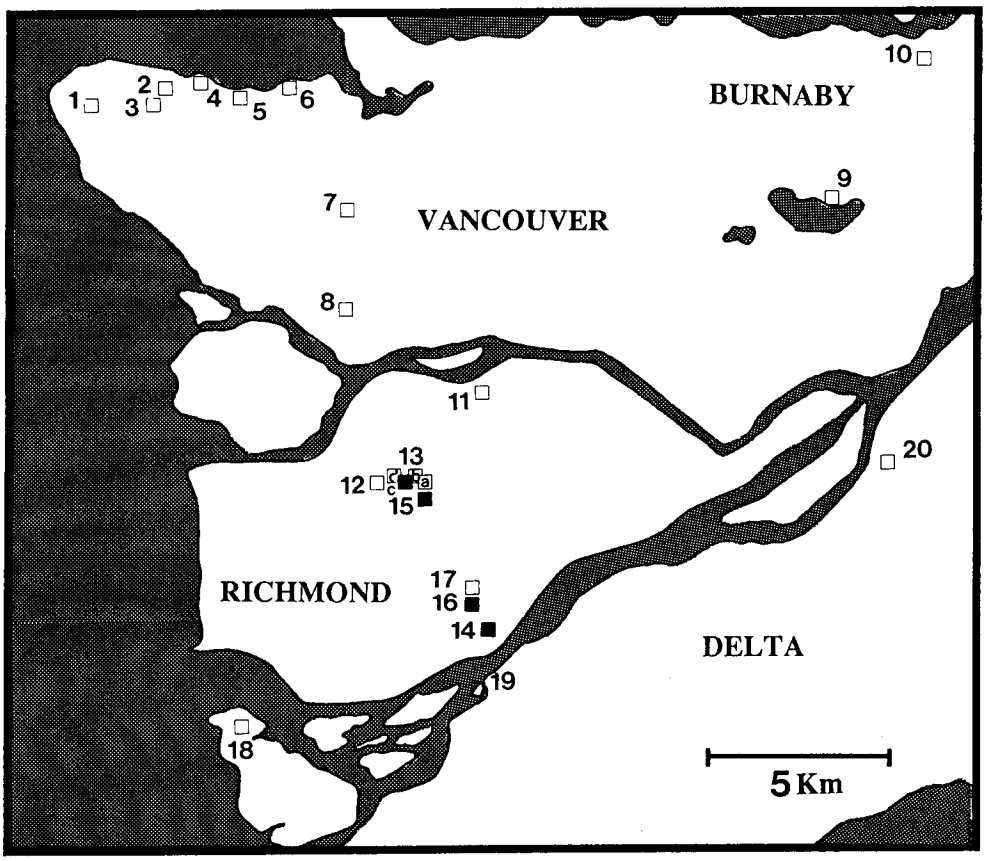


Figure 2.1. Study sites in the lower mainland. Solid squares indicate sites used in life table studies, open squares indicate winter moth sampling sites. Vancouver sites (1-8); 1. University of British Columbia, 2. West 9th and Alma, 3. West 13th and Trimble, 4. Spanish Banks, 5. Locarno Beach, 6. Jericho beach, 7. West 35th and Granville, 8. West 61st and Granville. Burnaby sites (9-10); 9. Burnaby lake, 10. Simon Fraser University. Richmond Sites (11-17); 11. Knight street, 12. Department of National Defense lands, 13. Richmond Nature Park, 14. Birch stand I, 15. Blueberry plot I, 16. Blueberry plot II, 17. Blueberry plot III. Westham Island (18) and Delta sites (19-20); 19. Deas Island, 20. 112th Street (north). Ten sampling sites at Ladner and Chilliwack are not shown.

western edge consists mainly of briar (*Rubus* spp.) and some sporadic salal (*Gaultheria Shallon* Pursh). Some small birch (*B. papyrifera*) are interspersed among the blueberry bushes.

Richmond Nature Park (RNP, no. 13c in Figure 2.1)

Richmond nature park consists of an area of about 0.705km^2 and is of mixed forest vegetation consisting mainly of birch (*B. papyrifera*) and hemlock (*Tsuga heterophylla.* (Raf.) Sarg.). The undergrowth includes salal (*G. shallon*), blueberry (*V. corymbosum*), and red elderberry (*Sambucus racemosa* L.). Some parts of the park consist of boggy areas where the flora is dominated by Labrador tea (*Ledum groenlandicum* Oeder) and blueberry. Studies were carried out on the west side of the park.

Birch Stand I (BI, no. 14 in Figure 2.1)

This is an area of 125m x 50m, consisting of birch (*B. papyrifera*) woodland. It is surrounded by farmland. The birch trees are of a variety of ages, there is some sumac (*Rhus glabra* L.) and Hemlock (*T. heterophylla*) growing amongst the birch. The undergrowth consists largely of salal (*G. shallon*) and blueberry (*V. corymbosum*).

Sampling procedures

Larvae (Blueberry)

The sampling unit for larvae was a leaf cluster. Leaf-clusters consist of individual buds in the spring, which develop into leaf or flower clusters in later months. In 1991, buds were collected only on April 11th. In 1992, due to a mild winter and early spring and

thus an early bud burst, larval sampling commenced on March 11th. During 1992, sampling was carried out at regular weekly intervals. Samples were collected on March 11th, 23rd, 31st, April 8th, 15th, and May 5th. Sampling stopped after May 5th, since after this time pupation had begun. Estimates of early instar densities are from samples taken on April 11th in 1991 and on March 23rd in 1992.

In sampling, the two apical buds of branches were collected. This biased the results on larval densities within plots because winter moth larvae prefer apical buds (see Appendix 1), but did not affect between plot comparisons. Apical buds were sampled because in later months larval densities are expected to be low, and large numbers of larvae were required for estimation of parasite and pathogen incidences.

The buds/leaf clusters were randomly collected from four transects at each blueberry site. Eight buds were taken from each of 10 bushes, two from each of the cardinal points; a total of 320 buds were collected at each sampling period. Buds were dissected under a light microscope and the larvae counted. In 1992, data on bud development, larval numbers and instars were recorded. Instars were determined by measuring head capsule widths of each larva under a dissecting microscope (see Appendix 2).

Larvae (Birch)

Sampling of birch stands was carried out on April 11th in 1991 and on March 11th, 23rd, 31st, April 8th, 15th and May 5th in 1992. Outer branches of birch were clipped with a telescopic pruner which reached a height of ca. 15m. Branch samples consisted of two to twenty leaf clusters and were taken at each of the cardinal points of ten trees along three transects. A minimum of 240 buds and leaf clusters were collected for each birch site at

each sampling date. Each leaf cluster consisted of two to five leaves. Successive samples were taken from the same transects but not necessarily from the same trees. Samples of undergrowth were randomly taken along each transect. Larvae were counted from each sample and data were collected on bud development, larval development and leaf damage.

Larvae collected from all sites (blueberry and birch) were kept in individual plastic containers in an outside shed and reared through to pupation. After pupation, pupae were examined and scored as healthy, deformed, parasitized or dead due to unknown causes. Larvae were fed ample supplies of birch, blueberry or apple from non-infested areas, and leaves were changed every two to four days. A number of the larvae were frozen immediately and examined for viral or microsporidian disease. All larvae which died during rearing were also examined for pathogens. Smears were made from dead larvae and stained with Naphthalene black in 1991 and with both Naphthalene black and Giemsa, to aid in identification, in 1992. Examinations for microsporidia were carried out at every stage of the life cycle, except eggs in 1991. In 1992, eggs were teased apart, fixed in Methanol and stained in Giemsa. Larvae were stained as above. For adults the abdomens were severed, the contents were then moistened, fixed and stained with Giemsa.

Pupae (Blueberry and birch)

Pupal densities were estimated by using the pupal drop tray method (Varley and Gradwell 1968, Varley *et al.* 1973). Throughout pupation, drop trays were placed along the transects beneath the host plants at each site. Drop trays consisted of plastic trays filled with sifted peat. Each year trays were set out in late April and collected in early June. Trays were sifted to find cocoons. Cocoons were opened and the condition of the pupae recorded. Pupae were scored as healthy, parasitized or dead due to unknown causes. Pupae

were weighed and pupal cremasters were examined to distinguish winter moth pupae from those of Bruce's spanworm (Eidt and Embree 1968).

Adults (Blueberry and birch)

Densities of emerging adults were estimated in 1991 and 1992 by using two trapping methods. Sticky traps were used in both years at birch sites, but only in 1992 at blueberry sites. These consisted of bands of masking tape tightly wrapped about the tree or bush trunk. Tanglefoot was spread over the bands. Ten traps were placed at each site. Stocking traps were used only in 1991 at birch sites. Twelve traps were set up at each site and these were used to supplement data from sticky traps. The stocking traps were similar to those used by Embree (1965b) except that the females were captured live in containers at the top of the trap. These containers had funnels through which females could enter, but restricted them from leaving the trap. One trap was placed on each tree, in three transects of four trees. Traps were equally divided among the four cardinal points. Stocking traps were not suitable for blueberry plots because the blueberry stems were too narrow and low.

Adult females were collected from the traps at regular intervals. The diameters and circumferences of the trunks and the canopy areas of the trees were measured. The numbers of buds per unit area were visually estimated for each tree or bush. The fecundity of the females was examined by counting the number of oocytes in the body and comparing this with estimates from a number of published studies.

Data Analysis

Data were analyzed using 2-way ANOVAs with sites as one of the variables and years as a second variable. Where necessary, log and arcsine transformations were used to

reduce heterogeneity of variance. Where homogeneity of variance did not satisfy Barlett's test ($P < 0.05$), nonparametric Kruskal Wallis tests were applied. Following ANOVA, Tukey's HSD test was applied to test for mean seperation. The Mann-Whitney U test was used to test for mean seperations on all Kruskal Wallis tests. Comparisons of 1991 and 1992 were carried out for all life stages and mortalities. Only total pupal densities (prepupal densities) were compared over three years (1990 - 1992).

The magnitude and trends in mortality were demonstrated using k-values. The mortality of eggs and larvae (k_{larv}) was estimated as the difference between the log of the estimated egg potential each year per m^2 and the mean density of pre-pupae entering the soil each year. The egg potential each year was estimated by multiplying the number of adult females per m^2 that year by the average fecundity of females in the same year. The average fecundity was estimated by weighing pupae in 1991 and 1992 and using a relationship from Roland and Myers (1987) for pupal weight versus fecundity. The value for 1990 was estimated by multiplying an estimate of adults per m^2 (derived from pupal densities and pupal mortality estimates) by 150, an average fecundity for the species (Embree 1965a).

Mortality due to parasitism (k_{para}) was estimated as the difference between the log of the mean density of prepupae and the log of the density of those which were unparasitized. An important mortality factor, termed k_{prepu}, was observed each year. This was the difference between unparasitized prepupae dropping to the soil and healthy pupae in the soil, i.e. death due to unknown causes.

Pupal mortality (k_{pupa}) was estimated as the difference between the log density of healthy pupae in the soil and the density of emerging adults in the winter. For 1989 and 1990 estimates of the numbers of adults emerging were derived from predation estimates using the tether method (see Chapter 3). These estimates are meaningful since in 1991 and

1992 estimates of adult densities by both the tether method and the trapping of emerging females corresponded well.

Spread of winter moth and *C. albicans*

Random samples of birch were collected from 30 sites throughout the lower mainland of British Columbia (see Fig. 2.1). Ten sites at Langley and Chilliwack are not shown in Figure 2.1. These included sites at Cultus Lake, Mill Lake, Aldergrove Lake and Campbell River. Collections were made by clipping 40 branch tips from birch trees or lowgrowth bushes. Lowgrowth bushes included crabapple (*Malus sylvestris* Mill.) , cherry (*Prunus* spp.), and blueberry (*V. corymbosum*). Caterpillars were counted and reared individually in plastic cups in an outdoor shed. Caterpillars were given ample amounts of birch from non-infested trees. Leaves were changed every two to four days. Caterpillars were reared to pupation and the condition of the caterpillars was determined by examination of the pupae. Pupae were identified as winter moth or spanworm and scored as either healthy, parasitized or dead due to unknown causes.

2.3 Results

2.3.1. Damage to blueberry and birch

Damage to blueberry: Timing of bud burst is dependent on the variety of blueberry in question (Anonymous 1990). At Richmond sites, blueberry buds burst before birch in 1992. Five stages of development were identified (see Fig. 2.2), these were similar to early stages in Massie's system (see Holliday 1977).

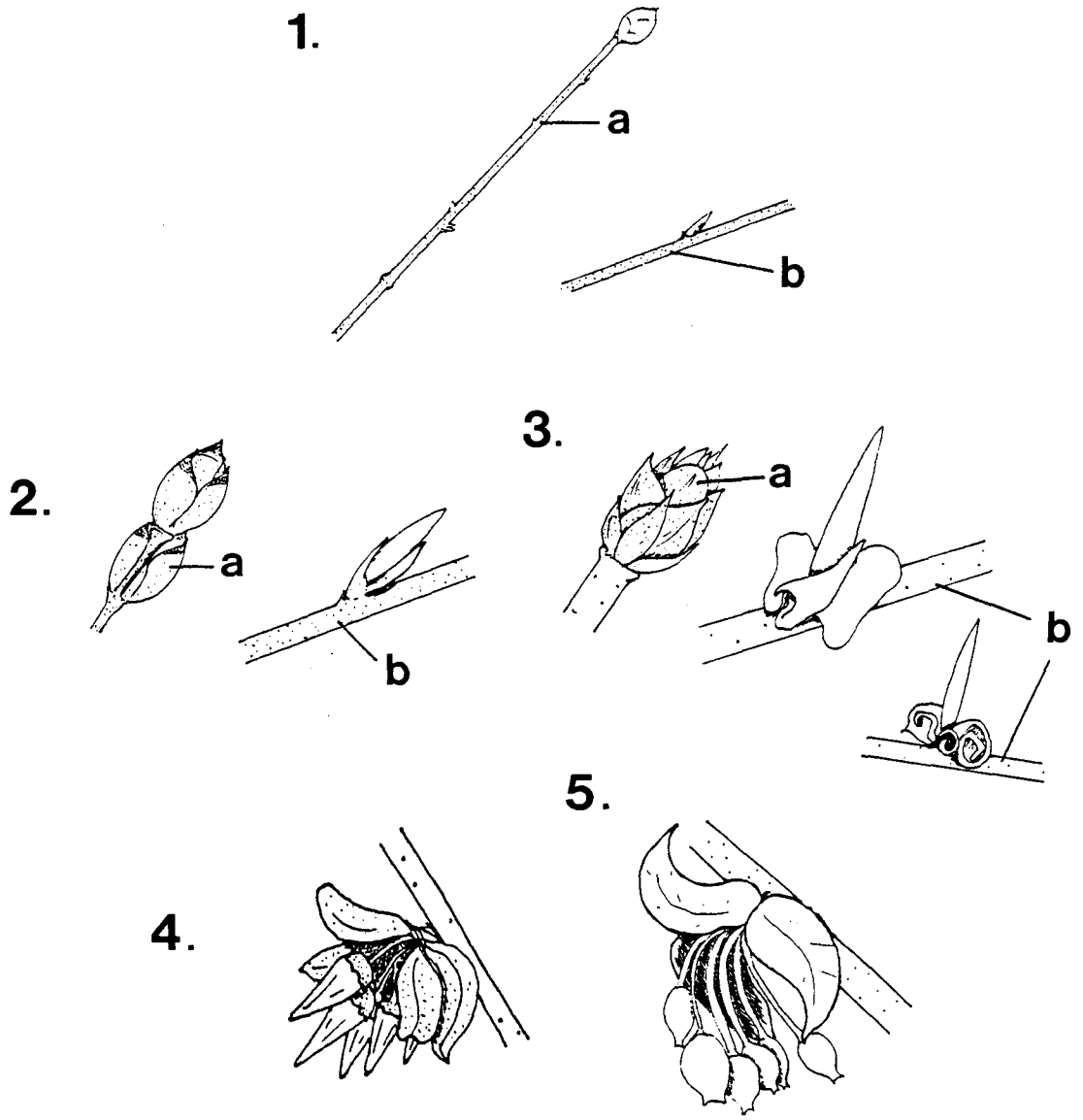


Figure 2.2. Stages in the development of highgrowth blueberry (*Vaccinium corymbosum*) flower clusters (a) and leaf clusters (b). See text for details.

Stage I: The closed bud stage. Flower buds appear sealed, are generally brown to red in colour and are between 2 and 3.5 mm in width (1a). Leaf buds are much smaller, between 0.5 and 1.5 mm in width (1b). Before burst, a greenish tinge appears at the edges of the individual scales, this occurs in both bud types.

Stage II: The flower buds swell to 4 - 4.5 mm and the scale tips turn pink. At this stage the scales are not tightly closed (2a). The scales then begin to shrink back and turn brown. Leaf buds swell to about 2mm and do not have a pink tinge (2b).

Stage III: Eventually the bud begins to loosen and open out (3a). In leaf buds two outer whorls roll back revealing a central leaf whorl (3b). This central leaf whorl lengthens and the leaves begin to enlarge (leaf buds can give rise to from 2 to 5 leaves).

Stage IV: For flower buds, this stage is marked by the elongation of the flower stalks and the protrusion of the young green flower petals (4).

Stage V: Elongation continues and the flowers turn white and open out. Stage five flowers have a bell shaped appearance and the leaves are completely expanded (5). Stages IV and V for leaves are marked by the continued expansion of the leaves.

Larvae attack Stage II buds, generally tunneling through the developing flower petals to eat the developing reproductive parts inside. Because of the tightness of the buds, frass accumulates between flower parts and may initiate fungal growth and thus spoilage of

the flower. At high densities the developing buds can turn completely brown and die. Leaves do not have the usual 'shot-hole' damage (cf AliNiazee 1986). Damaged areas are generally larger than discrete holes. Early in the season the caterpillars show a preference for flower buds, only later switching to the leaves. There is also a preference for apical buds (see Appendix 1).

Damage to birch: Five stages in the development of birch leaves were noted (Fig. 2.3), these stages corresponded to stages in Malaisse's (1964) system for beech, having a pseudoterminal bud type, i.e. leaves emerge one after the other from the base to the tip of the shoot.

Stage I: Buds are tightly closed, brown in colour and from 3 to 5 mm long and 2 to 3 mm wide (1).

Stage II: The buds lengthen, swell and turn green (2).

Stage III: The leaf scales open and the two outer leaves unfurl. A central inner whorl may be apparent at this stage (3).

Stage IV: The inner whorl begins to lengthen, and eventually the outer leaves (5 - 7mm) fold back. Protective leaf scales can be seen about the central whorl. The leaves continue to elongate (4).

Stage V: At about 10 - 14mm the central leaves begin to open, continue to expand and the petioles elongate (5).

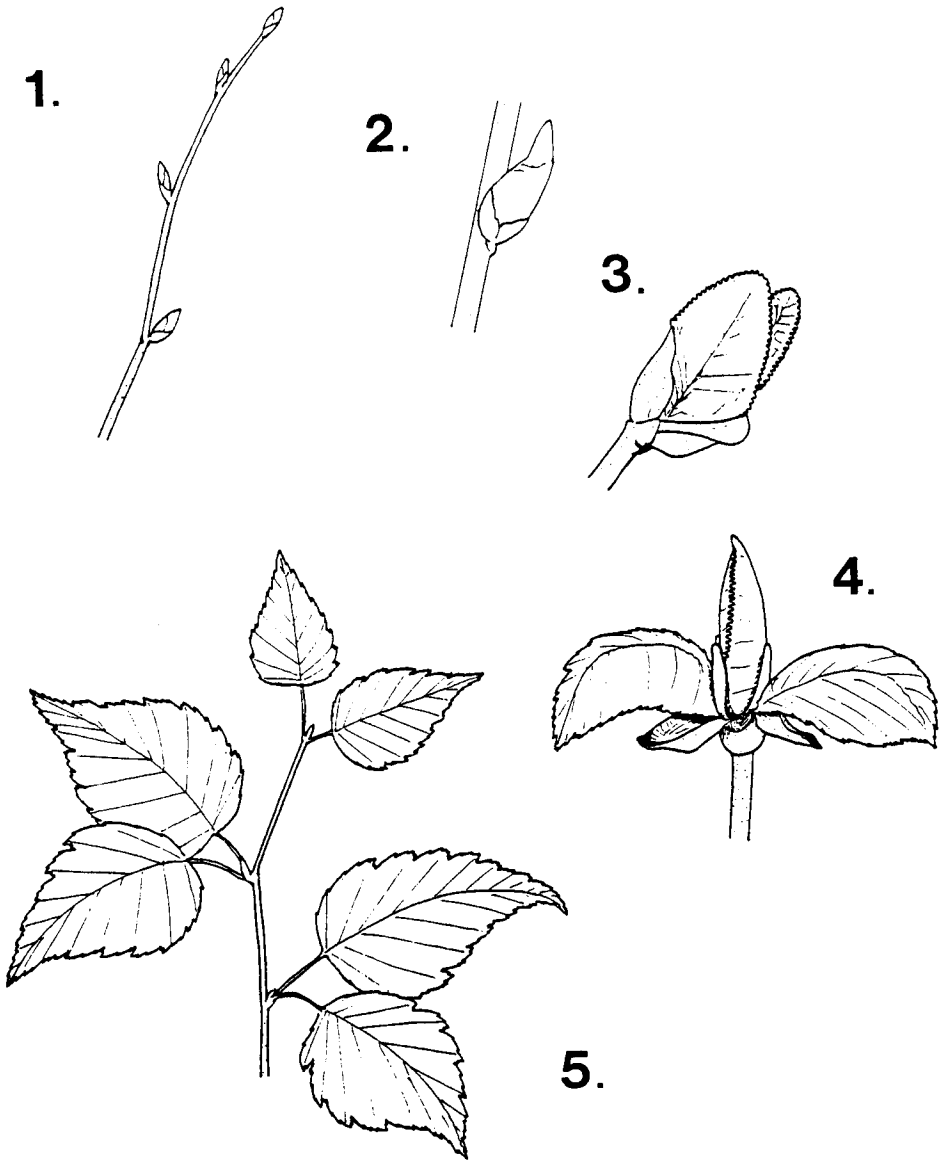


Figure 2.3. Stages in the development of birch leaves (*Betula papyrifera*). See text for details.

The development of buds varies with site, position of buds within sites and positions of buds on the individual branches. For example, at Birch site BI, outside branches were slower to develop than branches at 30 or 60m from the edge.

Damage to birch was visually estimated at each site, within trees and among leaves. In 1991, damage was estimated at about 50% to all leaves at BI and 30% at RNP. Larvae begin their damage on stage III buds. Within trees, lower branches generally had the most damage, presumably through downward larval migration throughout the season. This disagrees with Embree's (1965a) observations of winter moth on oak where larvae were predominantly on the upper branches (see also Eidt and Embree 1968 and Dubrovin 1990). There is a great variability in the damage encountered among trees and within sites. Differences among trees were most striking at RNP. Undergrowth in 1991 was often 100% defoliated and among birches young trees were particularly damaged, presumably due to their low size, rather than through any differential foliage quality. In 1992 similar patterns were observed with average damage to birch leaves at about 30%.

Growth on Blueberry and Birch: The pupal weights of winter moth on birch and blueberry were compared to investigate the suitability of these hosts for winter moth larvae. Growth on apple was also examined and compared since feeding on apple is known to result in heavy pupae (Holliday 1977, Roland and Myers 1987). The host plants were found to have a significant effect on the resulting size of pupae (1-way ANOVA on log transformed data $P < 0.001$). There was no significant difference in the weights of larvae reared in an outside shed on either blueberry or birch, or on a combination of blueberry and birch (see Table 2.1). However, larvae reared entirely on apple were significantly larger than those reared on blueberry and birch (Tukey test, $P < 0.001$). Therefore, it appears that birch and blueberry are less favourable host plants than apple for winter moth, but that growth on both blueberry and birch is equal.

Table 2.1 Mean pupal weights of winter moth, *Operophtera brumata*, reared on apple, birch and blueberry or switched between hosts. 'N' is the number of individuals reared through to pupation. All larvae were taken from wild populations.

Host plants		temperature regime (°C)	mean weight (g)	N
Initial host	Final host			
Apple		12 - 20	0.0284	22
Birch		12 - 20	0.0210	115
Blueberry		12 - 20	0.0185	36
Blueberry	Birch	12 - 20	0.0212	42

2.3.2. Population densities at Richmond

Data from 1989 already indicated high densities of larvae at Richmond. The population appears to have peaked in 1990, then underwent a general decline till 1992 when the population collapsed on both blueberry and birch.

Early instars

Analysis of bud counts indicate that larval densities were dependent on site and year (2-way ANOVA of log + 1 transformed data BI, RNP and BBII larvae for 2 years, site: $P < 0.001$, year: $P < 0.001$).

On blueberry changes in the year to year densities of early instars were examined from four years of data (1989 - 1992) available for the two sites (Fig. 2.4). From 1989 to 1990 a general increase in larval densities was apparent at the blueberry sites. For these two years the data are presented as the number of larvae per branch. It is not clear from the available data whether there is an increase or decrease in the blueberry populations from 1990 to 1991. Per branch counts are expected to be lower than per bud counts because only apical buds were sampled in 1991 and 1992. This suggests that a decline in the populations from 1990 to 1991 is most probable. A decline is also suggested from data presented by Sheppard *et al.* (1990), where winter moth larval densities of 2.2 per cluster were recorded at BBII in 1990.

Between 1991 and 1992 there has been a decline in the populations. Data for BBI are not available for 1991, but there has been an obvious decrease in the numbers of larvae present (pers. obs.). At BBII data were collected for both years and there is a significant decrease in the larval densities (T-test on log + 1 transformed data, $P < 0.001$).

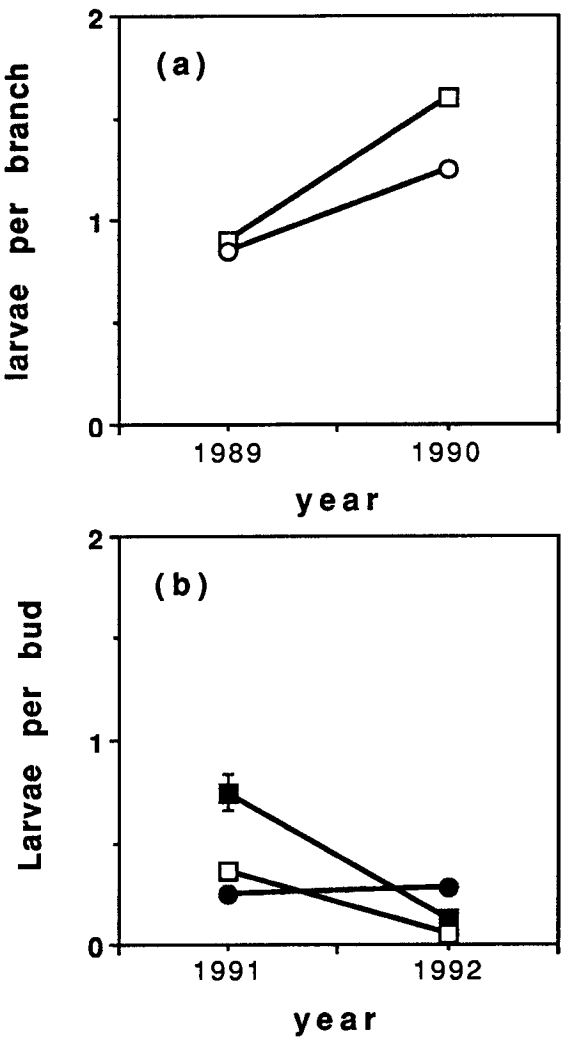


Figure 2.4. Densities of early instar larvae per branch in 1989 and 1990 (a), and per bud in 1991 and 1992 (b), at four sites (open circles = BBI, open squares = BBII, closed circles = BI and closed squares = RNP) in Richmond, B.C.. All standard errors are included but are negligible.

One-way ANOVA of 1991 data indicate that densities of larvae at BBII were not significantly different from RNP (Tukey test, $P = 0.108$), but were different from BI (Tukey test, $P < 0.001$). In 1992, both Blueberry sites were identical (Tukey test, $P = 1$) and were similar to densities encountered at RNP (Tukey test, $P = 0.2$). BI had significantly more larvae than all other sites in 1992 (Tukey test, $P < 0.001$).

Two years of data (1991 and 1992) are available for the birch sites (Fig. 2.4b). Local accounts and reports from the Forest Insect and Disease Survey suggest that birch sites also underwent a population decline between 1990 and 1991 (Wood and Van Sickle 1990, 1991). Between 1991 and 1992 a decrease in early instar densities is apparent at RNP, but at site BI there appears to be a slight increase in larval densities. Data were collected at the western side of BI in 1991. In 1992, this side was cut down and so sampling in 1992 was carried out at a new area. Observations of defoliation patterns in 1991 indicate however, that the western edge had received considerably less defoliation in 1991 than the eastern side (<10% damage to leaves and > 50% respectively).

Prepupae

Estimates of prepupae per m^2 are taken from pupal drop trays. Data on prepupal densities are available for all sites for each of the four years (Fig. 2.5). Densities of prepupae were dependent on site (Kruskal Wallis, $P < 0.001$) and year ($P < 0.001$). Densities were significantly different at the $P < 0.001$ level (Mann Whitney test) between blueberry and birch sites. On blueberry, the densities of prepupae undergo a similar trend to that observed among early instars. The numbers of prepupae at the two blueberry sites were similar (Mann Whitney, $P = 0.235$). From 1989 to 1990 there was a major increase in the populations, but after 1990 the populations underwent a general decline. In 1992

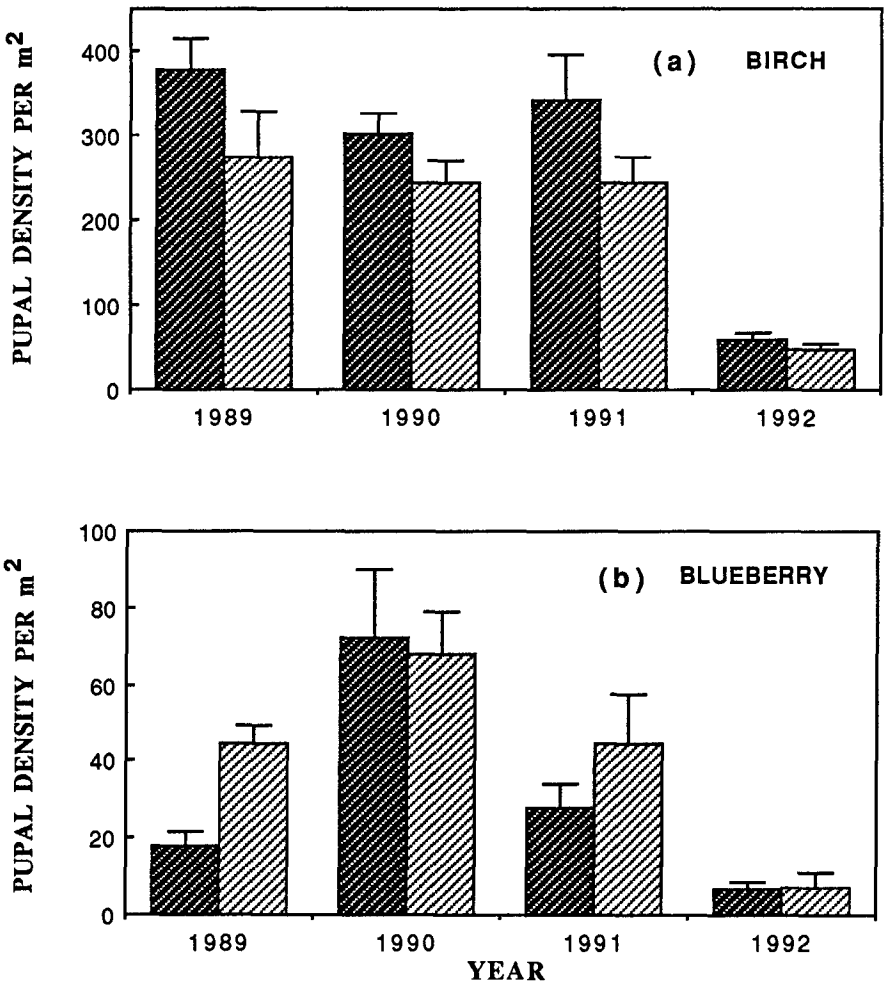


Figure 2.5. Densities of prepupae per square meter at (a) birch sites (dark shading = BI, light shading = RNP) and (b) blueberry sites (dark shading = BBI, light shading = BBII) at Richmond, B.C. bars indicate standard errors

populations at both blueberry sites collapsed. Densities of prepupae at the two birch sites were significantly different (Mann Whitney, $P = 0.038$). There was a decrease in density between 1990 and 1991 (Mann Whitney, $P = 0.036$) with a crash at all sites in 1992 (Mann Whitney test, $P < 0.001$).

Adults

Densities of emerging females are available for two years only at the birch sites (Fig. 2.6). There was a significant difference in numbers of emerging adults between the sites (Mann Whitney test, $P < 0.001$). However, there is no difference between the numbers of adults emerging in 1991 and the number emerging in 1992 (Mann Whitney test, $P = 0.113$). Significant differences were observed between densities of adults at all sites in 1992 (Kruskal Wallis, $P < 0.001$). Blueberry sites were similar in densities in 1992 (Mann Whitney, $P = 0.19$), but differed from birch sites ($P < 0.001$, Mann Whitney tests). The two birch sites also differed in 1992 (Mann Whitney test, $P = 0.036$).

Fecundity

Pupal size was dependent on site (2-way ANOVA on log transformed data, $P < 0.001$) but not on years ($P = 0.398$). In 1991, pupae from BI tended to be smaller (Table 2.2), although not significantly smaller than those from RNP (Tukey test, $P = 0.097$). Sufficient data were not available to test differences between birch and blueberry sites. In both years (1991 and 1992) pupae were heaviest at RNP. Counting of oocytes from females in 1991 indicated that fecundity was generally lower than expected from regressions taken from apple fed larvae, but more closely approached estimates from oak fed larvae. Therefore fecundity was estimated from Roland and Myers (1987) relationship of pupal weight to fecundity for oak fed larvae.

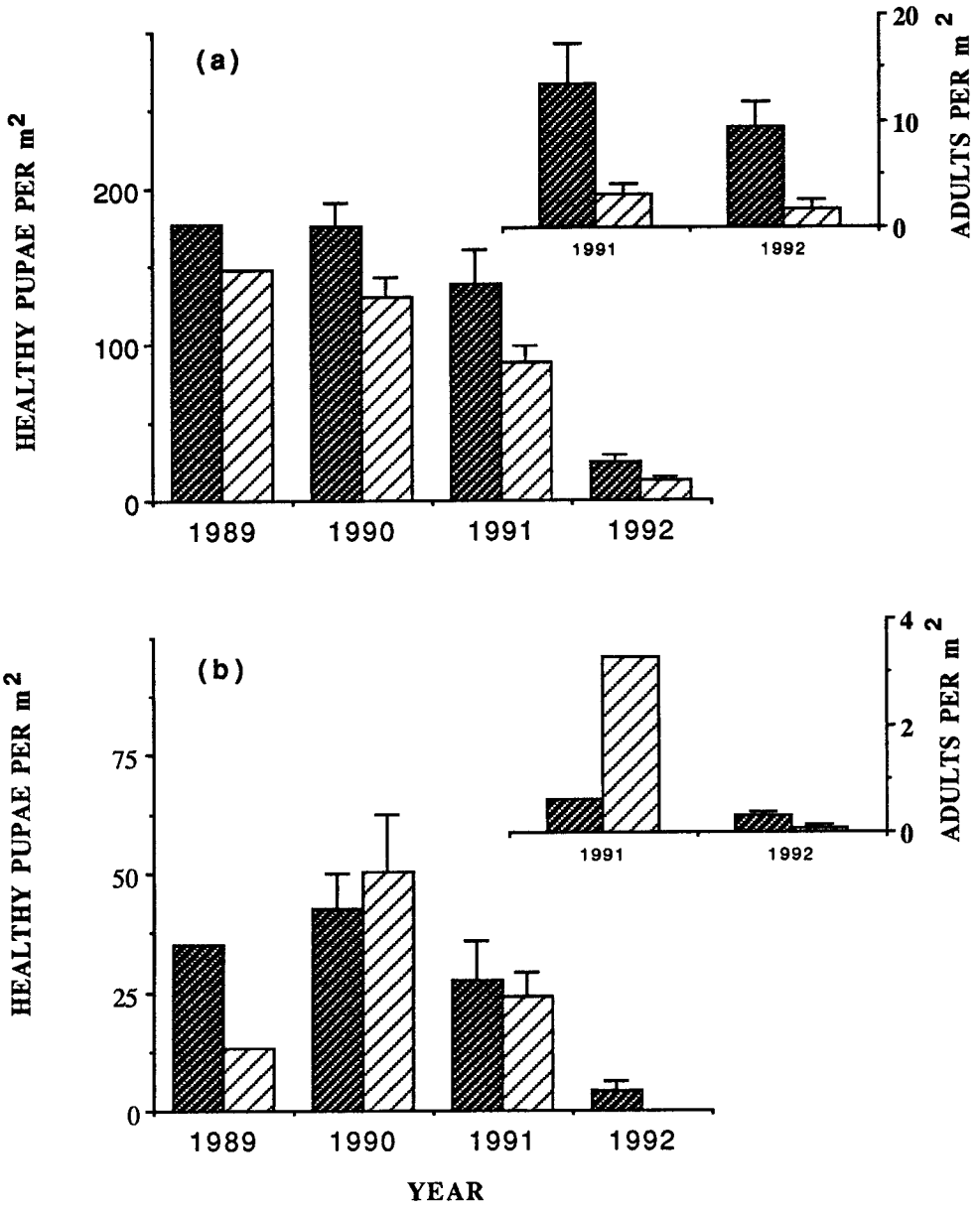


Figure 2.6. Densities of healthy winter moth pupae from 1989 to 1992 with corresponding adult densities from 1991 and 1992 at (a) two birch sites (dark shading = BI, light shading = RNP) and (b) two blueberry sites (dark shading = BBI, light shading = BBII) at Richmond, B.C., bars indicate standard errors.

Table 2.2. Mean pupal weights of winter moth *Operophtera brumata* from four field sites at Richmond B.C. during 1991 and 1992, and estimates of fecundity based on published relationships between weight and fecundity (eggs/female).

Site	Year	Mean Weight (g)	N	fecundity estimates			
				Roland and Myers (1987)		Hale (1989)	Holliday (1977)
				Oak	Apple	Apple	Apple
BI	1991	0.0251	83	128.41	175.55	178.6	171.77
	1992	0.0236	40	114.7	159.8	165.1	157.46
RNP	1991	0.0277	103	152.18	202.85	202.0	196.58
	1992	0.0290	39	164.06	216.5	213.7	208.98
BBI	1991	0.0224	10	103.74	147.2	154.3	146.02
	1992						
BBII	1991	0.0263	37	139.38	162.15	189.4	183.22
	1992	0.0214	2	94.60	110.7	145.3	136.48

It is apparent therefore, that each of the four study sites underwent a significant population decline in 1992. This decline was apparent at all life stages of the winter moth, except the adults. There has been no clear trend in fecundity changes during the decline.

2.3.3. Mortality on Blueberry and birch

Parasitism

Three parasitoid species were recovered from the Richmond populations. The most common species was identified as *C. albicans* (identified by J.E. O'Hara: Biosystematics Research Centre, Ottawa) and has been present at all four sites since 1989. *Agrypon* sp. was also present in small numbers at birch sites. This species was found among pupae from 1990 to 1992, at levels below 0.5%. Because of its low incidence it has been excluded from analysis. A third species, morphologically and behaviourally similar to *Ephialtes* spp. (see Wylie 1960b) was recovered from larvae late in the season at BI. The larvae of this parasitoid were observed feeding externally on winter moth larvae. Usually three to five larvae were found attached to an individual caterpillar. After the winter moth larvae had died, the parasitoids pupated. These parasitoids were found in 1991 and 1992. The parasitoid was rare and its effects are also considered to be negligible.

Parasitism by *C. albicans* fluctuated between years at all sites (see Figs. 2.7 and 2.8 and Appendix 3). Parasitism was dependent on site but not on year (2-way ANOVA on arcsine transformed data, $P < 0.001$ for sites and $P = 0.061$ for years (1991 - 1992). The lack of any significant difference between years may have been due to small sample sizes in 1992. The highest parasitism occurred at the birch sites in 1991 with about 50% of the pupae having parasitoids. Parasitism on blueberry was generally lower than on birch. The

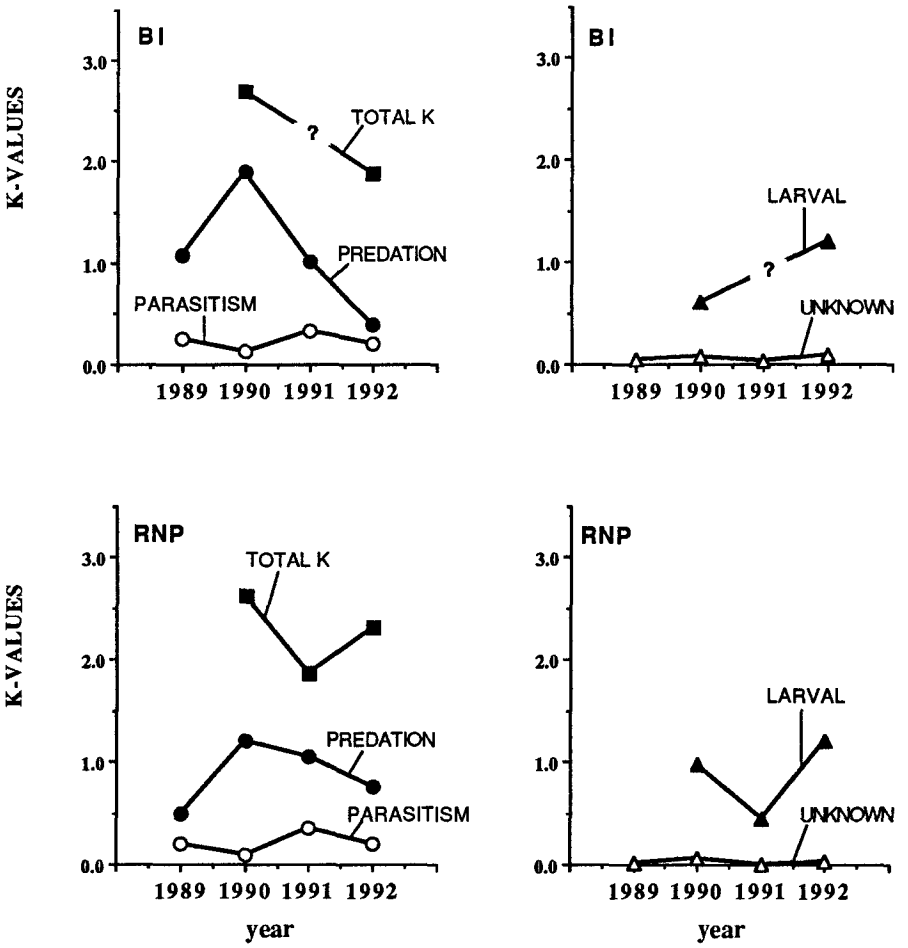


Figure 2.7. Mortality of winter moth at birch sites in Richmond. Closed circles indicate pupal predation (k_{pup}) estimated from tether experiments, open circles indicate mortality due to *C. albicans* (k_{para}). Closed triangles indicate larval mortality (k_{larv}) and open triangles indicate death of prepupae due to unknown causes (k_{prepu}), data are from BI, and RNP. Total generation mortality (K) is also presented.

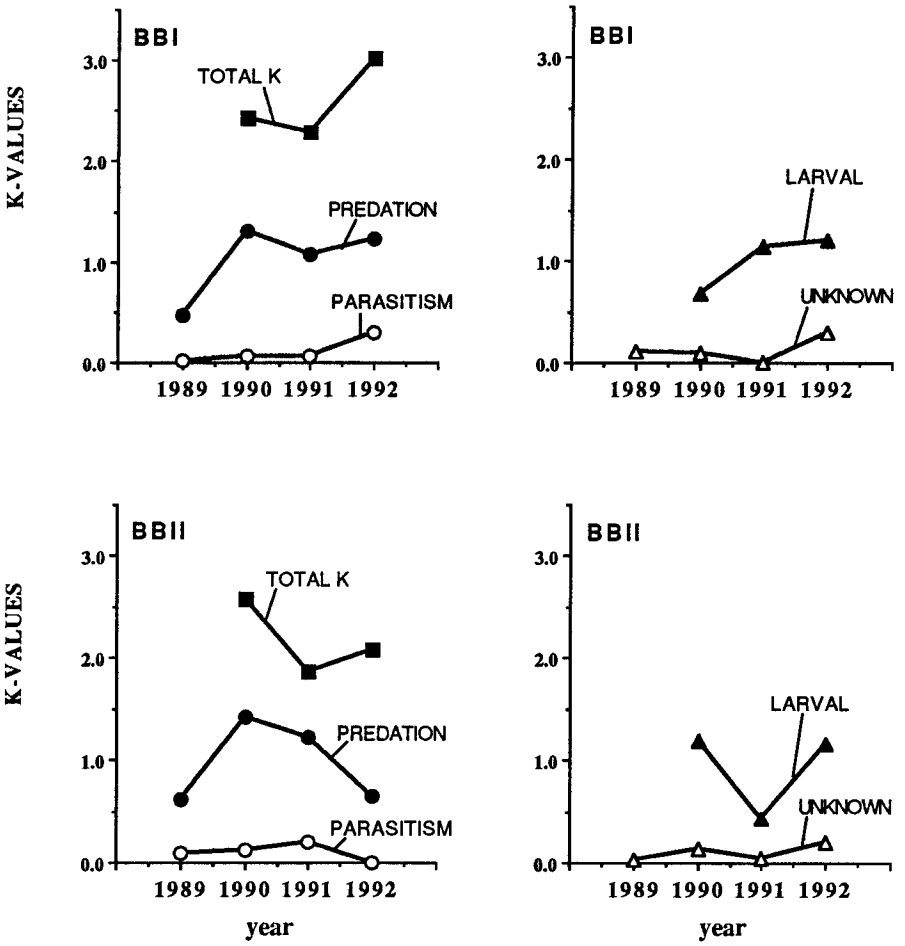


Figure 2.8. Mortality of winter moth at blueberry sites in Richmond. Closed circles indicate pupal predation (k_{pup}) as estimated from tether experiments, open circles indicate mortality due to *C. albicans* (k_{para}). Closed triangles indicate larval mortality (k_{larv}) and open triangles indicate death of prepupae due to unknown causes (k_{prepu}), solid squares indicate total generation mortality (K). Data are from BBI and from BBII.

highest levels on blueberry were encountered at BBII with 39% of pupae parasitized. There was no significant difference between birch sites each year (Tukey test, $P = 0.96$) and between blueberry sites each year (Tukey test, $P = 0.98$). Birch sites had significantly more parasitism than blueberry sites (Tukey test BI *vs* BBI and BBII, $P < 0.005$, BII *vs* BBI, $P > 0.005$ and BBII, $P = 0.018$).

There was no significant difference in the levels of parasitism encountered between blueberry sites over the 4 years, although a general increase in the levels is apparent until 1991. On birch levels appeared to peak in 1991. However, in 1990 the levels encountered are much lower than expected. Between 1991 and 1992 there was a decline in the levels of parasitism encountered at both sites ($P = 0.061$).

Disease

Examination of cadavers and live specimens indicated that the incidence of disease among the Richmond population was very low. All sites were negative for viral disease. Microsporidia were not identified from egg, pupal or adult stages at any of the sites. However, at site BBI microsporidian-like bodies were present among late larvae, but only during 1991 (see Appendix 4). It appears therefore, that viral and microsporidia diseases have had little effect on the lower mainland populations.

Pupal mortality

Many of the larvae which pupated were found to be either deformed or dead. Often dead pupae were found to have fungal hyphae. However, it is difficult to ascertain whether pupae had died due to fungal attack, or whether the fungi had simply attacked the pupal cadavers. The levels of dead or deformed pupae differed between sites and years (2-way

ANOVA on arcsine transformed data $P = 0.026$ for sites, $P < 0.001$ for years). BBI had significantly more dead pupae than any of the other sites (Tukey test, $P < 0.05$). In 1992, pupal death was high at all sites, but particularly high on blueberry (Tukey test, $P < 0.001$), (see Figs. 2.7 and 2.8 and Appendix 3). Because of these differences between birch and blueberry and because of the very high incidence of pupal death in 1992, it appears likely that death was mainly a result of asynchronies between larvae and leaf development.

Soil mortality

Soil mortality was estimated in 1991 and 1992 at birch sites, but only in 1992 at the blueberry sites. Stickybands and stocking traps indicated high mortality of winter moth between pupal drop and adult female capture. Tethered pupae (these are described in more detail in Chapter 3) indicate levels of pupal predation. Estimates for both soil mortality and pupal predation were very similar, indicating that most of the soil mortality was attributable to predation of pupae by generalist predators (see Table 2.3). The estimate of soil mortality for BBII in 1992 was much greater than that for pupal predation in the same year. However, this is probably inaccurate. There were also large discrepancies at BBI between the estimates of soil mortality and pupal predation, from emergence traps and tethers respectively. Difficulties in estimating soil mortality at blueberry sites may be due to the small numbers of emerging adults in the winter (see Fig. 2.6). This indicates that at low pupal densities emergence traps are inefficient.

Table 2.3 Estimates of soil mortality (from emergence traps), and mortality due to pupal predation (from tethers) at four sites in Richmond for two years at birch sites and one year at blueberry sites. The difference is attributed to mortality of prepupae on the ground and of adults after emergence and to death of healthy pupae in the soil. All estimates are presented as percentages.

SITE	BI		RNP		BBI	BBII
YEAR	1991	1992	1991	1992	1992	1992
Soil mortality	90.73	66.96	96.90	90.90	91.07	98.61
Pupal predation	90.28	58.75	91.00	82.5	94.32	77.63
Difference	0.45	8.21	5.90	8.40	-3.25	20.98

K-factor analysis

K-factor analyses indicate that pupal mortality (k_{pup}) has been an important source of mortality throughout the four years for which data are available. This mortality has been greater than mortality caused by *C. albicans* (k_{para}) at each site and each year. At three of the sites, k_{pup} appears to be weakly density dependent (Fig. 2.9). Pupal mortality (k_{pup}) appears to be temporally density dependent (except at BBI), since it is dependent on the yearly pupal densities at each site. However, since only four years of data are available, this trend is weak. Larval mortality (k_{larv}) and mortality due to unknown causes (k_{prepu}) increased in 1992 at each site. This increase was most apparent at the blueberry sites. Estimates of larval densities for BI in 1991 were not feasible since they gave values lower than the estimates of prepupae from drop trays. This however indicates that k_{larv} at BI in 1991 was probably also low.

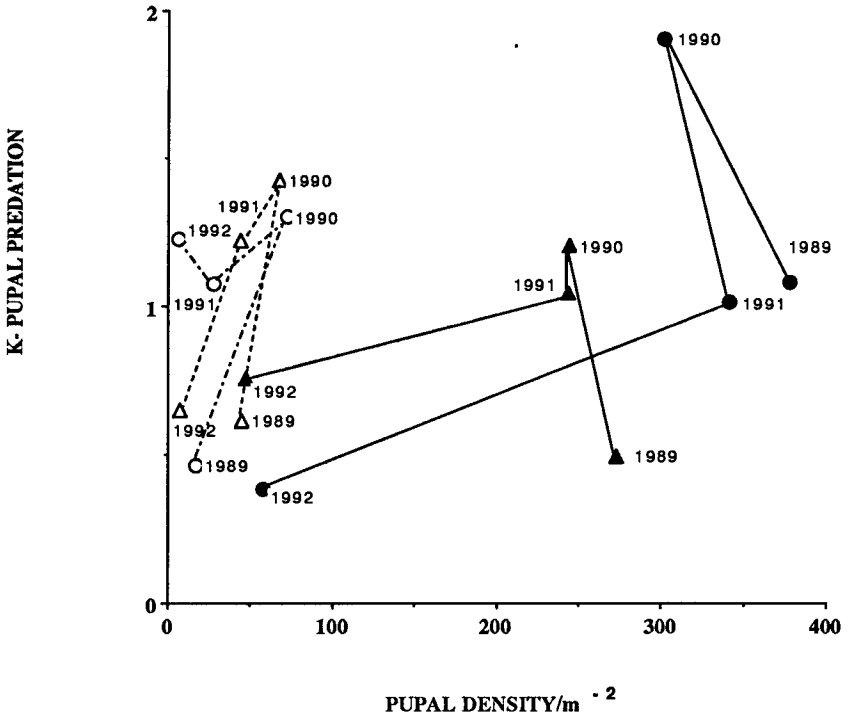


Figure 2.9. K-values of pupal predation plotted against the total densities of pupae in the soil. Closed circles indicate BI, closed triangles indicate RNP, open circles indicate BBII and open triangles indicate BBI. Trends indicate the occurrence of weak temporal density dependence at each site.

The similarities in the trends of k_{prepu} and k_{larv} suggest a link between these two mortalities. I suggest that this link is foliage quality, since both of these mortalities may be influenced by foliage quality (and thus asynchronies of bud burst). The total generation mortality (K) demonstrates similar trends at all four sites, with the lowest values in 1991. although it was likely to have been lower in 1989 when larval survival had not been estimated. Mortality due to parasitism (k_{para}) peaked at each site in 1991. In that year winter moth densities were already decreasing, so that a decrease in k_{para} should have been expected. Plotting k_{para} against prepupal densities (Fig 2.10) gives a counterclockwise trend for BBI. This suggests that k_{para} has a delayed density dependence, however, only four years of data are not sufficient to examine this fully. For birch sites there are no apparent trends. Greater success of *C. albicans* in 1991 may reflect better synchronization of *C. albicans* oviposition with the appropriate stage of winter moth larvae, or greater survival of *C. albicans* compared with winter moth from the previous year. A possible mechanism for this could be greater soil mortality of winter moth pupae.

Refugia against parasitism

Absolute densities of winter moth pupae are higher for birch sites than for blueberry sites. However, birch trees have more leaf clusters per unit area than blueberry sites. When the levels of parasitism are plotted against the densities of winter moth prepupae per leaf cluster it becomes apparent that parasites are more efficient on birch in spite of lower prepupal densities (Fig. 2.11). I investigated some possible refugia by which winter moth on blueberry may be avoiding parasitism, and examined whether a varied habitat could offer a further refuge at birch sites.

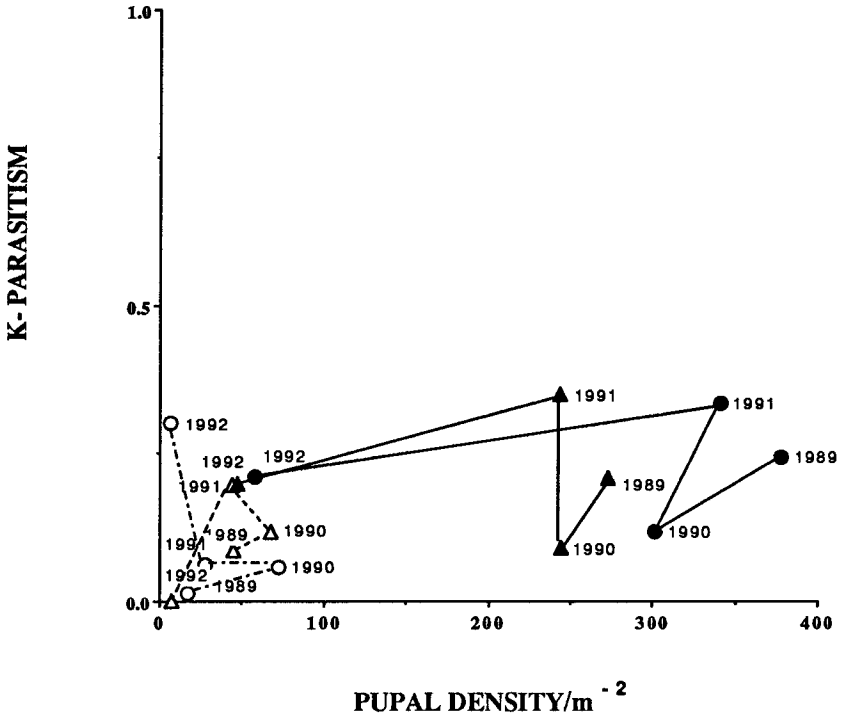


Figure 2.10. K-values of *C. albicans* parasitism plotted against the total densities of pupae in the soil, an indicator of prepupal densities. Closed circles indicate BI. Closed triangles indicate RNP, open circles indicate BBII and open triangles indicate BBI. Trends indicate a weak delayed density dependence at the blueberry sites, but no trends are apparent for birch sites.

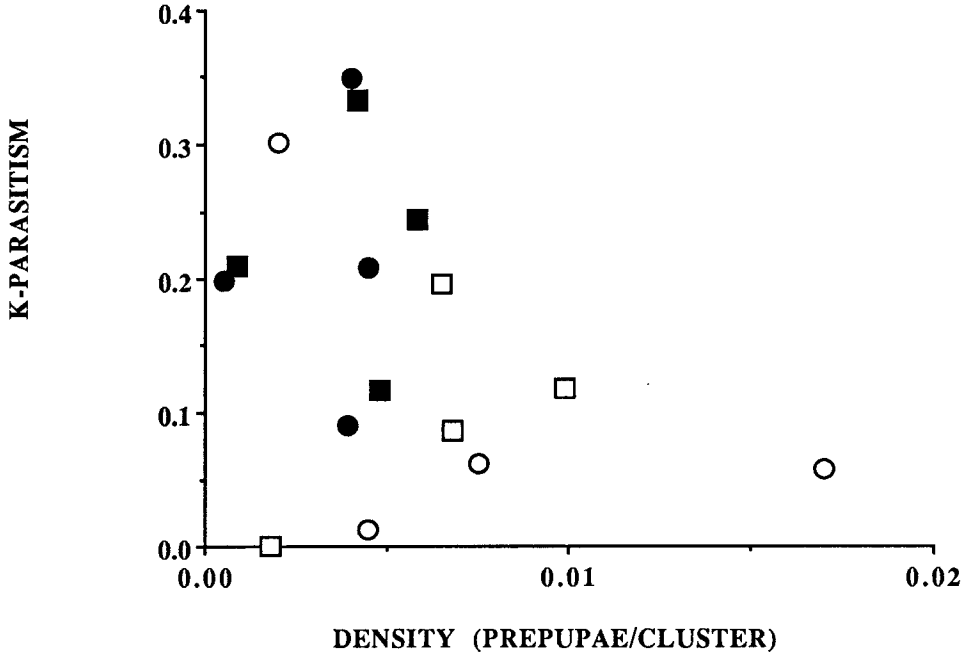


Figure 2.11. Mortality of prepupae due to *C. albicans* (K parasitism) plotted against prepupal densities per leaf cluster as estimated from total pupae in drop trays divided by the average number of buds per unit area, estimated visually, at each site. Results indicate disproportionately low levels of parasitism on blueberry (open circles = BBI, open squares = BBII, closed squares = BI and closed circles = RNP).

a) Refuge resulting from foraging behaviour

Larval development on blueberry appears slower than on birch (Fig. 2.12), but this was not significant. The large proportion of second instars in blueberry on April 15th (1992) is difficult to explain and is probably due to the small sample sizes taken from the blueberry sites. Later in the season there appear to be more larvae on the leaves of blueberry than on the flowers (see Fig. 2.13) , but this trend was significant at only one of the sites (BBII) (2 sample t-test on Log + 1 transformed data, P = 0.005).

Analysis of leaf damage indicates that winter moth larvae disperse their damage (Fig. 2.14). Early in the season most of the damage to leaves is below 5%, as the season progresses the modal damage levels increase. The modal proportions of damage differ among sites based on the densities of larvae at each site. Similarly, high density areas have the highest modal damage levels.

b) Habitat refuge, birch canopy *versus* undergrowth

Cyzenis albicans adults were active and their eggs were found on the birch leaves on April 8th in 1992. Parasites were recovered from both undergrowth and canopy caterpillars (8% and 12% respectively). Few of the larvae reared in the outdoor shed, from either canopy or undergrowth, pupated and therefore it was not possible to adequately estimate levels of parasitism.

There remains a possibility that the undergrowth may act as a refuge, by supporting later instar larvae. Figure 2.12b indicates the occurrence of larval instars at four sampling dates. The distribution of instars in the undergrowth closely follows that of the canopy for all dates except April 8th. At one site only (the high density site) high numbers of fifth

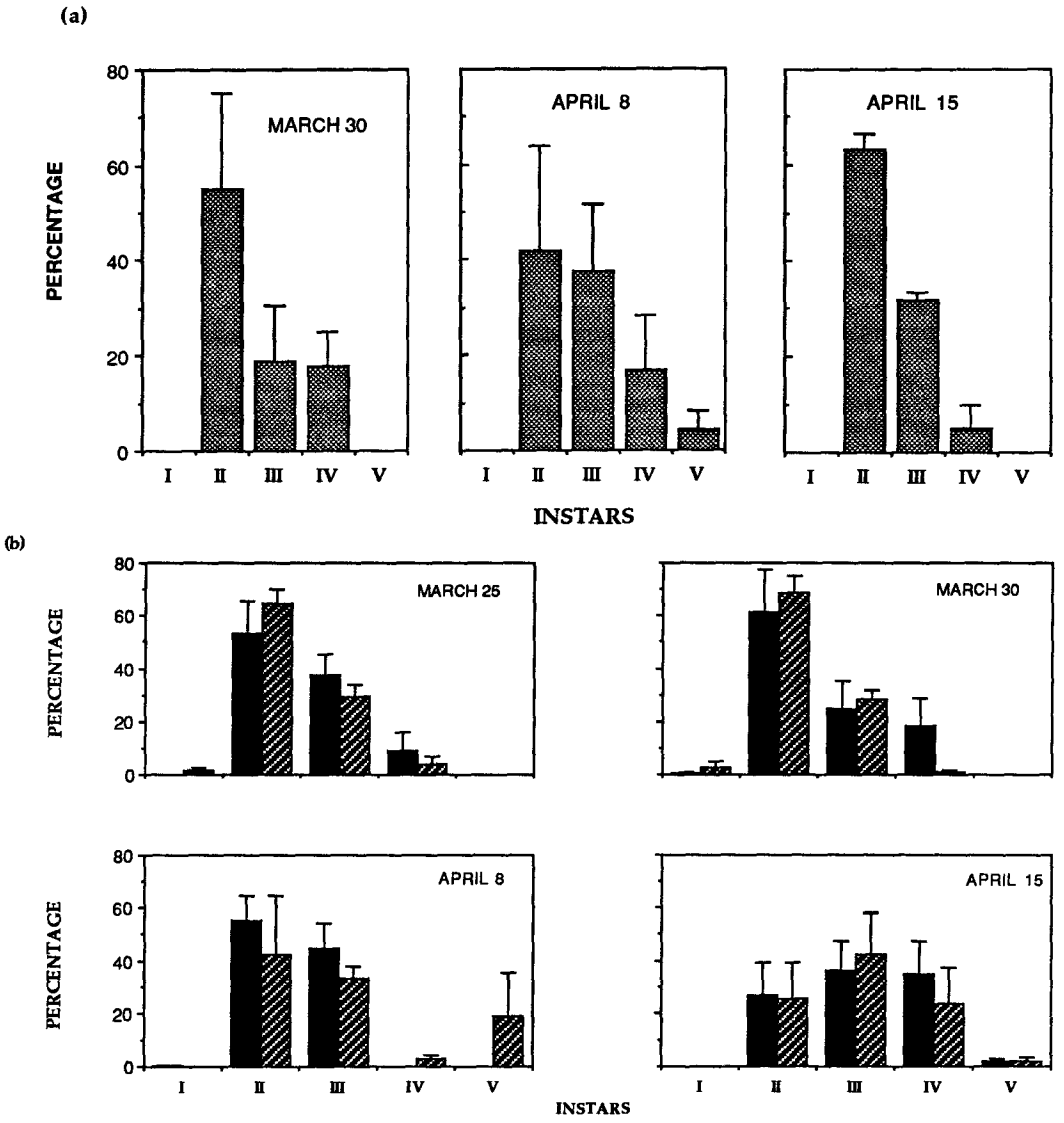


Figure 2.12. Percentage of winter moth larvae at each instar a) on blueberry at three sampling dates and b) percentages of winter moth larvae in birch sites at each instar over four sampling dates. Solid bars indicate larvae in the canopy, shaded bars indicate larvae in the undergrowth. Standard errors are included. There is no significant difference in the development of larvae on blueberry or birch or in either canopy or undergrowth.

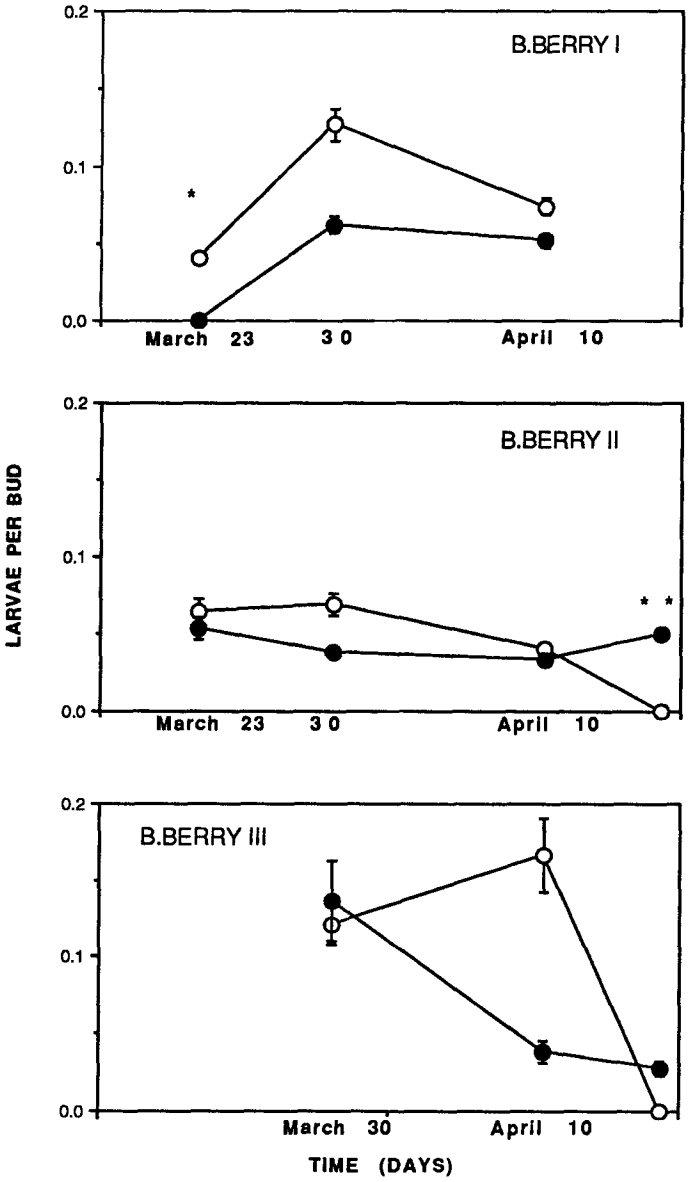
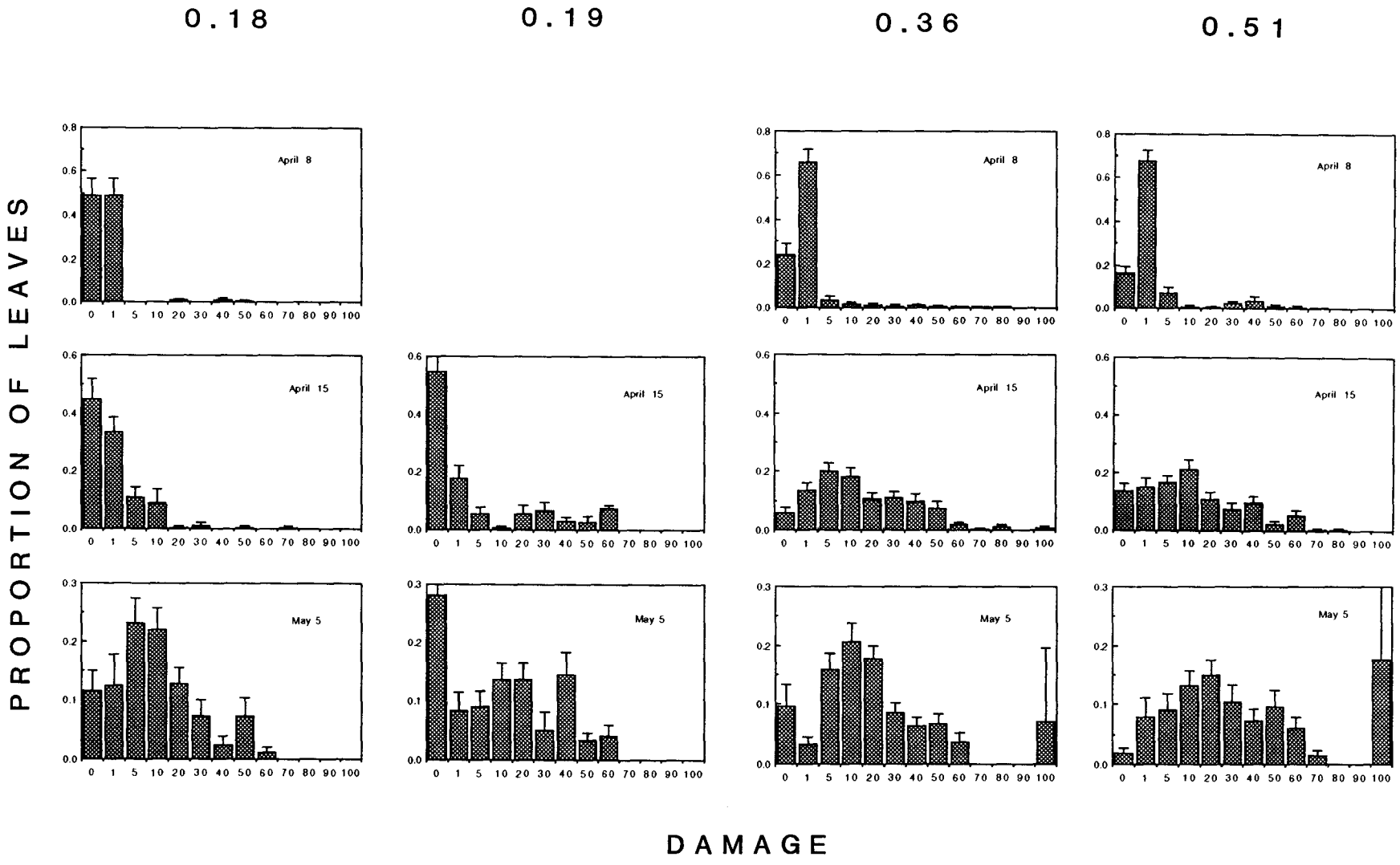


Figure 2.13. Occurrence of winter moth larvae on flower or leaf clusters at three blueberry sites in 1992. Open circles indicate densities on flower clusters and closed circles indicate densities on leaves. Error bars are included. There is an apparent shift from foraging on flowers to foraging on leaves as the season progresses. Data was log+1 transformed and analyzed with a two sample t-test; * = P = 0.05, ** = P = 0.005.

Figure 2.14. Progression of damage to birch leaves at four different densities of winter moth larvae over three sampling dates. Densities of early instar larvae per cluster are presented at the top. Bars indicate the proportion of leaves in each damage class, with associated standard errors. Leaves with one hundred percent damage generally had died as a result of larval attack.


0.18
0.19
0.36
0.51
PROPORTION OF LEAVES
DAMAGE
April 8
April 15
May 5
0 1 5 10 20 30 40 50 60 70 80 90 100

instars were found in the undergrowth but differences were not significant. Therefore, a suggested developmental difference between canopy and undergrowth caterpillars is unlikely.

2.3.4 Winter moth and *C. albicans* spread

Winter moth is continuing to spread throughout the greater Vancouver area. Larvae were present at 18 of the 20 sampling sites (see Tables 2.4, 2.5 and 2.6). Bruce's spanworm alone was found at the Langley sites. Larval densities were highest at Richmond, but varied greatly over small distances. At Richmond Nature Park, numbers were lower at the eastern side (11 - 14). The southern areas of Vancouver (south of 41st Avenue), had high densities of winter moth causing moderate damage to ornamental and shade trees. At all other sites (1 - 7) Vancouver, (18) Westham Island, (19) Deas Island and (20) Delta, numbers were low. Larvae were not found at Burnaby (9 - 10).

Parasitism by *C. albicans* also appears high in Richmond. Figure 2.15 indicates the highest levels of parasitism encountered throughout the four years of study. Parasitism was highest on birch. Figure 2.15 also includes incidences of parasitism from 1990 for Tsawwassen and Ladner. Sampling at these sites was discontinued after 1990 but it appears that the Tsawwassen levels of parasitism are the highest encountered in the lower mainland. In Vancouver, parasitism remains low, at below 10%, with sufficient sample sizes only in the southern areas. No parasites were recovered from northern Vancouver (north of 41st Avenue), Westham island, Deas Island or Delta. However, numbers of larvae reared through to pupae were very low at these sites.

Table 2.4. Winter moth early instar larval densities (per cluster) at Richmond sites during 1991 and 1992, with associated levels of parasitism by *C.albicans* and death of prepupae due to unknown causes from 1990 to 1992. Host plants are indicated. Brackets indicate standard errors of larval estimates and sample size for parasitism and "unknown" mortality estimates. Asterix indicates that pupae were taken from drop trays, otherwise pupae were reared from collected prepupae.

SITE	HOST	LARVAL DENSITIES		PARASITISM			DEATH (UNKNOWN)		
		1991	1992	1990	1991	1992	1990	1991	1992
KNIGHT ST.	BIRCH				59 (27)			22 (27)	
D.N.D.	BIRCH		0.0112 (0.0079)	0 (6) *	0 (5) *	0 (3)	0 (6) *	0 (5) *	0 (3)
	BLUEBERRY		0.0119 (0.0118)						
(RNP) EAST I	BIRCH	0.7432 (0.0881)	0.1236 (0.0201)			37 (42) *			36 (42) *
(RNP) HWY. 99	BIRCH		0.2318 (0.0302)			11 (19)			68 (19)
(RNP) WEST I	BIRCH			19 (348) *	55 (384) *	37 (103) *	28 (348) *	9 (103) *	36 (103) *
(RNP) WEST II	BIRCH	0.0111 (0.0064)	0.0218 (0.0093)			0 (1)			0 (1)
BIRCH I	BIRCH	0.2500 (0.0377)	0.2805 (0.0062)	24 (218) *	54 (448) *	38 (206) *	15 (218) *	8 (448) *	20 (206) *
B.BERRY I	BLUEBERRY		0.0926 (0.0176)	12 (93) *	14 (16) *	50 (6) *	18 (93) *	0 (16) *	50 (6) *
B.BERRY II	BLUEBERRY	0.3579 (0.0348)	0.0502 (0.0148)	24 (269) *	36 (89) *	0 (15) *	13 (269) *	2 (89) *	42 (15) *
B.BERRY III	BLUEBERRY		0.1250 (0.0352)						

Table 2.5. Winter moth early instar larval densities (per cluster) at Lower Mainland sites during 1992, with associated levels of parasitism by *C.albicans* and death of prepupae due to unknown causes for 1990 to 1992. Host plants are indicated. Brackets indicate standard errors of larval estimates and sample size for parasitism and "unknown" mortality estimates.

SITE	HOST	LARVAL DENSITIES	PARASITISM			DEATH (UNKNOWN)		
		1992	1990	1991	1992	1990	1991	1992
WESTHAM ISLAND	BIRCH	0.0065 (0.0064)			0 (10)			20 (10)
	CRABAPPLE	0.0698 (0.0275)						
DEAS ISLAND	BIRCH	0.0124 (0.0114)		0 (5)			0 (5)	
DELTA	OAK							
TSAWWASSEN	BIRCH		80 (20)			0 (20)		
LADNER	BIRCH		28 (162)			7 (162)		

Table 2.6. Winter moth early instar larval densities (per cluster) at Vancouver sites during 1991 and 1992, with associated levels of parasitism by *C.albicans* and death of prepupae due to unknown causes. Host plants are indicated. Brackets indicate standard errors of larval estimates and sample size for parasitism and "unknown" mortality estimates.

SITE	HOST	LARVAL DENSITIES		PARASITISM			DEATH (UNKNOWN)		
		1991	1992	1990	1991	1992	1990	1991	1992
U.B.C.	BIRCH		0.0041 (0.0040)		0 (7)	0 (2)			50 (2)
9TH ALMA	BIRCH		0						
13TH TRIMBLE	BIRCH		0.0077 (0.0077)						
SPANISH BANKS	APPLE	0.06 (0.0336)				0 (2)			0 (2)
	BIRCH	0	0.0039 (0.0039)						
LACARNO BEACH	BIRCH		0.0078 (0.0077)			0 (3)			66 (3)
JERICO BEACH	BIRCH		0.0152 (0.0106)		0 (46)	0 (1)		48 (46)	0 (1)
35TH GRANVILLE	BIRCH			14 (21)	0 (41)		0 (21)	61 (41)	
49TH OAK	BIRCH			8 (49)			6 (49)		
61ST GRANVILLE	BIRCH		0.1914 (0.0256)			2 (44)			18 (44)
VANCOUVER	BIRCH			10 (49)			4 (49)		

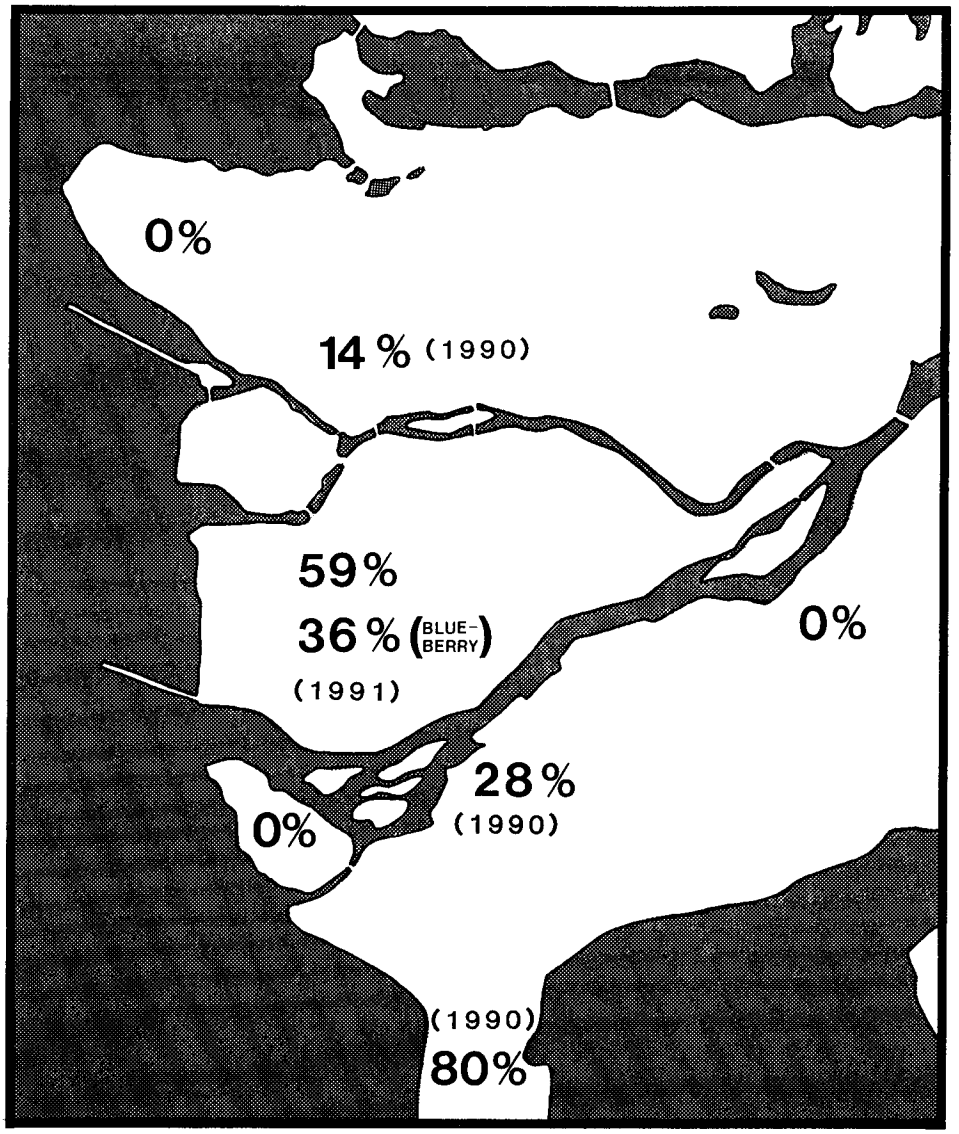


Figure 2.15. Highest incidences of parasitism by *C. albicans* encountered at seven regions in the lower mainland, over the four year study period. The year in which parasitism was highest is presented in brackets. Birch was the host plant at each site except at Richmond where blueberry was also sampled (as indicated), and Westham Island where both birch and crabapple were sampled.

2.4 Discussion

Winter moth has reached high levels on both blueberry and birch in Richmond. The population was already high when this study was initiated in 1989. Since 1990 there has been a decline in the population with an eventual population crash in 1992 on both blueberry and birch. The decline in 1992 was significant at all life stages except adults.

Parasitism - Host Plants

Overall average prepupal densities per leaf cluster on unmanaged blueberry are similar to those on birch stands (see Fig. 2.11). Significantly lower levels of parasitism also occur on blueberry. The possible reasons for this include: i) differences in the synchrony of host on the different plants with parasitoids, ii) differences in the foraging behaviour of caterpillars on the different host plants or iii) differences in the chemical cues for oviposition of *C. albicans* on blueberry and birch.

A large asynchrony between the occurrence of fourth and fifth instar winter moth and the oviposition of *C. albicans* could explain the reduced parasitism of caterpillars on blueberry. Such an asynchrony has been implicated in the lack of success achieved by *C. albicans* on apple in Nova Scotia when compared to its success on oak (Roland 1986a, 1986b). Parasitism of winter moth larvae on oak reached levels as high as 80%, while on apple levels generally remained lower than 5% (only in the early 1960's, did parasitism reach comparable levels (50%) on apple in Nova Scotia [MacPhee *et al.* 1988]). In Victoria, parasitism on apple was generally higher than in Nova Scotia (ca. 50%), but still lower than on oak (ca. 70%). Reasons for the discrepancies between the two regions are unknown, but they may be due to climatic differences. Examination of the development rate of caterpillars in 1992 indicated no differences between development on birch and

blueberry (see Fig. 2.12). However, this represents only a single year in which sample sizes were small. Therefore, different development rates on blueberry and birch can not be ruled out.

Differences in the foraging behaviour of larvae on birch and blueberry could result in different levels of parasitism by *C. albicans*. Roland (1986a, 1986b) found that *C. albicans* oviposits differently on oak and apple. In the field he observed more eggs on oak foliage than on apple foliage in response to similar levels of damage. Also, *C. albicans* eggs were more clumped on oak foliage at all levels of scale measured (among clusters, within trees and among trees). In spite of this, the resultant levels of parasitism on apple and oak were not different in Victoria. One of the reasons he suggested for this was that caterpillars may be eating more foliage on apple than on oak.

Larval feeding behaviour and the morphology of host plant leaves, as well as the morphology of the entire plant, could have profound influences on the success of *C. albicans* in parasitizing winter moth larvae. Feeding behaviour differs among winter moth caterpillars on different host plants. Shot-hole damage described by AliNiazee (1986) for filberts, is apparent on oak but not on birch or blueberry. These differences are probably due to differences in the morphological or chemical qualities of the leaves. Therefore, although there may be less eggs on apple leaves there could be a greater chance that the moth larvae will ingest them, or start to feed from the site where the eggs are because of the chemical or morphological condition of the leaf. This may explain discrepancies between the actual number of *C. albicans* eggs and the resultant levels of parasitism.

Caterpillars generally disperse their damage, and thus depart from what would be predicted from optimal foraging theories (see references in Mauricio and Deane Bowers 1990). Two suggestions have been put forward to explain this pattern. Firstly, that

dispersal of feeding damage may help to avoid predators (Heinrich 1979). Secondly, that it may be a response to changes in plant chemistry as the caterpillars feed (Feeny 1976). Regardless of the reasons for the dispersal of damage, it should result in reduced aggregation of eggs, less likelyhood of a caterpillar ingesting eggs, and possibly less superparasitism. On birch, caterpillars ate small amounts of leaves (< 5%) before moving to new undamaged leaves. As the season progressed, the damage to the individual leaves increased due to density effects and the larger size of caterpillars. This suggests that the larvae are visiting previously damaged leaves. This revisiting of damaged leaves is expected to be more common at high densities. On blueberry this trend was not observed because larvae feed of flower buds early in the season, making it difficult to examine the progression of damage. However, an important observation in 1992 was the switch from feeding on blueberry flowers early in the season to feeding on blueberry leaves about early to mid April. This was at the time when *C. albicans* adults were ovipositing. Possible reasons for this shift include: i) size constraints (at this time flower clusters may be unable to accommodate the larger winter moth instars); ii) sudden physiological changes in the flowers and thus changes in nutritive quality; or iii) avoidance of predation from insects, mainly wasps attracted to the flowers. This shift meant that the larvae moved to foliage that had received little or no damage and thus were less likely to have *C. albicans* eggs.

The switching behaviour observed on blueberry is more likely to cause a refuge against parasitism if *C. albicans* oviposition on blueberry is similar to that on oak. If, as on apple, oviposition is not aggregative, then the resulting parasitism from lightly damaged leaves could be high. Because birch and blueberry leaves are morphologically more similar to apple leaves, as opposed to oak (i.e. lack of undulating edges, etc.), I expect that the foraging behaviour on blueberry will be more like that on apple. I suggest, based on photographs of damage to oak and observations of damage to blueberry, birch and apple leaves, that the amount of damaged surface exposed for oviposition increases faster with

oak leaf damage than with apple. This is because caterpillars appear to avoid the tough veins of oak leaves but generally eat through the veins of apple. Also oak leaves are generally larger than apple, birch, and blueberry leaves, so that corresponding amounts of damage to oak induce more surface area for *C. albicans* to lay eggs.

The fact that *C. albicans* is able to aggregate its eggs in response to levels of damage on oak, but not on apple (Roland 1986a, 1986b), suggests differences in the synomones released from these hosts in response to damage. Sugars at the edges of damaged oak leaves stimulate *C. albicans* oviposition (Hassell 1968), and an airborne chemical attractant causes aggregation (Roland *et al.* 1989, Roland 1990a). Which cues are present in birch and blueberry is not known. Presumably the contact oviposition stimulant is present in both these hosts, but an airborne factor may be lacking. If the airborne factor is absent, the lack of oak trees in the vicinity of these study sites may explain why parasitoid levels are so low in Richmond when compared to studies in Nova Scotia or on Vancouver Island. Furthermore, the morphological complexity of blueberry bushes compared to birch, might reduce parasitism by decreasing direct contact of *C. albicans* with damaged leaves.

Habitat refuge

The possibility of refugia at birch sites were also investigated; a habitat refuge is the most probable type of refuge. Winter moth larvae are largely monophagous, although the species is polyphagous (Wint 1983). However, shifting of host plants can occur among larvae (Wint 1983, Roland 1986a and see results section). In the birch woodlands in this study, there was dense undergrowth of salal, red elderberry and blueberry. Of these, only blueberry was eaten. The blueberry plots had little or no undergrowth with only limited patches of salal. The possibility exists that larvae dispersing downward may move to fresh hosts, and therefore have fewer opportunities of ingesting *C. albicans* eggs. A second

possibility by which undergrowth could act as a refuge is by supporting quicker development of later instars. Finally, *C. albicans* may be more attracted to damage in one of the hosts over the other, with one host plant acting as a sink for *C. albicans* eggs and the other creating a refuge for winter moth larvae in mixed stands.

Undergrowth was found to be important for early instar larvae since bud-burst was generally sooner in the undergrowth. Early in the season there appeared to be a higher incidence of second instars in the undergrowth than in the canopies (pers. obs.). Later sampling however revealed no differences in the development of undergrowth and canopy larvae (see Fig. 2.12). Sampling on April 8th did show a higher number of fourth and fifth instars in the undergrowth, but this was not significant and was probably due to downward larval dispersal rather than to differences in the development rates of larvae in the undergrowth and canopy. Mass rearing of caterpillars from both undergrowth and canopies demonstrated no differences in the incidences of parasitism.

It is difficult to suggest why *C. albicans* is more successful in parasitizing larvae on birch than on blueberry. There is no strong evidence to suggest that there are differences in synchronies of larvae and leaf development on either blueberry or birch, or that the mixed vegetation of birch stands presents a refuge. In this study, caterpillar foraging behaviour appears as the most likely determinant for the lack of*C. albicans* success on blueberry. The switching behaviour of larvae possibly reduces the success of the parasitoid. A more thorough examination of the morphological and chemical nature of these hosts and a better understanding of the chemical stimuli involved in *C. albicans* oviposition is needed to help forecast the success of the parasitoid on these hosts.

Larval mortality

Larval mortality and 'death due to unknown causes' was high in 1992. At three of the four sites k_{larv} was the greatest mortality factor. At the remaining site (BBI) k_{larv} was similar to k_{pup}, the highest mortality factor at that site. A number of factors are responsible for larval mortality. These include predation by birds (Embree 1965a, Roland *et al.* 1986), or arthropods (I have observed predation of winter moth larvae by spiders on numerous occasions), viral or other diseases (Wigley 1976), starvation (Tenow 1972, Wint 1983) or dispersal to unfavourable sites (Holliday 1977). In Britain, larval mortality was the key factor influencing winter moth populations, and resulted mainly from asynchronies between bud burst and egg hatch (Varley and Gradwell 1968, Varley *et al.* 1973).

Many authors have investigated the importance of synchrony between host plants and herbivores (West 1985, Feeny 1970, Hunter *et al.* 1991, Valentine *et al.* 1983). On oak, apple and alder, winter moth favour young leaves (Feeny 1970, Holliday 1977, Kikuzawa *et al.* 1979, Wint 1983). Topp and Kirsten (1991) found that on willows, which continue to produce leaves throughout the summer, larvae that feed on young leaves later in the season, developed more quickly, but were lighter than those feeding on young leaves earlier in spring. Feeny (1970) analyzed oak leaves during development of both the leaves and the winter moth larvae. Early feeding coincided with maximum leaf protein content and minimal leaf sugar content, demonstrating nitrogen availability as a possible limiting factor to spring feeding. There was also an increase in the amount of oak leaf tannins during the summer. However, Feeny suggested that leaf toughness was the most important factor inhibiting late season feeding by larvae. Wint (1983) also found leaf toughness to most consistently affect pupal weights.

Because of the wide range of winter moth host plants, it is difficult to suggest a single factor which may inhibit late season development. It is likely that a combination of factors are important. The early spring of 1992, with consistently high temperatures, suggests that leaf development may have been faster that year, and could have had important consequences for the winter moth.

Authors working with winter moth on Sitka spruce suggest that nutrient levels and asynchronization of bud-burst and larval hatch has no influence on larval densities (Watt and Macfarlane 1991, Hunter *et al.* 1991). Five years of field data showed poor synchronization of bud-burst with eclosion. Larvae survived for up to four weeks before bud-burst declining to low densities only after bud-burst (Watt and MacFarlane 1991). These observations may be a result of Sitka spruce being taxonomically a very different host plant from most other winter moth hosts that have been studied. Spruce, since it is evergreen, has needles available even before bud-burst. These needles are less preferred and nutritionally less desirable for the winter moth (Hunter *et al.* 1991). However, they may support larvae for some time. Unfortunately, Watt and MacFarlane (1991) do not present information on the condition of larvae when the buds did burst, nor has there been any feeding experiments to investigate survival of larvae on old foliage of spruce. Though the results with Sitka spruce show poor synchrony, they do not undermine the importance of the phenological relationship between winter moth and its host plant, in this case Sitka spruce.

Kikuzawa *et al.* (1979) suggest that asynchrony with bud burst is not likely to be an important factor in winter moth population dynamics on alder, since these have pseudoterminal buds. Birch also has a pseudoterminal bud type. However, the concomitant increases in larval mortality and in pupal deformities in 1992 on both blueberry and birch,

suggest that there may have been a large asynchrony of larval eclosion and bud-burst on both hosts in that year.

Poor synchrony of larval eclosion with bud burst, as suggested for 1992, implicate starvation and dispersal losses as important sources of mortality in that year. Edland (1971), in perhaps the most detailed study of winter moth larval dispersion, found that both first and second instar larvae disperse. He implied that first instar larvae were dispersing in response to larval densities at individual stands. In stands of infested trees, 80% of the first instar larvae dispersed while on individually colonized buds there was no dispersal. Hunter (1990) found from laboratory trials that winter moth dispersal was independent of density. However, in his experiments he used buds that were unopened and so were an unfavourable food source. As such he could not really test for density dependent dispersal. I looked at dispersal of first instars on stage two blueberry buds and found no evidence for density dependence. Larvae, however, dispersed at a faster rate from smaller buds, suggesting that food limitation may be the major dispersal stimulus (see Appendix 1).

Edmonds (in Cox and Potter 1986) found that daily ballooning was closely related to egg hatch of Douglas-fir tussock moth, which usually had occurred one to two hours earlier. This may occur in winter moth also, since winter moth has diel hatching (Embree 1970). Many authors suggest that newly hatched larvae of a number of species are predisposed to disperse, even in the presence of preferred foliage (Cox and Potter 1986, McManus 1973, Capinera and Barbosa 1978). This might explain Edland's (1971) observations, with large numbers of larvae dispersing from heavily infested stands, simply because greater numbers of larvae were available to disperse. Wint (1983) suggested that food deprivation may be important. He found that after one day of starvation larval activity begins to increase, but eventually declines if starvation continues. In 1992, starvation may have been severe especially for early instars due to an early spring. Many of the larvae

which dispersed may have died due to lack of available food after dispersal or due to ground predation (see Weseloh 1985). On blueberry stands, mortality of dispersing larvae may have been high due to a lack of suitable undergrowth. Of the birch sites, RNP is likely to have had most mortality because of the low tree density (see Table 3.1) (Holliday 1977).

The concurrent increases in 'death due to unknown causes' and larval mortality are important to note. Death of prepupae due to unknown causes included death due to desiccation, failed pupation, deformed pupae failing to emerge and possibly unidentified pathogens. The most common causes of death among prepupae were failure to pupate and deformities. These imply poor nutrition and thus unfavourable foliage quality. Larvae that survived to prepupae may have lacked nutrients essential to survive pupation. Furthermore, because of lower densities of larvae in 1992 than in the previous year, one should expect an increase in pupal size. This was not observed. The occurrence of lighter pupae in 1992, in spite of lower densities again indicates poor foliage quality (see Morris 1972, Danthanarayana 1975, Barbosa and Capinera 1977, Heliövaara *et al.* 1989). Larger pupae occurred only at RNP in 1992, suggesting that the different histories of defoliation or the different ages of the trees at the two birch sites (see Table 3.1) may have had an effect.

Changes in leaf quality either due to current or proceeding years of defoliation have been noted for many plant hosts, but especially among birch (see references in Haukioja 1990). These changes may influence herbivore quality. One such induced response that may have important consequences for populations of early feeders is that previous defoliation can affect the timing of spring bud-burst (Heichel and Turner 1976). For birch, some authors suggest that damage to apical buds (as occurs with winter moth attack) actually has ameliorative effects on subsequent larval feeders (Haukioja 1990). There may have been an induced response among the birch at BI, because of extensive defoliation in 1990. Whether damage to blueberries induces responses is unknown.

Roland and Myers (1987) found reduced fecundity of winter moth which had fed on apple heavily defoliated in the previous year. Those which had fed on previously moderately defoliated plants had increased fecundity. Roland and Myers discounted long term effects of foliage quality on winter moth fecundity as causing winter moth decline. Kikuzawa *et al.* (1979), studying winter moth on alder in Japan, suggest that reductions in fecundity may have lead to a decline in outbreak there. This reduced fecundity could be attributed to a lack of food in the previous year. Unfortunately, it is difficult to suggest whether there actually was a decrease in fecundity, because comparisons of adult weights on alder from non-outbreak years were not presented. Laasonen and Laasonen (1987) suggest that there may be induced resistance of birch (*B. pendula* (Roth.)) to larvae of *Operophtera fagata* (Scharf.). This finding was based on observations of increased numbers of dry or wrinkled larvae as an outbreak in Isosauri (Finland) continued. However, they suggest that other unidentified (annihilating) factors also played a role in the outbreak decline. It is difficult to suggest what may be occurring on either birch or blueberry in this study. Current year larval mortality shows no indication of being density dependent (see Figs. 2.7 and 2.8), discounting current year induced responses, and long term data are not available to examine a delay in density dependence which would result from long term induced responses.

Disease

In Britain, disease is an important factor responsible for larval mortality (Wigley 1976). Circumstantial evidence from Canada has suggested that parasitoids may be responsible for transmitting disease in winter moth populations (Embree 1966, Cunningham *et al.* 1981). In Nova Scotia, no disease was apparent among winter moth populations until after the introduction of *C. albicans* and *A. flaveolatum.* It has been

suggested that the virus appearing in the population of winter moth at that time was transmitted from the native Bruce's spanworm (Embree 1966). Polyhedrosis virus is occasionally prevalent among spanworm in both eastern and western Canada. Decline of spanworm outbreak in the Maritimes and Quebec has been attributed to this virus. The NPV has been described as a simply embedded (unicapsid) NPV and is classified as *Baculovirus* subgroup A (Ives and Cunningham 1980), which is taxonomically very similar to that of the NPV from winter moth in England (Wigley 1976). It is not unreasonable to suggest that cross infection may have occurred.

The presence of parasitoids, intimately associated with the winter moth populations, may be necessary for viral transmission. Winter moth larvae killed by virus release viroids into the environment. The parasitoid attracted to host damage could transport the virus on it's body surface and contaminate new areas. One problem with this idea is that *C.albicans* oviposits when late instars are present. Late instars are more resistant to virus, necessitating larger amounts of virus to successfully kill a caterpillar (Wigley 1976). The presence of early instars in the population may be important in maintaining the infection and increasing the quantity of innoculum in the environment. I tried cross contamination experiments in 1991 using fourth instar larvae of winter moth and spanworm. I used winter moth NPV from Britain and spanworm NPV from eastern Canada at heavy doses. There was no indication of cross infection in spite of high mortality of primary hosts. Lack of sufficient numbers of spanworm larvae prevented more extensive experimentation (see Appendix 4).

The incidence of disease in the lower mainland population is low, and certainly disease played no role in the 1992 decline. Microsporidia were found at BBI in 1991. Larvae exhibited pronounced symptoms and there was 100% mortality of infected larvae. A number of microsporidia (Phylum Microspora, see Poinar and Thomas 1984) have been found to infect winter moth. In 1956, Kreig described *Thelohonia cheimatobiae* from

winter moth populations in Germany. Canning (1960) described 2 species, *Cytosporogenes operophtera* and *Orthosoma operophterae*, from larvae at Wytham Wood in England. A third species, *Nosema wistmani,* purr. & Skat. was identified in 1979 (see Canning *et al.* 1985a for a review of recent taxonomic changes and species descriptions). Microsporidia are normally transmitted between hosts when spores are ingested (Canning and Barker 1982, Canning *et al.* 1985b). The microsporidia found in 1991 were not identified and failed to turn up in eggs, larvae or adults in 1992. It is possible that this infection was accidental from another species of Lepidopteran.

Pupal mortality

Pupal mortality (k_{pup}) has been the most consistent mortality factor over the four years of study and at each of the four site. Pupal mortality has been more important than parasitism in bringing about population decline in Richmond. These results are in agreement with Roland's (1988) observations for Victoria, and with the situation in Britain (Varley *et al.* 1973). However, the four sites differ in the trends observed in pupal mortality. This is probably because of different predator assemblages at the different sites (see Chapter 3). Predation at all sites, except BBII, appears to be temporally density dependent (see Fig. 2.19), but there is insufficient data to strongly support this assumption. This differs from the situation in both Nova Scotia and Victoria, where pupal mortality increased during the decline in outbreak of the winter moth, and was thus inversely density dependent (Embree 1966, Roland 1988). Pupal mortality in the lower mainland may have been high for some years and did not go through such an inverse density dependent process; possible mechanisms behind this process will be addressed in subsequent chapters.

Some differences between the mortality occurring in Richmond and that which occurs in Britain, Nova Scotia and on Vancouver Island include a high rate of parasitism (which differs from the situation in Britain), and the lack of a period of inverse density dependent predation (as occurred in Nova Scotia and Vancouver Island). Therefore, this system appears to be somewhat midway between that of Britain and those of the other sites in Canada.

In 1992 the outbreak declined in Richmond. However winter moth is continuing to spread in the Lower Fraser Valley. Examination of tree bands in southern Vancouver indicate that densities of winter moth are now very high. In the winter of 1992 the numbers of adults per m^2, estimated from sticky traps, was double that at BI ($18.7 \pm 6.88 m^2$ *vs.* $9.48 \pm 2.3 m^2$), the highest level recorded from Richmond. Parasitism by *C. albicans* is still very low, about 3% in 1992. It will be interesting to see whether *C. albicans* will reach high levels of parasitism in southern Vancouver and cause population decline, as Embree (1991) would expect, or whether there will be a population decline with low levels of parasitism, as has occurred in some areas of Nova Scotia and Vancouver Island (Roland 1988) and in Oregon (Kimberling *et al.* 1986). Levels of predation are not expected to be high in Vancouver, since the urban environment is not conducive to large numbers of predators (i.e. ants, beetles, etc.).

CHAPTER 3
PREDATION OF WINTER MOTH PUPAE IN THE LOWER FRASER VALLEY OF BRITISH COLUMBIA.

3.1 Introduction

Long term studies by Varley and Gradwell (1963a, 1968, 1973) at Whytham wood, in England, indicated that winter moth soil mortality is density dependent and thus regulates winter moth populations. This 'soil mortality' included all mortality incurred from the time of pupal drop until adult females were caught ascending trees in winter. Populations in Canada are also regulated by soil mortality (Roland 1986a, 1988, 1990b, 1992, McPhee *et al.* 1988, Pearsall 1992 and see Chapter 2). East (1974) found at Whythm Wood a total soil mortality of 81% of which 62% was incurred to the pupae, 14% to prepupae and 5% to adults. Pearsall (1992) suggests that in Nova Scotia only a very small amount of soil mortality (between 3 and 37%) is due to mortality of adults or prepupae. Similar results were also found in this study (see Chapter 2). Pupal mortality is therefore most important and has been attributed mainly to predation by generalist predators.

Generalist predators have often been recognized for their potential to regulate prey populations (Luff 1983). Reasons for this include the fact that they have broad diets which buffer fluctuations in the abundance of their prey, and that they are not significantly limited by the maximum attack rates of their functional responses (Hassell 1966, Hassell and May 1986). At Whytham wood a number of studies have been carried out in an attempt to identify the generalist predators of winter moth. Frank (1967a) using serological and radioactive tracer techniques identified the carabids, *Pterostichus madidus* (F.) and *Abax parallelopidus* (Pill. et Mitt.) and a staphylinid, *Philonthus decorus* (Gr.), as important. The carabids *P. cupreus* (L.) and *P. melanarius* (Ill.) and larvae of the elaterid *Athous*

haemorrhoidalis (F.) were also shown to consume pupae, but were not sufficiently abundant at the site to be of much consequence. Frank also found small mammals, including the mouse *Apodemus sylvaticus* (L.) the vole *Cleithrionmys glareolus* (Schr.) and the shrew *Sorex araneus* (L.) to take pupae. Unlike invertebrate predators, these were found to actively search out the winter moth pupae. Frank (1967b) estimated that 39% of healthy pupae in the soil were being predated, with *P. decorus* responsible for most of this (53.6%), and *P. madidus* and *S. araneus* responsible for most of the remaining predation.

Graphing *P. decorus* abundance against winter moth population density at Whytham Wood showed signs of cycling which is expected from a delayed numerical response (Frank 1967b). Kowalski (1976) demonstrated an aggregative numerical response of *P. madidus* and a numerical response of *P. decorus* to winter moth density. However, he suggested that heavy losses of *P. decorus*, due to predation by small mammals in the winter, may have impeded a generation response. This stabilization of the *P. decorus* population inhibits the occurrence of a delayed density dependent effect promoting stability of the winter moth population. Buckner (1969) suggested that small mammals, particularly *S. araneus,* were causing much greater mortality than predaceous beetles at Whytham Wood. East (1974) however, has refuted this, estimating that carabids were responsible for up to 38%, staphylinids 30%, and small mammals only 4% of the predation at Whytham Wood. Small mammals may be more important as predators of carabids and staphylinids (see Parmenter and MacMahon 1988 and Grüm 1979) setting the levels of the generalist predator populations.

There are few studies of winter moth predators in Canada. Embree (1965b) estimated soil mortality in Nova Scotia at between 37% to 92% over the period of winter moth decline. He suggested as much as 31% of this was due to small mammal predators (he did not investigate other predators). Pearsall (1992 and in press) studying pupal predators in Nova Scotian apple orchards, found high levels of predation (68.6%), as much as 70% of

which she attributed to beetle predators. She indicated *Carabus granulatus* (L.), *C. nemoralis* (Mull.), *Pterostichus coracinus* and *Harpalis rufipes* (DeGeer) (all carabids introduced from Europe) as likely predators and suggested that there is a functional response of these predators to winter moth density.

Roland (1986a, 1988, 1990b) working on Vancouver Island, estimated soil mortality to be as high as 86% at the University of Victoria research orchard and 95% at Mt. Tolmie Park (his oakwood site). Roland (1990b) suggested that beetles of 0.5 - 1.5mm in width are responsible for the bulk of predation losses (since these could fit through a 2mm mesh). Examination of predated pupae implicated carabid or staphylinid larvae. Three carabids (*Pterostichus melanarius*, *C. nemoralis* and *Calathus fuscipes* (Goeze) and two staphylinids, *Staphylinus aeneocephalus* (DeGeer) and *Ocypus melanarius* (Heer), all of European introduction were also implicated as important predators due to their abundance at the sites. He did not investigate the importance of small mammals. Mortality of pupae on Vancouver Island was spatially density dependent. However, using beetle removal experiments, Roland (1986a) suggested that winter moth was not affected by the abundance of beetle predators. This points to a lack of either aggregated or numerical responses. Mortality of *C. albicans* pupae was reduced and there were higher incidences of virus infected or otherwise dead pupae in the absence of beetle predators. This suggests that virus killed or otherwise failed pupae are normally preferentially taken by predators. These results point to differences in the predation occurring between unhealthy and healthy winter moth pupae which may be important in the dynamics of the system.

Roland (1986a, 1988) reanalysed Embree's data from Nova Scotia and suggested that pupal mortality had been more important in bringing about the winter moth decline than was previously suggested. A similar trend had occurred on Vancouver Island. On both occasions, pupal mortality had increased rapidly from low levels before *C. albicans* introduction, to high levels at the time of winter moth decline. This occurred in spite of 25

years of parasitoid free high populations in Nova Scotia, but only 6 years on Vancouver Island. He has suggested that somehow *C. albicans* may have influenced soil mortality and brought about this decline (both in Nova Scotia and on Vancouver Island). Roland (1986a) proposed three mechanisms by which this may have occurred;

1) the availability of pupae (*C. albicans*) over a longer period of time, 10 months as opposed to 5 - 6 months for unparasitized pupae, may allow predators to build up a numerical response to winter moth populations,

2) unparasitized pupae may be more likely to be taken by predators, than parasitized pupae, therefore, as the proportions of parasitized pupae in the soil increase the remaining unparasitized pupae become increasingly susceptible to predation, and

3) that parasitoids act as vectors of disease, infecting fifth instar larvae and leading to pupal death and thus increasing soil mortality.

These mechanisms are not exclusive. The third mechanism could not be tested in Richmond since the incidence of disease was too low to suggest that it may play any role in population decline (see Chapter 2).

This part of the study has two main objectives: firstly, to look for possible predators of winter moth and *C. albicans* pupae on the Lower Fraser Valley, comparing predators and predation at the blueberry and birch sites. and secondly, to examine the possibilities of a link between *C. albicans* parasitism and pupal predation, addressing Roland's first two mechanisms. I will examine patterns of predation in the Lower Fraser Valley from four years of data and compare observations here with those of Nova Scotia and Vancouver Island.

3.2 Procedures

Study sites

A total of eight sites have been examined throughout the four years for which data are presented. In 1989 and 1990, seven sites were studied, these were; BI, RNP, RNPa (a bog site), BBI, BBIa (a commercially harvested site immediately adjacent to BBI), BBII and DND. In 1991, RNPa and BBIa were not studied and in 1992, two further sites, BIa (a site immediately adjacent to BI but with markedly different habitat) and RNPII, were studied, but DND was not studied. BBIa, RNPa and DND will only be mentioned in the sections on field planting of pupae and trends in predation. These sites are indicated in Figure 3.1 and habitat descriptions are presented in Table 3.1 (see also Fig. 2.1 and information in Chapter 2).

Pitfall trapping

Pitfall trapping was carried out at BI, RNP, BBI and BBII in 1991 and 1992, a further two sites, BII and RNPII, were trapped only in 1992. In 1991, traps were set up on June 18th and trapping was discontinued on September 4th. In 1992, traps were set out from May 14th until the spring of 1993. Each site had 20 traps laid out in two transects of 10 and spaced at approximately 15m intervals.

Traps consisted of 500ml plastic goblets. Holes were dug with a core sampler so that the goblets fitted neatly into the holes. The earth around the mouth of the traps was compacted so that no part of the traps were protruding from the soil surface. Slits were made at the sides of the goblets to drain water. In 1992, 1cm^2 wire-mesh was placed over the mouth of each trap to prevent entry of small mammals (shrews, voles and mice). The mesh was kept in place by wire pegs. The mesh was removed from traps at the birch sites

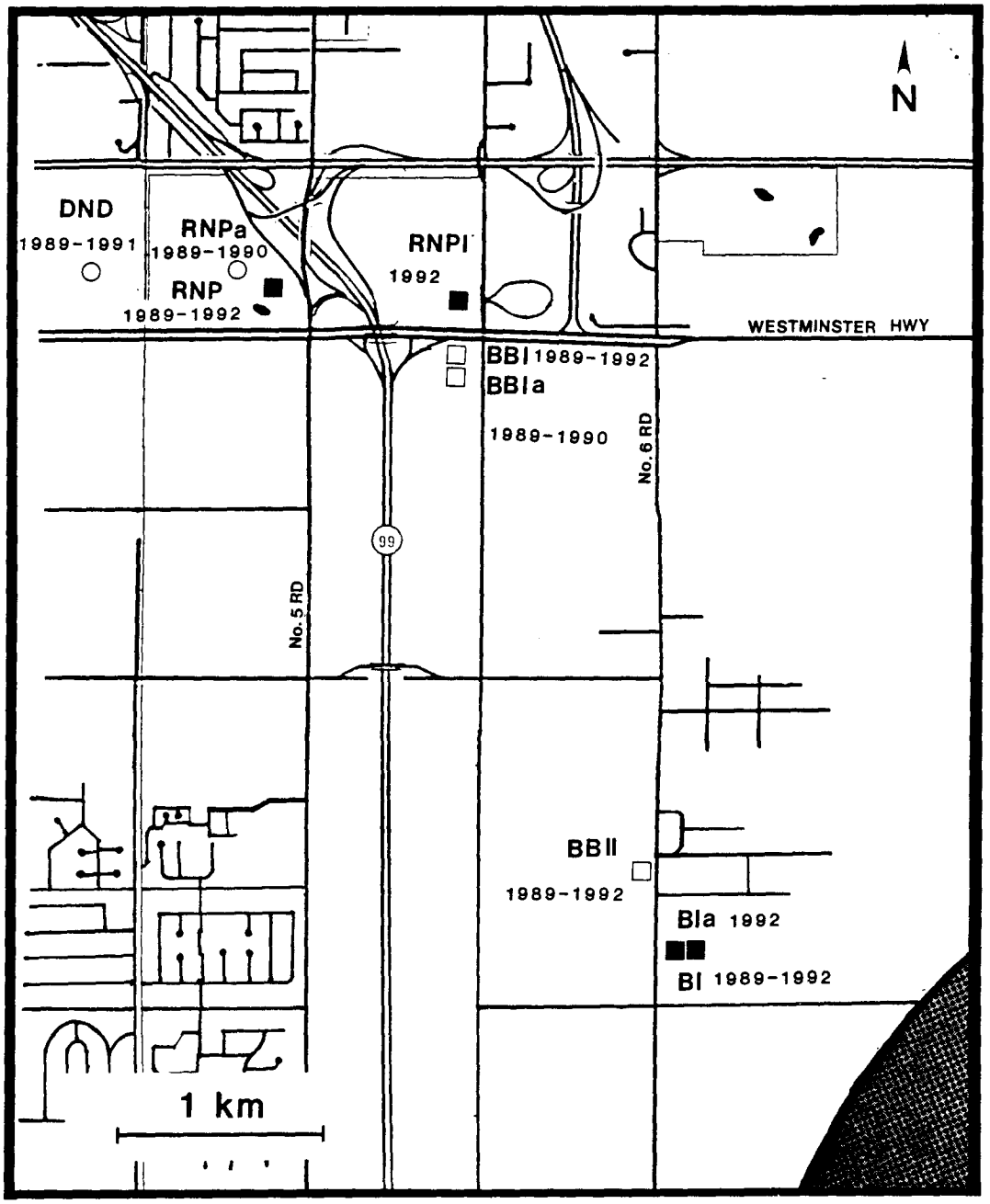


Figure 3.1. Predation study sites at Richmond Open circles indicate bog sites, open squares indicate blueberry sites and closed squares indicate birch sites. The years in which studies were conducted at each site are presented. Highway 99 is indicated by an encircled'99'.

Table 3.1. Habitat characteristics at nine sites in Richmond. Studies on winter moth pupal predation have been carried out at these sites between 1989 and 1992. Densities of birch and hemlock are presented as the number of plants per $50m^2$. Percentage cover of salal, labrador tea and heather are also presented. For undergrowth blueberry, percentage cover is presented while for blueberry plots the numbers of plants per $50m^2$ are presented (indicated by an asterix). Ten randomly chosen plots of $50m^2$ were sampled at each site.

HABITAT								
SITE	Birch			% Cover				
	small	medium	large	Hemlock	Salel	B.berry	lab.tea	heather
Blueberry I	3.1				13	10.2*		
Blueberry Ia						7.08*		
Blueberry II	1.2				5.7	7.08*		
Department of National Defence lands	46.3	0.2			sporadic	23.9	47	2
Richmond Nature Park (Bog) (a)		0.6		3.8	7.5	23.5	62	
Richmond Nature Park	2.7	10.1	7	0.3	59	8.5		
Richmond Nature Park II		1	5.5	0.75	43.75	5		
Birch I	11.6	15.7	3.4	0.1	76.3	6.7		
Birch I (a)	33.1	35.8	4.1	0.4	25.6	14.5		

in the autumn to prevent leaf litter from concealing the trap entrances. In 1991 trap catches were removed every two weeks. In 1992 trap catches were removed weekly till October 7th, and from then at irregular intervals. All predacious beetles were identified to species level and recorded. Spiders, woodlice, milipedes, centipedes and non predaceous insects such as Collembola, flies, etc. were not recorded.

The number of predatory beetles at each site in each year were analysed using the Shannon-Weiver diversity index (H' and H'_{max}) and the species evenness index J' ($J'=H'/H'_{max}$) (Ludwig and Reynolds 1988) Also a coefficient of community index was used (c= 2w/a+b [where a is the total number of individuals in sample a, b is the total number of individuals in sample b, and w is the sum of the lower scores for each species]) (Screiber et al. 1987). The Shannon-Weiver index is the proportion of individuals occurring in the species. The species evenness index is a measure of relative diversity. It measures the expression of species dominance, which is 1-J'. A low value indicates low dominance, a high value indicates high dominance. The coefficient of community index is used to compare similarities in the faunal composition of communities. Values approaching zero are dissimilar, those approaching one are similar.

In 1991, baited pitfalls were set up to examine the possibility of predators responding to olfactory stimuli to locate winter moth pupae. Traps consisted of goblets with muslin bags of bait, the bait consisted of either 1) 4 moth pupae without the cocoon or, 2) 4 fly pupae without the cocoon, suspended from a skewer which lay across the mouth of the trap. Ten traps, five of each type, were set up at each site. The traps were collected at the same time as the control traps (unbaited) on three dates (July 3rd, July 17th and August 1st).

Subsoil traps

In 1991 and 1992, subsoil traps (Fig. 3.2) were set out to identify possible subsoil predators. These traps were specific for small sized predators (mainly beetle larvae) and indicated whether subsoil predators may be responding to olfactory stimuli emitted from the pupae. The basic trap design consisted of a mesh over a mason-jar lid (the trap top), which was tightly secured to a petri-dish lid with drain-holes (the trap bottom). A circular sheet of plastic was coated with tanglefoot and placed in the petri-dish. Bait was suspended by flower wire between the mesh and the tanglefoot. Six trap types were used. In 1991, each baited trap had 4 pupae and empty cocoons were not used as bait. In 1992, owing to a shortage of available pupae, baited traps had each only 2 pupae and traps with a 0.01mm mesh were not used. In 1991, each site had 30 traps, 10 of each type. In 1992, only birch sites had traps each with 20 traps, 5 of each type (Table 3.2). Traps were collected weekly in 1991 and on every second week in 1992.

Table 3.2. Subsoil trap types used in experiments at Richmond, in 1991 and 1992.

TRAP TYPE		MESH SIZE	BAIT	YEAR
TYPE I	1mm complex	1mm	Complex of pupae	1991
TYPE II	0.01mm complex	0.01mm	Complex of pupae	1991
TYPE III	1mm control	1mm	None	1991/1992
TYPE IV	1mm moth	1mm	*O. brumata* pupae	1992
TYPE V	1mm fly	1mm	*C. albicans* pupae	1992
TYPE VI	1mm cocoon	1mm	Empty cocoon	1992

SUBSOIL-PREDATOR TRAP

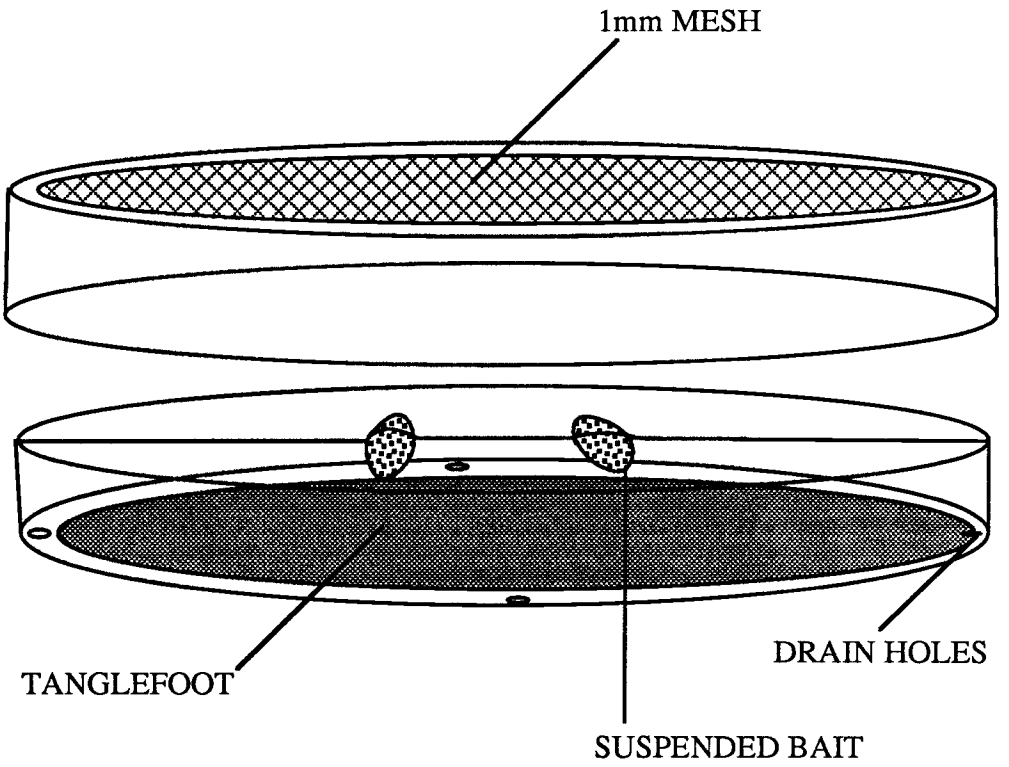


Figure 3.2. Subsoil predator trap used in predation studies at Richmond, B.C..

Field planting of pupae

Pupae were set out at each of the four main field sites from late June until October each year from 1989 to 1992 to estimate the levels of predation at each site. Pupae were also planted at BBIa, RNPa and DND in 1989 and 1990 and at DND also in 1991. Tethers consisted of groups of four pupae attached by flower wire to a central wooden skewer. Pupae were spaced at about 10cm intervals along the wire. Scures were placed along transects at intervals of about 5m, and cocoons were covered with a layer of humus about 3cm deep.

From 1989 to 1991, 20 scures were placed at each of the sites. Pupae attached to the scures were not examined and so the pupae are taken to represent the natural winter moth-*Cyzenis* pupal complex. In 1992, pupae were examined before tethering. A hole was made at one end of the cocoon and the pupa taken out with a forceps, all pupae were weighed and categorized. Five types of pupae were set out in the field; 1) small moth pupae (0.01 - 0.02g) and 2) small fly pupae (<0.01g) were set out at both blueberry and birch sites, 3) large moth pupae (0.02 - 0.03g), 4) large fly pupae (0.01 - 0.02g), and 5) 20 dead pupae (death due to unknown causes) were set out at each of the birch sites.

Tethers were set out after pupation was complete, generally about 1-2 weeks later. In 1989, they were set out on June 25th, in 1990 on June 26th, in 1991 on June 29th and in 1992, on June 25th. Pupae were examined each week in 1990 and 1992 and only once in 1989 and 1991. All pupae were collected on October 7th each year before adult winter moth emergence. In 1992, extra pupae were placed out at the field sites on July 29th, to maintain $N > 20$.

In 1991 and 1992, pupae were out-planted in beetle exclosures (Fig. 3.3) to estimate the levels of pupal predation due to subsoil invertebrates other than adult ground beetles. Ten exclosures were set out at each site. The exclosures were similar to the traps used for subsoil predators. Exclosures consisted of two mason-jar lids covered with 1mm mesh, 4 pupae were suspended between the lids by flower wire. In 1992, pupae were separated into fly or moth groups. The exclosures were examined weekly in 1991 and every two weeks in 1992.

Arena studies

In 1991 and 1992, arena studies were carried out to identify which beetles could eat winter moth and *C. albicans* pupae. Arenas consisted of 5l. plastic containers which were covered with a lid of 1mm mesh. The containers had 2cm of moistened peat with dry leaves for beetle cover. Pupae were placed in the containers either as pupae without cocoons at the top of the peat, or cocooned pupae buried beneath the soil. In 1991, groups of four pupae were used in each experiment and experiments were replicated five times. In 1992, only two cocooned pupae were used in each arena. Whenever cocooned pupae were being used they were only opened for examination of the pupal condition after the trials. This prevented biases from disturbance of the pupae or cocoons.

Beetles were taken from pitfall traps, fed on canned dog-food for some time and then starved for two days before being placed in the arenas. The peat was frequently sprayed with water since the beetles are very susceptible to desiccation. Beetles were left in containers for one week.

BEETLE EXCLOSURE

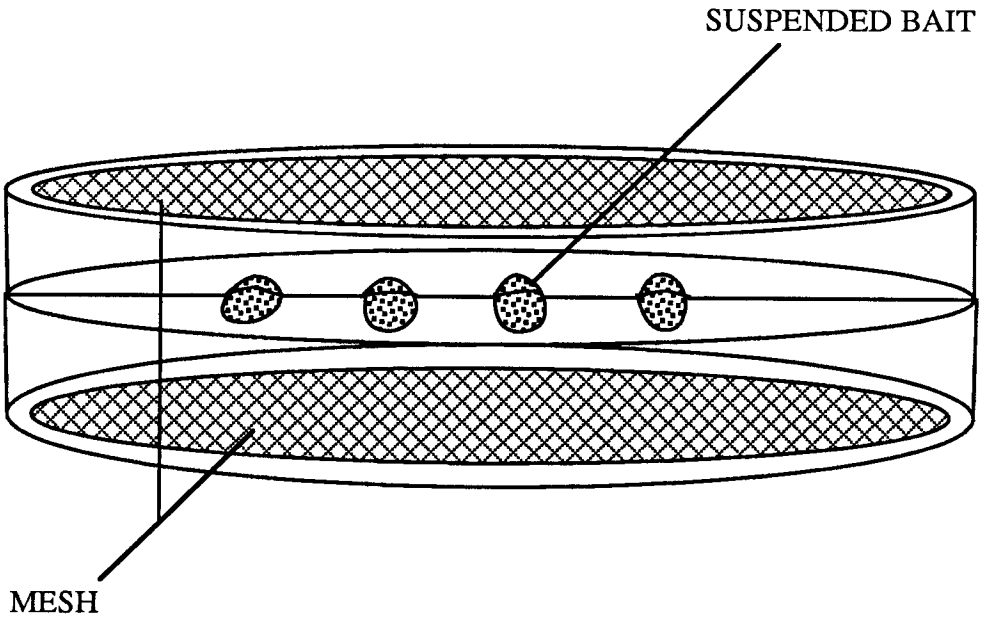


Figure 3.3. Beetle exclosure used in predation studies at Richmond, B.C..

3.3 Results

3.3.1 Trends in predation

Figure 3.4a indicates the levels of predation at 3 blueberry sites in Richmond, between 1989 and 1992. Sites BBI and BBII have been discussed extensively in Chapter 2. BBIa is a commercial blueberry plot immediately adjacent to site BBI, studies at BBIa ceased after 1990.

Data from 1989 and 1990 indicate that there was a dramatic increase in predation of the winter moth-*Cyzenis* pupal complex at all three blueberry sites in 1990. This increase coincides with increases in the winter moth population at that time (see Fig. 2.6b). In 1991, levels of predation at BBI and BBII changed little from levels observed in the previous year. At both sites a slight decrease is apparent. There was a further decrease in predation levels at BBII in 1992. This corresponded with the a decline in the winter moth population there. At BBI however, pupal predation increased in spite of a decline in the winter moth population.

Trends in the predation of the winter moth-*Cyzenis* pupal complex at two bog sites (RNPa and DND) and two birch sites (RNP and BI) are presented in Figure 3.4b, the two birch sites having been discussed extensively in Chapter 2. Studies ceased at RNPa (a bog site at Richmond Nature Park) in 1990 and at DND, a second bog site, in 1991. Both of these sites are known to have had very low densities of winter moth (at DND prepupal densities were as follows: 1989 = $0m^{-2}$, 1990 = $0m^{-2}$ and 1991 = $2.22m^{-2}$, [N = 20 pupal drop trays]: see also Table 2.7). Winter moth may have been kept out of these sites either due to a lack of suitable host plants or due to a very high predation pressure. By 1990, predation at both sites had increased to about 100%. In 1991, there was a slight decline in

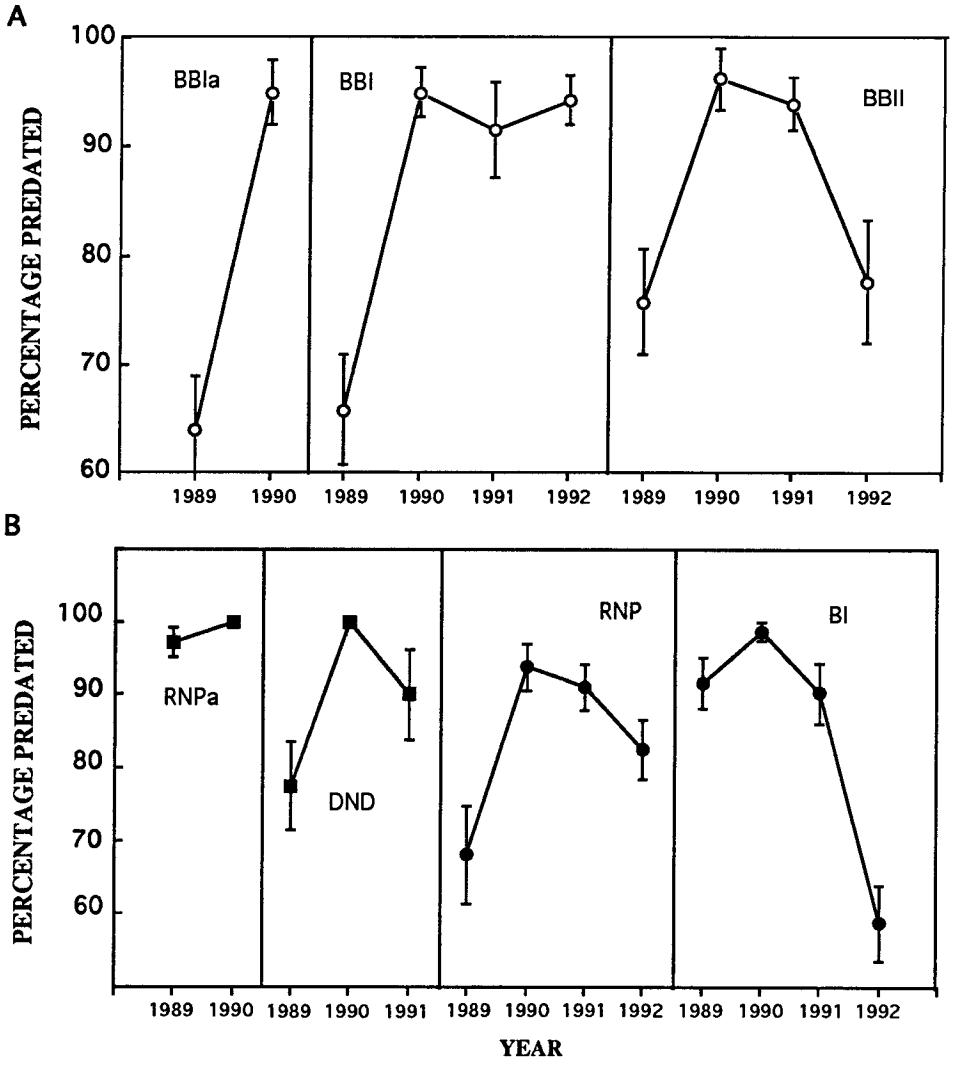


Figure 3.4 Levels of predation on the winter moth-*Cyzenis* complex. Predation estimated from tethered pupae at a) Three blueberry sites and b) two bog sites (squares) and two birch sites (circles). Bars indicate standard errors.

the levels of predation at DND. The predators at both these bog sites were not studied in detail. However, ants were abundant at the sites and are presumed to be the main predators.

At the two birch sites, similar trends to those occurring at BBII were observed over the 4 years. Between 1989 and 1990, levels of predation increased, underwent little change in 1991, and declined in 1992. This decline in predation was most dramatic at BI.

Changes in the levels of predation at each site (except at site BBI in 1992) reflected the changing densities of winter moth. This may be due to different predator assemblages at the sites. Predation therefore appears to be temporally density dependent at each of the four main study sites. This density dependence operates at current year densities, i.e. there is not a delay (see Figure 2.9). However, similar levels of predation were observed at sites with very different densities of winter moth pupae. Therefore, predation is not spatially density dependent. Interestingly, in spite of very different densities of winter moth at each of the sites, the levels of predation were similar each year.

3.3.2 Predator assemblages

A total of 951 beetles were caught in pitfall traps in 1991, and 3190 beetles in 1992. Higher catches in 1992 were due to a longer trapping period with more pitfall traps (26740 trap days in 1992 compared with 5740 in 1991). Since trapping began earlier in 1992, there was increased diversity at each site (Table 3.3), this was due to the large numbers of staphylinids, beetle larvae and small sized beetles (i.e. *Bembidion* sp. and *Agonum* sp.) which were abundant only in May and early June. Table 3.3 presents trapping results from four sites over two years, with additional sites, BII and RNPII trapped in 1992. Non-predatory beetles are not presented in the table. These included Silphidae, Histeridae, Hydrophilidae and *Tachinus* sp. (Staphylinidae), all of which are attracted to carrion, and Elateriodea, Curculoidea, etc., which are herbivorous. Very small staphylinids are also

Table 3.3. Predatory beetles trapped at four sites in Richmond B.C. during 1991 and at six sites in 1992. The Shannon-Weiver Diversity Index (H') and Species Dominance (1-J', where J' is Pielou's Evenness Index), are presented for each site (Ludwig and Reynolds 1988). B.L.'s are beetle larvae and S's are staphylinids.

SPECIES	Total number caught									
	BBI		BBII		RNP		RNPI	BI		BII
	1991	1992	1991	1992	1991	1992	1992	1991	1992	1992
Amara aurata	45	81					1	2	6	
A.littoralis	55	22							5	1
A.laevipennus		3								
Calathus fuscipes	1				4			2		
Callisthenes wilkerii										1
Carabus granulatus		11	7	21			5	8	81	37
C.nemoralis		11	15	5			1		11	5
Harpalus affinus	36	29					9			
H.rufipes				2			2			
Pterostichus algidus								3	16	5
P.herculaneus					42	82	111	227	342	316
P.melanarius	2	10	13	36			2	4	11	8
Scaphinotus marginatus			8	60	1	23	88	25	106	104
Bembidion sp.		7				6	260			16
Agonum sp.										5
B.L. 1 (Staphylinidae)		3		1			1		1	1
B.L. 2 (Carabidae)				2			3			3
B.L. 3 (Elateroidae)				14						12
B.L. 5 (Carabidae)										1
B.L. 6 (Carabidae)				5					1	1
B.L. 7 (Carabidae)	16	11	15	20			1		2	3
B.L. 8 (Carabidae)										
B.L. 10 (Lampyridae)				1						
B.L. 11		2		3			3		2	4
B.L. 12 (Lampyridae)				1						
B.L. 13										
B.L. 14 (Lampyridae)				2						
B.L. 15				1		1			1	
B.L. 16			3							
S. 3 (*Philonthus* sp.)		1		12		3	9		3	31
S. 4 (*Philonthus* sp.)				1		1	2			
S. 5 (*Philonthus* sp.)							5			
S. 11 (*Philonthus* sp.)							1	3		1
S. 12							7			
S. 15 (*Queduis* sp.)								1		
Total number caught	155	191	61	187	47	116	511	275	623	566
Total trap days	1400	4480	1400	4480	1400	4340	4480	1540	4480	4480
Diversity index (H')	1.37	1.95	1.67	2.11	0.40	0.90	1.37	0.70	1.33	1.94
Species dominance (1-J')	0.20	0.18	0.03	0.24	0.64	0.48	0.52	0.68	0.49	0.33

excluded from the table. These were deemed too small to be functionally capable of feeding on winter moth pupae. This was borne out in arena studies. *Notiophilus* sp., *Leistus ferruginosis* Mann., and *Loricera decempunctata* Eschs. have also been excluded. These are diet specialists which feed on Collembola and mites (see Hengeveld 1980a, 1980c, Thiele 1977). Therefore, Table 3.3 represents the potential predator population at the sites (Appendix 5 is an expanded version of Table 3.3 and includes all groups that were trapped).

Some distinct differences between the beetle assemblages at the different sites are immediately apparent. In both 1991 and 1992, the highest diversities were at blueberry sites. Birch sites had low diversities since these were dominated by two species *P. herculanieus* Mann. and *S. marginatus*. Fisch.. Among the birch sites, BII and RNPI had the greatest diversities. This may be due to less ground cover vegetation at both of these sites. Vegetation may have inhibited beetle movement at the other birch sites. Diversity indices have often been criticized as being biologically meaningless. Species evenness however, is more realistic since it is a comparison of H' against H'_{max}. Species evenness (J') at birch sites varied from 0.33 to 0.68, while at blueberry sites J' varied from 0.03 to 0.24, indicating that birch sites are dominated by few species. The most commonly captured species was *P. herculaneus*. This was the most abundant species at all the birch sites. Two other *Pterostichus* species, *P. algidus* Lecon., and *P. melanarius* generally occurred with this species, but at much lower numbers. *P. melanarius* was the only *Pterostichus* species occurring at the blueberry sites, and was not as common as those at birch sites. All three *Pterostichus* species were active at the sites throughout the year, although they were most abundant before mid-August. Birch sites had higher numbers of staphylinids and of the cychrisized form[1], *S. marginatus*.

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[1] Cychrisization refers to the narrowing of the head and thorax of beetles as an adaptation for predation of snails.

Figure 3.5 indicates that in general, sites tended to be different in terms of their faunal compositions. Site BBI had a very different assemblage of beetles when compared to all other sites. Four beetle species which occurred at BBI appear to be most suited to blueberry habitat, these include *Amara aurata* DeJean, *A. litteralis* Mann., *A. laevipennus* Kirby, and *Harpalus affinus* (Schr.) (see Appendix 6 and Lindroth 1961-1969). These species (except *A. laevipennus*) were very abundant at BBI, but were only occasionally captured at the other sites. *Scaphinotus marginatus* which was common at the other sites was completely absent from BBI.

The very different assemblages of beetles at BBI and BBII is surprising. The predator assemblage occurring at BBII was more similar to those occurring at the birch sites. These included the species *L. decempunctata* (see Appendix 5) and *S. marginatus*. The *Amara* species and *H. affinus* did not occur at BBII. However, these two blueberry sites represent very different habitats. The blueberries at BBII are completely overgrown and the ground is therefore moist. BBI on the other hand, is a dryer habitat. It is periodically mowed and so it is more similar to commercial blueberry plots. Most of the species found at BBI are favoured by its dryer habitat (Lindroth 1961-1969, Jeannel 1967). BBII had a diverse array of beetle larvae (see also later sections). Carabid larvae were the most commonly captured larvae, larvae of the larger species (i.e. *Carabus* spp.) appear to be surface active. Pitfall trapping is not a good indicator of the abundance of beetle larvae. However, these data clearly suggest a higher incidence of surface active larvae at BBII.

The pitfall trapping was not designed to examine abundances of small mammals. However, throughout the course of the trapping period a number of small mammals were caught. In 1991, numbers were particularly high, a total of 73 small mammals, mainly shrews, being captured. In 1992, covering the traps with wire mesh reduced the number to 29. In 1991, most of the small mammals were trapped on the first week of trapping, 33 at BI and 6 at RNP. Birch stands had more small mammals than blueberry sites, total catches

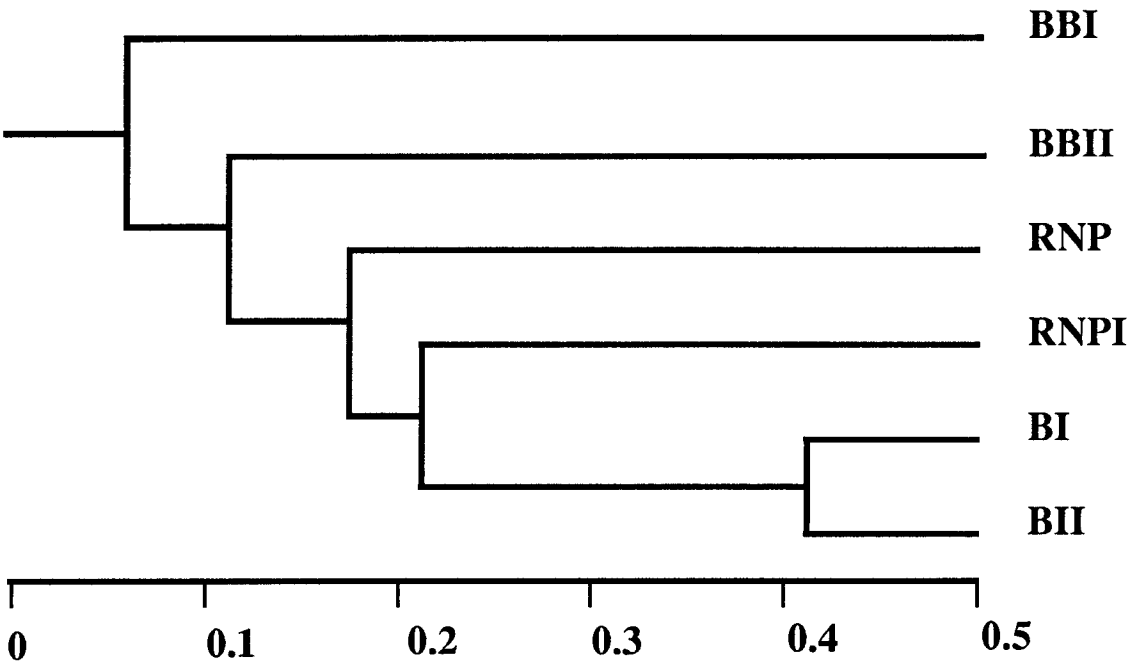

Figure 3.5. Cluster diagram (average linkage) of six sites based on the similarities of their predatory beetle faunas. Pitfall catches are from May 14 till December 3, 1992. Note that similarity coefficients do not exceed 0.5.

being BI = 45 and RNP = 14, in 1991 with BI = 2, BII = 7, RNP = 13 and RNPII = 6, in 1992. At the blueberry sites catches were as follows; in 1991, BBI = 5, BBII = 9 and in 1992, BBI = 1 and BBII = 0. Therefore small mammals, either through predation of pupae or ground beetles, are potentially very important in the dynamics of the system. The influence of small mammals is expected to be greater at birch sites than at blueberry sites.

3.3.3 Predatory beetles

It is difficult to know which beetles are predators of winter moth pupae. Here a number of experiments and observations are compiled to suggest which beetles may be important.

Arena studies were carried out in 1991 and 1992. Only the more abundant beetles were tested. These included *A. aurata, A. littoralis, C. granulatus, C. nemoralis, H. affinus, P. algidus, P. herculaneus, S. marginatus* and two common staphylinids. In 1992, only *C. granulatus, C. nemoralis* and *A. littoralis* were tested. Arena studies were difficult to undertake because mortality of the beetles in the arenas was high. Furthermore, to standardize the experiments, beetles were pre-starved for two days. This may have resulted in beetles, in arenas, feeding on winter moth pupae when in the wild they normally would not. The results therefore simply indicate which species are functionally capable of consuming winter moth pupae.

Three species were found to be facile at consuming pupae (see Table 3.4). These were *H. affinus, P. algidus* and *P. herculaneus*. All these species appeared to favour winter moth pupae, as 50% of winter moth pupae were consumed by *H. affinus* while only 30% of the *C. albicans* pupae were taken. *P. herculaneus* took 100% of the winter moth pupae, but only 20% of the *Cyzenis* pupae and *P. algidus* took 50% of the winter moth pupae and 30% of the *Cyzenis* pupae. The larger *Carabus* species have been noted elsewhere for their

Table 3.4. Ground beetle predators of winter moth-*Cyzenis* pupal complex. '+' indicates that predation was observed, '-' indicates predation did not occur and 'n.t.' indicates that no trials were undertaken. Naked pupae are pupae which have had the hibernaculum removed.

BEETLE PREDATORS	Naked *O.brumata* pupae	Naked *C.albicans* pupae	Cocooned pupae (complex)
Amara aurata	n.t	n.t	+
A. littoralis	n.t	n.t	+
A. laevipennus	n.t	n.t	n.t
Calathus fuscipes	n.t	n.t	n.t
Callisthenes wilkerii	n.t	n.t	n.t
Carabus granulatus	+	+	-
C. nemoralis	+	+	-
Carabus sp. larvae	-	-	+
Harpalis affinus	+	+	+
H.rufipes	n.t	n.t	n.t
Pterostichus algidus	+	+	+
P. herculaneus	+	+	+
P. melanarius	n.t	n.t	n.t
Scaphinotus marginatus	+	-	-
Staphylinids (*Philonthus* spp.)	-	-	-

potential to consume pupae (Roland 1986a, Pearsall 1992). Unfortunately, both species had very poor survival in arenas and were not seen to consume cocooned winter moth pupae. *Carabus* larvae did however consume pupae, but this was only noted on one occasion. Similarly the *Amara* species were found to consume pupae, but this occurred only on one occasion with *A. littoralis* (one pupa being consumed), and *A. aurata* (two pupae consumed). Buried winter moth pupae were taken on both occasions.

Scaphinotus marginatus was not successful in handling winter moth pupae. Only on one occasion did an individual eat a pupa. This pupa did not have a cocoon and was not buried. *S. marginatus* is a snail eater and predation of pupae is unlikely. It may however represent an important mortality factor for pupating prepupae. All the staphylinids that were tested did not consume winter moth pupae.

A number of observations were made in the field of ants and beetle larvae eating winter moth pupae, beetle larvae were particularly voracious predators and included the larvae of staphylinids, *Carabus* species and *Pterostichus* species.

No differences were observed between the catches from baited pitfalls and controls. In general the mean trap catches from baited traps were lower than means from unbaited. This is because of the low number of baited traps (N=5 for each type *vs.* N=20 unbaited, at each sites). There were no significant differences between trap catches within each site on each collection date.

3.3.4 Subsoil traps

Exclusion cages indicated that large numbers of pupae are consumed by insects that can fit through a 1mm mesh. However, the exclusion of larger beetles did reduce the amount of predation. In 1991, 25% of pupae were taken from exclusion cages at BI and

15% at RNP. In 1992, levels of 15% and 20% were found at BI and RNP respectively. At blueberry sites 40% were taken at BBI and 15% at BBII. Exclusion cages were not set out at the blueberry sites in 1992. These results suggest that exclusion of beetles greater than 1mm wide drastically reduces predation. The highest incidences of predation from exclusion cages were at BBI (40%) which may be due to the very different predator assemblage there, possibly with generally smaller beetle larvae.

Perhaps the most striking evidence that beetle larvae are important predators of winter moth-*C. albicans* pupae comes from 1991 exclusion traps. A number of beetle larvae and occasionally ants, were caught in these traps (see Table 3.5). There was no significant difference between the catches at different sites (2-way ANOVA on log +1 transformed data, P = 0.604). However the differences between the trap types were significant (P = 0.01). The 1mm baited exclusion traps caught significantly more than either the unbaited controls (P= 0.025, Tukey test) or the 0.1mm baited traps (P= 0.046, Tukey test). This difference was due mainly to more beetle larvae in the baited traps. There was no difference between the traps when ant catches were taken alone (2-way ANOVA, P= 0.57), but differences were significant for beetle larvae alone (2-way ANOVA, P= 0.005), with significantly more beetle larvae in the baited 1mm traps than in controls or 0.1mm baited traps (Tukey test, P< 0.05 level).

In 1992 due to a shortage of pupae, exclusion traps were only set out at the birch sites. There was no effect of either sites or trap types on catches (2-way ANOVA on log+1 transformed data, sites P= 0.941, traps P= 0.129). However traps did indicate (see Table 3.6) that beetle larvae may be attracted to empty cocoons, as the highest numbers of beetle larvae were caught in traps baited with empty cocoons.

Table 3.5. Mean numbers of ants and beetle larvae caught in exclusion traps during the summer of 1991. Three trap types were used, unbaited (control), baited 0.1mm and baited 1mm subsoil traps. Results are from ten traps at each site.

SITE	CONTROL		BAITED 0.1mm		BAITED 1mm	
	larvae	ants	larvae	ants	larvae	ants
BI	0	0	0	0	0.7	0.1
RNP	0	0.2	0	0	0.6	0
BBI	0	0	0.2	0.2	0.1	0.2
BBII	0.4	0	0	0	1.1	0.5

Table 3.6. Mean numbers of ants and beetle larvae caught in exclusion traps during the summer of 1992. Four trap types were used, unbaited (control), *Cyzenis* baited (fly), winter moth baited (pupa) and hibernaculum baited (cocoon) 1mm subsoil traps. Results are from five traps at each site.

SITE	CONTROL		1mm fly		1mm pupa		1mm cocoon	
	larvae	ants	larvae	ants	larvae	ants	larvae	ants
BI	0	0	0	0	0	0	0.2	0
RNP	0	0	0	0	0.2	0	0.8	0

This evidence suggests that predatory beetle larvae may respond to olfactory stimuli emitted from the winter moth or *C. albicans* pupae and that these stimuli may emit from the cocoon itself.

3.3.5 Timing of attack

Tether experiments in 1990 indicate that most of the predation on the winter moth-*Cyzenis* pupal complex occurred from June to August at each site. Within the first five weeks after pupae were set out, predation had reached 80% (Fig. 3.6). After early August the rate decreased.

In 1991, tethered pupae were only examined on August 6th. By this time predation had reached about 50% at blueberry sites and 65% at birch sites. The predation rate in 1991 therefore appears to have been considerably slower.

In 1992, a similar trend to that of 1990 was observed at all sites (see Figs. 3.7 and 3.8). Most of the predation occurred before August (that is, during the first 5 weeks). Interestingly, predation during the first week after tethering in 1992 appears to have been very low (less than 10% at blueberry sites) with rates increasing rapidly only on the second week. Pupae at the birch sites were not examined after the first week.

3.3.6 Predation on different pupal types

In 1992, the rates of predation were different for different types of pupae. In general, *C. albicans* pupae were more highly predated, though this was dependent on the site and size of pupae in question. At RNP (Fig. 3.7a) there was no difference between the levels of predation on different pupal types (1-way ANOVA on arcsine transformed data, $P = 0.546$). However, at BI (Fig. 3.7b) there were differences (1-way ANOVA on arcsine

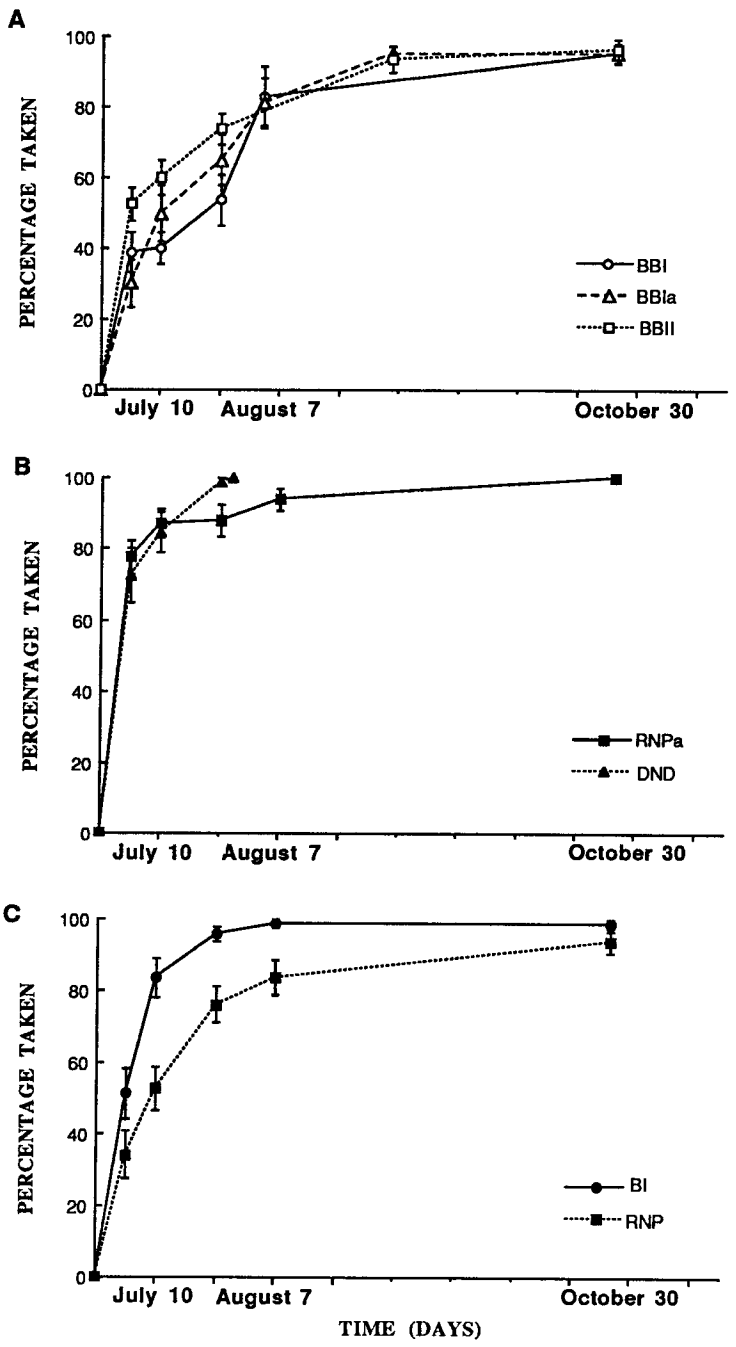

Figure 3.6. Predation of tethered pupae at a) three blueberry sites, b) two bog sites and c) two birch stands in Richmond B.C., during the summer of 1990. Bars indicate standard errors.

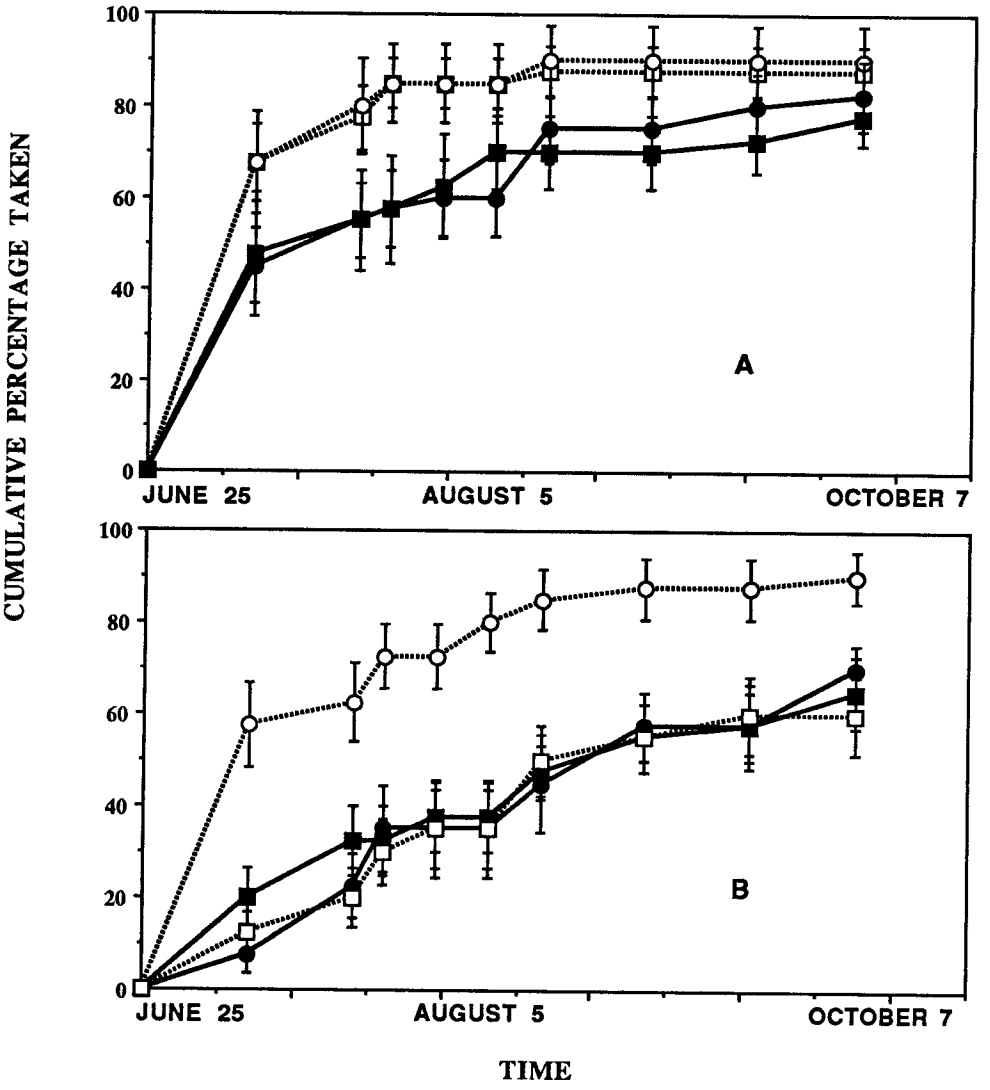

Figure 3.7. Cumulative predation of pupae at two birch sites a) RNP and b) BI, during the summer of 1992. Open circles indicate predation of small *Cyzenis* pupae (<0.01g), open squares indicate large *Cyzenis* (0.01-0.020, closed squares indicate small winter moth pupae (0.01-0.02g) and closed circles indicate predation on large winter moth pupae (0.02-0.03g). Bars indicate standard errors.

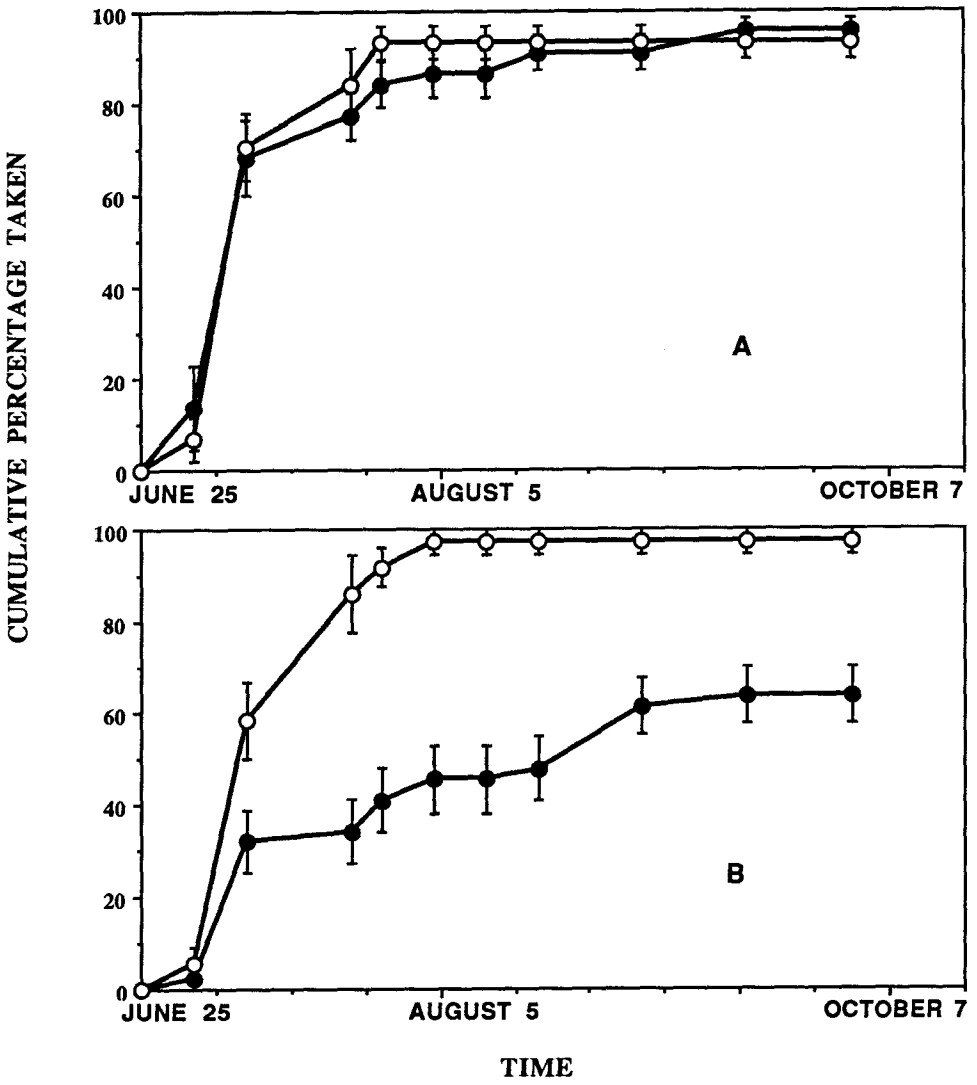

Figure 3.8. Cumulative predation of pupae at two blueberry sites, a) BBI and b) BBII, during the summer of 1992. Open circles indicate predation of small *Cyzenis* pupae (<0.01g) and closed circles indicate predation on large winter moth pupae (0.02-0.03g). Bars indicate standard errors.

transformed data, P = 0.008). Small *C. albicans* pupae were more highly predated than large winter moth pupae (P = 0.028, Tukey test) and large *C. albicans* pupae (P = 0.038, Tukey test), but not the small winter moth pupae (P = 0.07, Tukey test). At BBI (Fig. 3.8a) there was no difference in the predation of *C. albicans* and winter moth pupae (T-test on arcsine transformed data, P = 0.741). However, at BBII (Fig 3.8b) *C. albicans* were significantly more predated (T-test on arcsine transformed data, P = 0.008).

Looking at predation of pupae across sites, there were no differences in the predation of small *C. albicans* pupae (1-way ANOVA arcsine transformed data, P = 0.734). Predation of large winter moth pupae was dependent on site (1-way ANOVA on arcsine transformed data, P = 0.001). There was significantly more predation at BBI (P = 0.005, Tukey test) than BI or BBII (P < 0.005 level, Tukey test), but this was not different from RNP (P = 0.212). More large flies were taken at RNP than BI (T-test on arcsine transformed data, P = 0.012), but there were no differences between predation of small winter moth pupae at birch sites (T-test on arcsine transformed data, P = 0.105).

All these results suggest that different predators are responsible for predation at the different sites and that pupae of different sizes or types (i.e. *C. albicans*, healthy, etc.) may be taken by different predators within each site. *Cyzenis* pupae are more highly predated.

Dead pupae were set out on July 29th at the birch sites. These consisted of pupae taken from pupal drop trays and were deformed or dead due to unknown causes. Within two weeks these had received 100% predation.

The fact that predation levels are highest early in the season indicate that beetles are the most likely predators, since these were the most abundant at that time. At BI, BBI and BBII there appears to be a bimodal trend in levels of predation, with levels becoming low at the beginning of August and increasing again one week later (Figs. 3.9 and 3.10). This

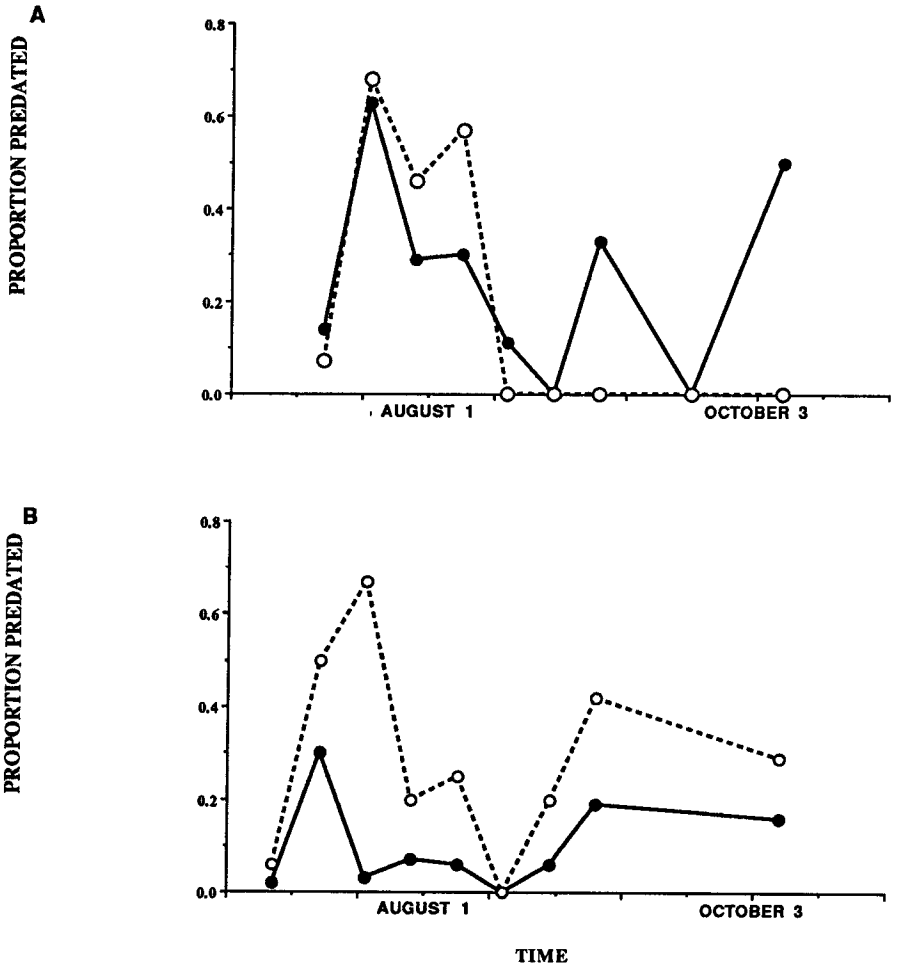

Figure 3.9. Comparisons of the weekly predation levels of small *Cyzenis* pupae (open circles) and large winter moth pupae (closed circles) at two blueberry sites, a) BBI and b) BBII in Richmond B.C..

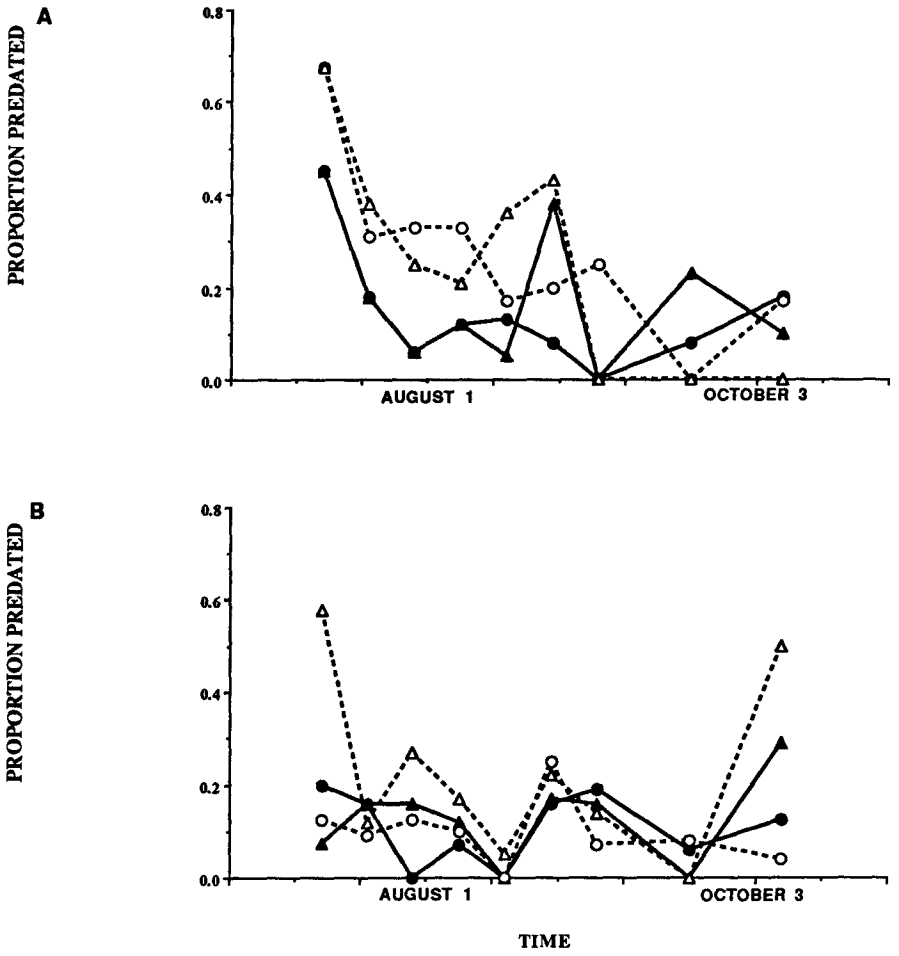

Figure 3.10. Comparisons of the weekly predation levels of small *Cyzenis* pupae (open triangles), large *Cyzenis* pupae (open circles), small winter moth pupae (closed triangles) and large winter moth pupae (closed circles) at two birch sites, a) RNP and b) BI in Richmond B.C..

suggests that *Pterostichus* spp. may be important since these also appear to be bimodal in occurrence (see later). To test this, weekly predation levels were regressed against different components of the predator complex. For the birch sites, predation levels on large winter moth pupae, smaller winter moth pupae, large *C. albicans* pupae and smaller *C. albicans* pupae were regressed against abundances of 1) *Pterostichus* spp., 2) *Pterostichus* spp. and *Carabus* spp. together, 3) *Pterostichus* spp., *Carabus* spp. and *S. marginatus* and 4) all beetles together. Of 32 regressions, only one was significant (at site BI all beetles against predation of small *C. albicans* pupae, $R^2 = 0.491$, $P = 0.035$). At RNP abundances of carabids against predation of pupae showed positive relations, but were not significant. For fly pupae abundances of beetles had no effect. This suggests that beetles may have been important in the predation of winter moth pupae there, but that other factors which do not follow the abundances of beetles were responsible for fly predation. A similar pattern emerged when looking at BI, except for predation of small fly pupae. Although these results do not identify the predators, they do indicate that different predators are responsible for predation of winter moth and *C. albicans* pupae, or that there is a different functional response to the different pupal types among predators.

Similar regressions were carried out for BBII, regressing weekly *C. albicans* and pupal predation (excluding the first week) against abundances of 1) *Pterostichus* spp., 2) *Pterostichus* spp. and *Carabus* spp. together, 3) *Pterostichus* spp., *Carabus* spp. and *S. marginatus* , 4) all beetles together and 5) beetle larvae only. Of 10 regressions 2 were significant. Pupal predation against abundance of beetle larvae ($R^2= 0.596$, $P= 0.023$) and fly predation against all beetles caught ($R^2= 0.550$, $P= 0.035$). This again suggests that the predators are different for flies and pupae in blueberry sites. Regressions for BBI were not carried out because sufficient pupae were not available to keep $N> 20$ for the tethers.

3.3.7 Seasonal abundance of predatory beetles

Trapping was carried out from mid May in 1992 to April of 1993 to estimate the seasonal abundances of important predatory beetles. Figures 3.11 to 3.13 indicate that the seasonal patterns were similar for most of the species. Most of the activity was in the early months of trapping, until mid August or early September, with a decline through winter. At BBI there were no adult predatory beetles active after September. Declines in the activities and abundances of beetles corresponded well with observations from 1991. Similarities in the occurrence of *Amara* spp. and *H. affinus* at BBI during both years suggests that these species may be linked by similar biologies (similar trends have been noted by Holliday and Hagley 1978). Beetles at BBII had very similar patterns of seasonal occurrence to those at BBI, except that small numbers of *P. melanarius* were active through the winter months at BBII. However, there was a noticeable drop in the numbers of *P. melanarius* caught in later months. At birch sites the important predatory beetles were *Pterostichus* species. These were found to be generally abundant throughout the year though the numbers went into decline from December to February when there was snow on the ground. At all four birch sites there was a general decline in the numbers of *Pterostichus* in early August. A similar decline in 1991 was not observed, but this may be because traps were collected only every two weeks in 1991. The bimodal nature of the abundance curves of *Pterostichus* spp. suggests that there may be two generations in a year, those adults active early in the year representing those that emerged from overwintering larvae, and the later ones from larvae of the previous spring.

3.3.8 Annual abundance of predatory beetles

Changes in the abundances of predatory beetles between 1991 and 1992 were examined using data collected from the final week of June till the first week of September each year. Only those beetles that were deemed possible predators (see previous sections

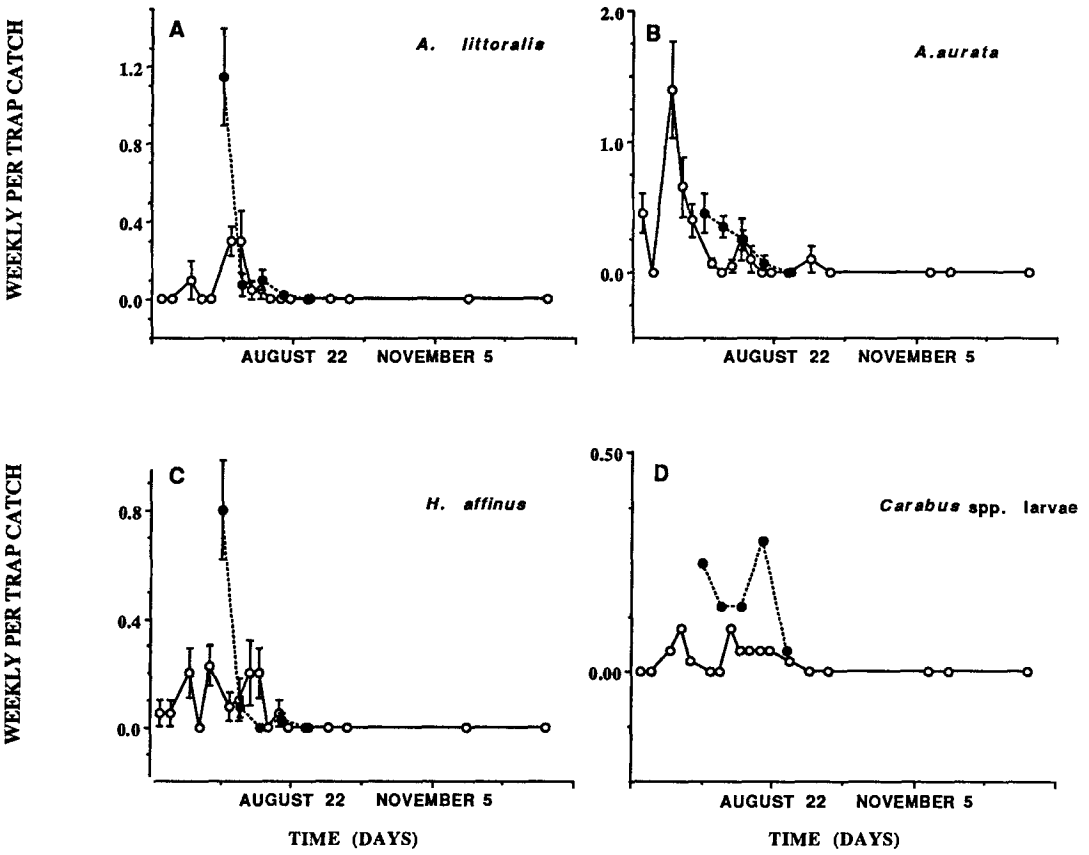

Figure 3.11. Seasonal abundance of Four predators at BBI, a) *A. littoralis*, b) *A. aurata*, c) *H. affinus* and d) beetle larvae from pitfall traps. Solid circles indicate abundances in 1991, open circles indicate abundances in 1992 and bars indicate standard errors.

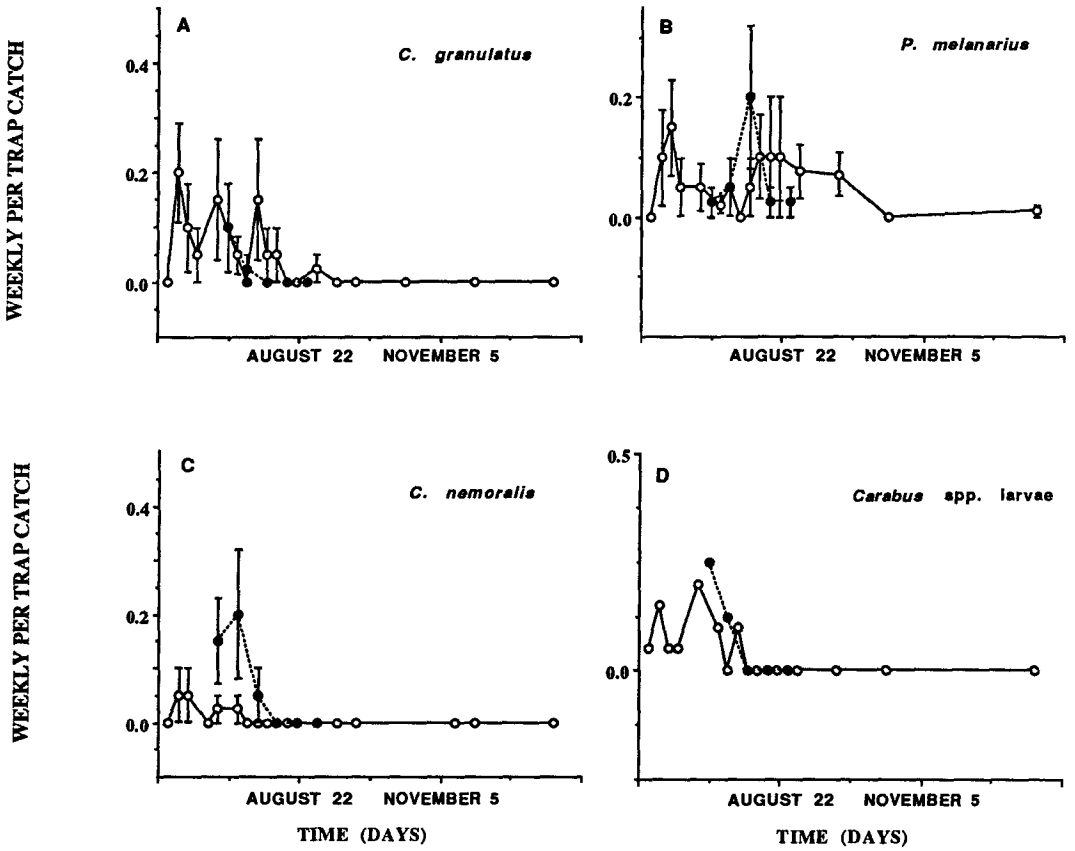

Figure 3.12. Seasonal abundances of four predators at BBII, a) *C. granulatus*, b) *P.melanarius*, c) *C. nemoralis* and d) *Carabus* spp. beetle larvae from pitfall traps. Solid circles indicate abundances in 1991, open circles indicate abundances in 1992 and bars indicate standard errors.

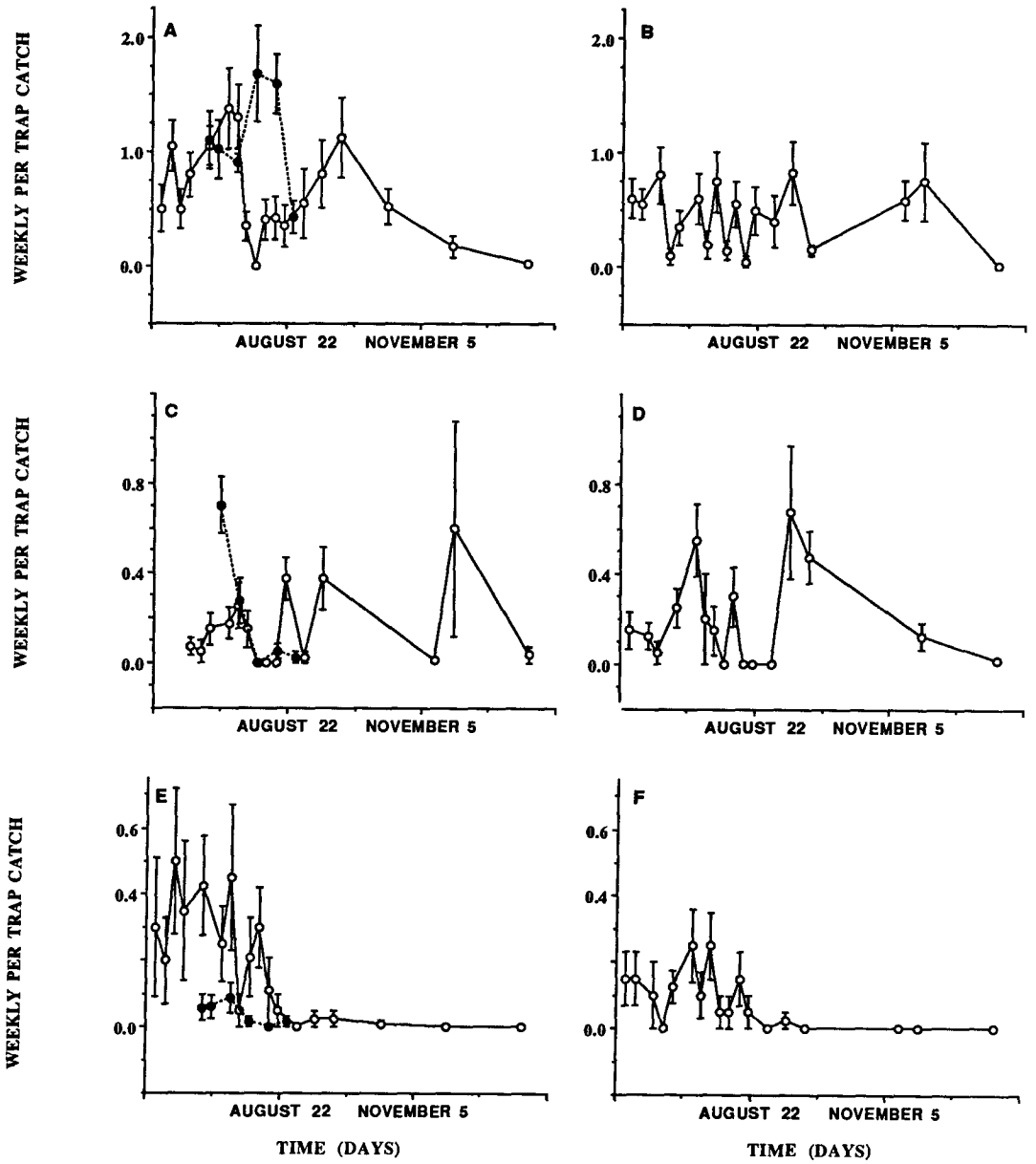

Figure 3.13. Seasonal abundances of *Pterostichus* spp. at a) BI, b) BIa, c) RNP, and d) at RNPI, with abundances of *C. granulatus* at e) BI and f) BIa. Solid circles indicate abundances in 1991, open circles indicate abundances in 1992. Bars indicate standard errors.

and later discussion) were examined. These included all *Pterostichus* spp., *Amara* spp., *Harpalus* spp., all beetle larvae, *Carabus* spp., all medium to large sized staphylinids, *Agonum* spp. and *Bembidion* spp.. These latter three groups were represented by only very few individuals during this trapping period.

There was a decline in the total abundance of predatory beetles only at one of the four sites for which two years of data are available (Fig 3.14). However, the changes in abundance at all sites, were not significant (2-way ANOVA on log+1 transformed data, years P= 0.36). The abundances between sites were significantly different (sites P< 0.001). BI had significantly more beetles than all the other sites (P< 0.001, Tukey test), BBI had less than BI but more than either BBII or RNP (P< 0.001, Tukey test). There were no differences between RNP and BBII (P= 0.594, Tukey test). The apparent increases of predators in 1992 can be attributed mainly to predatory staphylinids and small beetles. These may have had lower numbers in 1991 due to wetter weather conditions, or due to differences in the trap collection periods, i.e. they may have been eaten by larger beetles in the traps 1991.

When looking at the individual species at each site, there are no apparent trends (Fig. 3.15). *Pterostichus* spp. decreased at birch sites, but increased at blueberry sites. There were no significant differences between the abundances of these species in the two years (2-way ANOVA on log+1 transformed data, P = 0.496 for years) *Carabus* spp. increased at all sites where they occurred, medium staphylinids increased and large *Carabus* larvae increased at all sites except BBI where they decreased. Catches of the smaller carabids and other beetle larvae were too small to give a good indication of changes in their abundances. Those species which occurred predominantly at BBI, underwent significant declines in abundance (T-test on log+1 transformed data, *A. aurata*, P = 0.023, T-test, *A. littoralis*, P = 0.016 and *H. affinus*, P=0.019) (see Fig. 3.16).

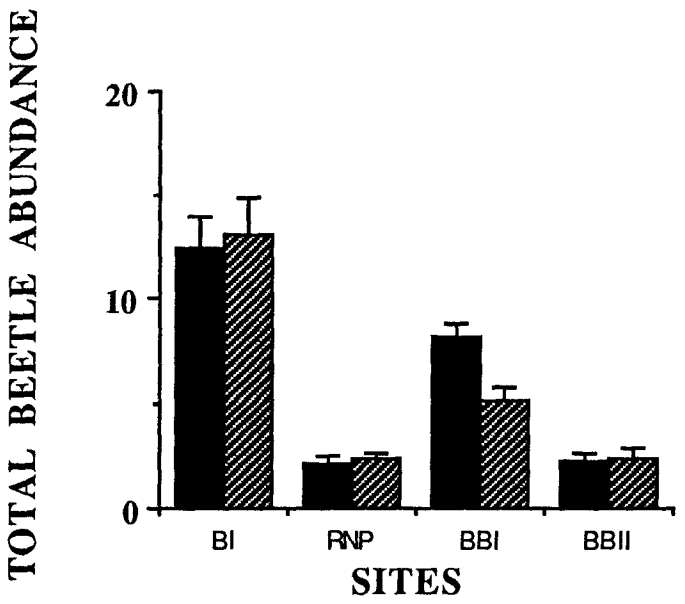

Figure 3.14. Summer abundance of predatory beetles at four filed sites in Richmond. Solid bars are abundances of beetles per trap in 1991, shaded bars are abundances of beetles per trap in 1992. Standard errors are presented.

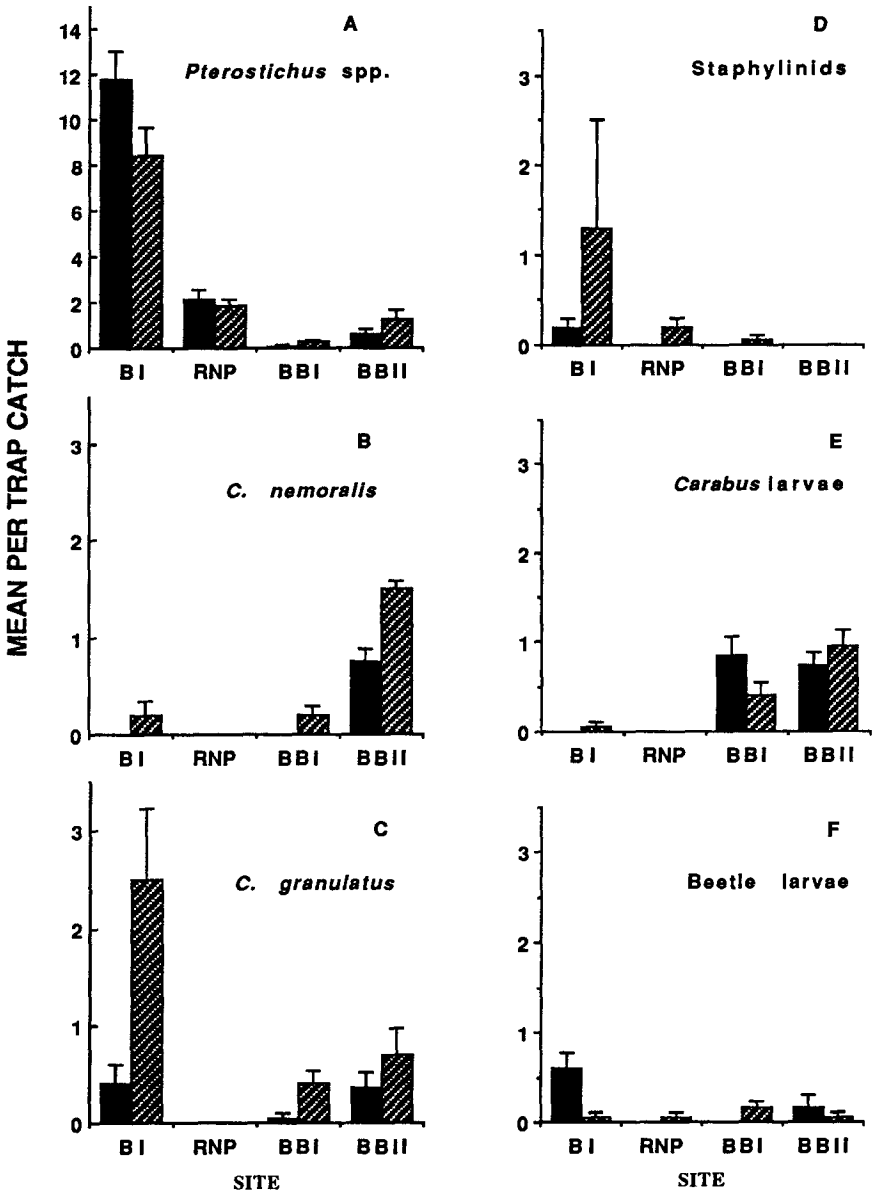

Figure 3.15. Changes in the abundances of a) *Pterostichus* spp., b) *C. nemoralis*, c) *C. granulatus*, d) staphylinids, e) *Carabus* spp. larvae and f) beetle larvae excluding *Carabus* spp.. Solid bars are 1991 abundances, shaded bars are 1992 abundances. Standard errors are presented.

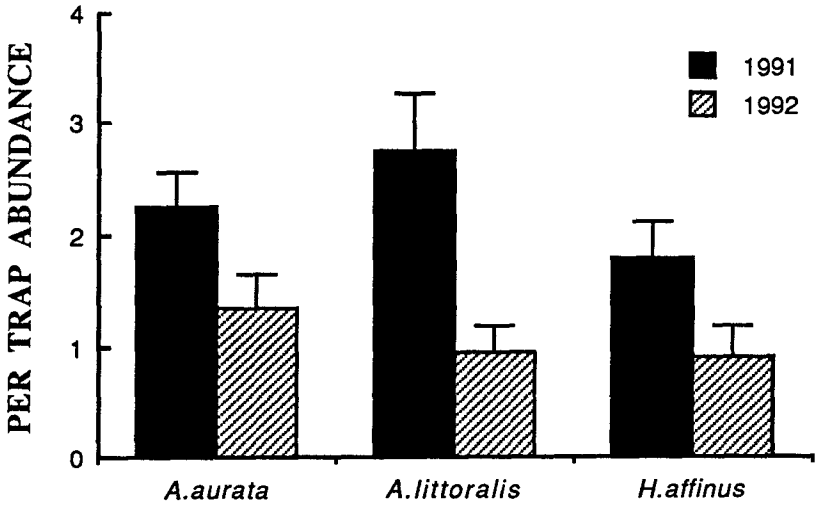

Figure 3.16. Changes in the abundance of three predators at BBI in Richmond, between 1991 and 1992.

It is apparent therefore that although the total abundances of the beetles changed little, the proportions of individual species changed at each site (see Table 3.7). Some species declined while other species increased in importance. At the birch sites, the most obvious changes were with *Pterostichus* spp.. In 1991, these made up 100% of predatory beetles at RNP and 95.8% at BI. Although high in 1992, the proportions had dropped considerably. At the blueberry sites *P. melanarius* increased in importance. The *Carabus* spp. also demonstrated significant shifts in the proportions, *C. nemoralis* particularly underwent dramatic shifts with a decrease at BBI and a large increase at BI. In general however, the shifts in importance were small at blueberry sites. *A. aurata, A. littoralis, H. affinus* and *P. melanarius* the more important predators changed little.

3.3.9 Distribution of sizes in the winter moth-*Cyzenis* pupal complex

In a previous section I indicated that the pupal type had an effect on predation. *Cyzenis albicans* pupae tended to be more highly predated than healthy winter moth pupae. Among *C. albicans* pupae the smaller individuals were most highly predated. Chapter 2 has indicated that winter moth pupal weights change between years, are different at different sites and are dependent on the host plant. *Cyzenis albicans* pupae are always significantly smaller then their healthy host pupae (see Fig 3.17). Furthermore, the sizes of *C. albicans* pupae tend to follow the sizes of the host pupae at the particular site (see Table 3.8). This is not surprising given the parasitoid's life cycle. A two-way analysis of variance of *C. albicans* pupal weights indicated that they are dependent on site, but not on year (site; $P = 0.028$ and year; $P = 0.259$ on log+1 transformed data), in a similar manner to healthy winter moth pupae.

Cyzenis albicans pupae appear to have greater constraints on their size, (the greatest range I have recorded is a maximum of 0.027g and a minimum of 0.004g). This results in a considerable proportion of the available pupae in the soil being of a small size (i.e. below

Table 3.7. Changes in the proportions of different beetle species in 1991 and 1992, at four field sites in Richmond. Total numbers indicate the numbers of beetles caught in pitfall traps between late June and early September of those years. PT = *Pterostichus* spp., CG = *C. granulatus*, CN = *C. nemoralis*, MS = medium staphylinids, AA = *A. aurata*, AL = *A. littoralis*, BLC = *Carabus* spp. larvae, BL = beetle larvae, HA = *H. affinus*, CF = *Calathus fuscipes* and HR = *H. rufipes*.

Site	Year	Total no.	PT	CG	CN	MS	AA	AL	BLC	BL	HA	CF	HR
BI	91	420	95.80	3.18		1.02							
	92	264	65.77	0.42	19.51	10.29	0.81	1.56	0.42	1.22			
RNP	91	43	100										
	92	47	78.72			17.02				4.26			
BBI	91	157	1.24	0.66			28.71	35.02	10.81		22.90	0.66	
	92	93	5.38	8.60	4.30	1.08	29.0	20.4	8.60	3.24	19.40		
BBII	91	55	24.28	12.98	28.02				28.12	5.47			1.33
	92	66	38.98	22.99	5.36				31.05	1.62			

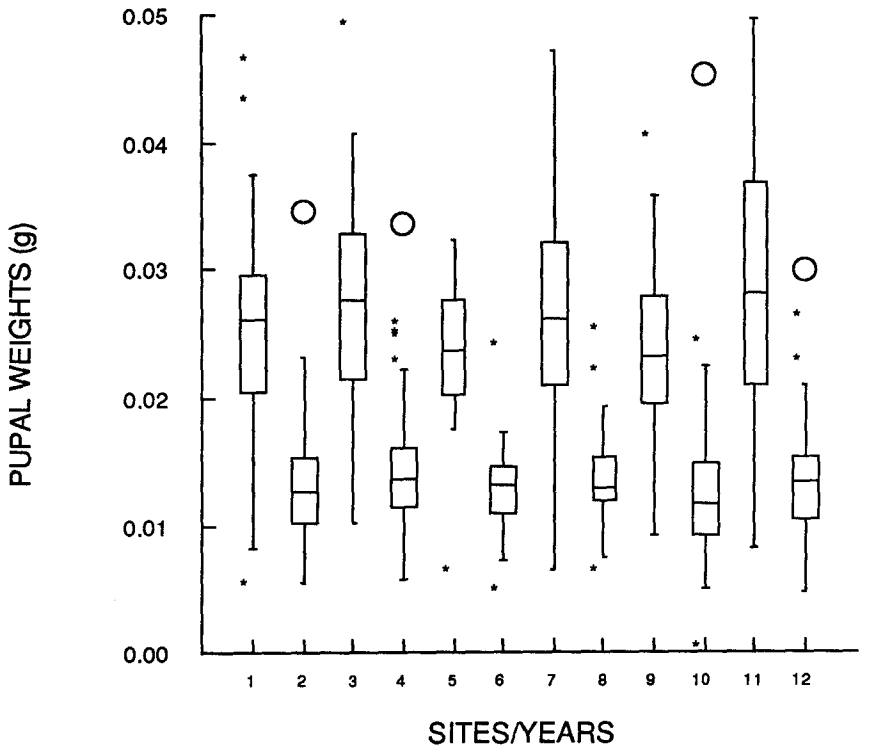

Figure 3.17. Distribution of pupal weights in the winter moth-*Cyzenis* pupal complex at Richmond. Key to plot: 1 = BI 1991 winter moth, 2 = BI 1991 *Cyzenis*, 3 = RNP 1991 winter moth, 4 = RNP 1991 *Cyzenis*, 5 = BBI 1991 winter moth, 6 = BBI 1991 *Cyzenis*, 7 = BBII 1991 winter moth, 8 = BBII 1991 *Cyzenis*, 9 = BI 1992 winter moth, 10 = BI 1992 *Cyzenis*, 11 = RNP 1992 winter moth, 12 = RNP 1992 *Cyzenis*. Asterix indicate outlying points, circles indicate far outlying points.

Table 3.8. Weights (± standard errors) of winter moth pupae at two birch sites in 1991 and 1992 and at two blueberry sites in 1991, with corresponding *Cyzenis* pupal weights at each site.

Site	Year	winter moth(g)	*Cyzenis*(g)
BI	**1991**	$25 \pm 0.8 \times 10^{-3}$	$13 \pm 0.2 \times 10^{-3}$
	1992	$24 \pm 1.2 \times 10^{-3}$	$12 \pm 0.4 \times 10^{-3}$
RNP	**1991**	$28 \pm 0.7 \times 10^{-3}$	$14 \pm 0.3 \times 10^{-3}$
	1992	$29 \pm 1.8 \times 10^{-3}$	$13 \pm 0.6 \times 10^{-3}$
BBI	**1991**	$22 \pm 2.2 \times 10^{-3}$	$13 \pm 0.5 \times 10^{-3}$
BBII	**1991**	$26 \pm 1.4 \times 10^{-3}$	$14 \pm 0.8 \times 10^{-3}$

0.02g) (see Fig. 3.18). Without parasitoids, less than 2-6% of the pupae would be below 0.01g, when parasitoids are present this can increase to over 16% (see Table 3.9). Furthermore, about 20% of the pupae would be below 0.02g, while with parasitoids this could reach 40-50%, depending on the levels of parasitism, and the winter moth host plant conditions. This alteration in the distribution of pupal sizes could have a considerable influence on the dynamics of the system, and on the interactions of the predators with the winter moth.

3.4 Discussion

Generalist Predators

Winter moth populations in Richmond are heavily influenced by pupal mortality. In Chapter 2, soil mortality, estimated as the difference between the number of prepupae dropping to the ground in summer and the number of the adults emerging from the soil in winter, corresponded well with estimates of pupal predation from outplanted pupae. Studies in Britain and Nova Scotia, indicated that the main predators of winter moth pupae are carabid and staphylinid beetles with varying importance being attributed to small mammals (Buckner 1969, Frank 1967a, 1967b, East 1974, Pearsall 1992). In this study, I have observed a number of new species as capable of predating winter moth pupae, these included *C. granulatus* and *H. affinus* which have been introduced from Europe and *A. aurata*, *A. littoralis*, *P. algidus* and *P. herculaneus* which are native to western North America.

Amara spp. and *H. affinus* were abundant at BBI, the site which is most representative of commercial blueberry habitat. In arena studies with winter moth pupae, *H. affinus* was an especially voracious predator and *Amara* spp., although less successful, did attack the pupae. Therefore, these species may play an important role in the predation of

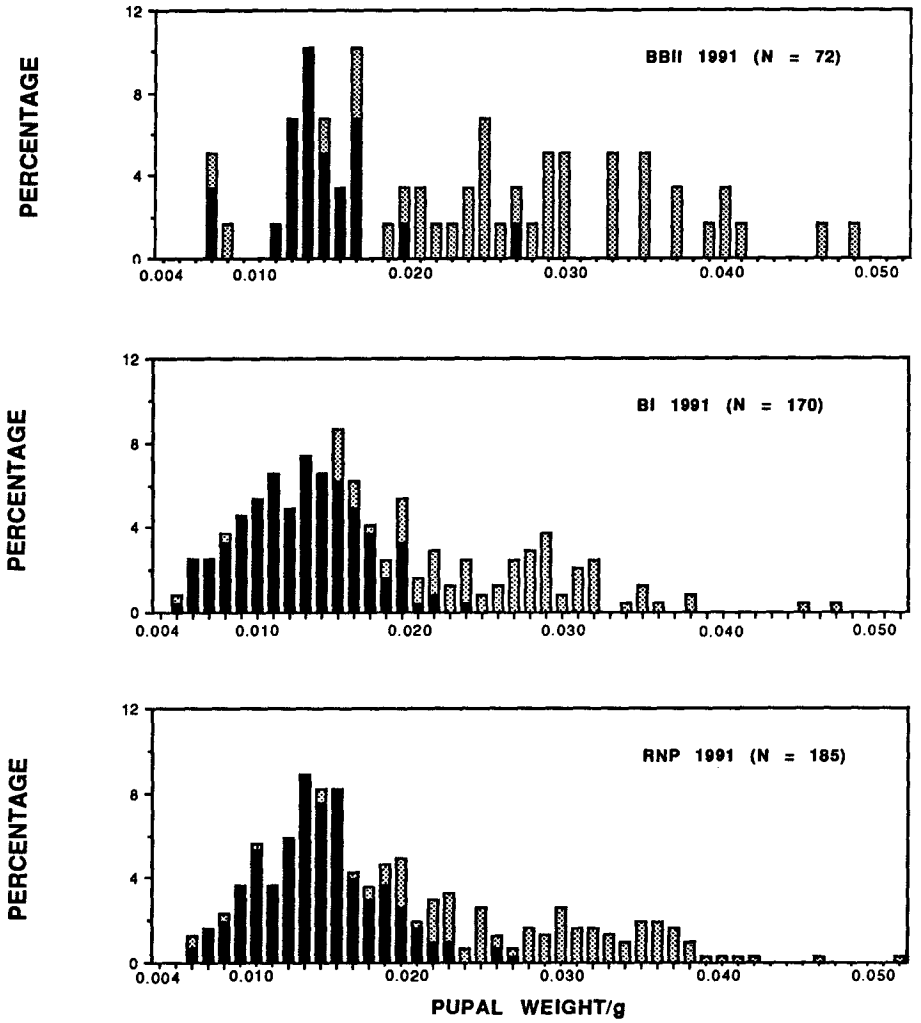

Figure 3.18. Effects of parasitism by *Cyzenis* on the overall sizes of pupae in the winter moth-*Cyzenis* pupal complex at Richmond at a) BI, b) RNP and c) at BBII in 1991. Black bars indicate *Cyzenis* pupae, grey bars indicate winter moth pupae.

Table 3.9. Proportions of pupae in different size categories from the winter moth-*Cyzenis* pupal complex at Richmond, with suggested proportions for the same populations in the absence of parasitism (i.e. taking only the proportions of winter moth pupae of each size category from each sample).

Pupal Type	Weight	RNP		BI		BBII
		1991	1992	1991	1992	1991
PARASITIZED						
Cyzenis	(< 0.01)	6.7	7.3	16.1	16.2	3.4
Cyzenis	(0.01-0.02)	44.5	28.4	39.4	22.4	35.6
Cyzenis	(>0.02)	3.9	2.4	1.4	1.5	1.7
winter moth	(<0.01)	1.3	1.6	1.0	2.8	3.4
winter moth	(0.01-0.02)	6.7	12.7	8.7	11.2	8.5
winter moth	(0.02-0.03)	21.0	23.9	26.7	35.3	29.8
winter moth	(>0.03)	16.0	23.8	6.6	10.8	17.6
HEALTHY						
winter moth	(<0.01)	2.8	2.5	2.4	4.7	5.7
winter moth	(0.01-0.02)	14.9	20.5	20.2	18.6	14.3
winter moth	(0.02-0.03)	46.7	38.6	62.0	58.8	50.3
winter moth	(>0.03)	35.6	38.4	15.4	18.0	29.7
N	Moth	103	39	83	40	37
	Fly	82	47	87	110	35

winter moth pupae. This is surprising since *Amara* spp. and *Harpalus* spp. are usually considered as phytophagous (Lindroth 1968, Johnson and Cameron 1969, Thiele 1977, Holliday and Hagley 1978, Hengeveld 1980c). Hengeveld (1980b) has recently disputed this. He suggests that the idea is based on few studies, with small numbers of specimens collected by dubious methods. On examining carabid gut contents, he found no clear distinction between the diets of *Amara* or *Harpalus* and those of carnivorous species. These species may undergo seasonal diet shifts. Cornic (1973) found that in July, the time of maximum oviposition, 20 - 40% of *H. affinus* specimens had insect remains in their guts, much of these remains were of lepidopteran and dipteran larvae. This corresponds with the time when winter moth pupae are in the ground and receiving most predation.

Pterostichus species are perhaps most likely to be efficient predators. A number of these have already been implicated in the predation of winter moth in Britain and Canada. *Pterostichus* species, particularly *P. herculaneus,* were very abundant at all birch sites, and *P. melanarius,* an introduced species, was abundant at blueberry sites. Frank's (1967a) serological investigations in Britain indicated that *P. melanarius* consumes winter moth pupae in the field.

Carabus granulatus and *C. nemoralis* were common at all sites. It is difficult to suggest what interactions these have with winter moth pupae. *Carabus* spp. are perhaps more likely to feed on soft bodied animals such as slugs, worms and caterpillars, which they digest preorally (Thiele 1977, Hengeveld 1980b). Thiele (1977) indicates that *Carabus* spp. consume most insects they come across, both adult and larvae. But subterranean pupae may have substantially less predation. This is suggested from Lareau's (1987) observations that *Carabus* spp. are not found deep in the surface litter. Whether *Carabus* species can handle winter moth pupae in the field is difficult to determine. They were not very successful in arena studies when compared to either *H. affinus* or *Pterostichus* spp., although Roland (1986a) found no difference between pupal predation by *C. nemoralis* and

P. melanarius. They are much more likely to be important predators of prepupae or fallen caterpillars. The extent of prepupal predation at Richmond is unknown, but is expected to be low since pupal predation accounts for most of the soil mortality (see Table 2.3).

Hengeveld (1980 a, 1980b) analyzed the guts of 6337 carabids of 24 species and found that all 24 species were polyphagous to some extent. He grouped his species into those approaching either generalist or specialist natures. In general, the Harpalinae were the generalists and the Carabinae were specialists. The Harpalinae includes species of the genera, *Harpalus, Amara, Pterostichus* and *Bembidion*. The specialist Carabinae include *Leistus, Notiophilus* and *Loricera*. The Carabini (*Carabus, Calosoma* and *Cychrus*) could be distinguished within the Carabinae, as these specialize on larger prey such as snails, worms and caterpillars. Of the species I have implicated as predators of winter moth in Richmond, only *C. granulatus* and *C. nemoralis* are specialists. The others all belong to the Harpalinae. Evans (1977) found that the size of the metatrocanters, the length of the legs and the running speeds were all greater in the Carabinae than in the Harpalinae, the latter having a greater ability to push under wedges. Furthermore, the Harpalinae have poorly developed sight and seem to recognize their prey more by olfactory means. These characteristics suggest that the Harpalinae are more capable of locating and attacking subsoil pupae. Frank (1967a) however, found no differences between catches of *A. parallelopedus* and *P. madidus* in either pitfalls baited with winter moth pupae or control (unbaited) traps. He suggests that if the beetles are capable of detecting the scent of pupae it is not over any long distance. Comparisons of baited and unbaited pitfalls in this study suggest similar conclusions.

The amounts of food that carabids eat is an important consideration in their success at controlling winter moth. Generally only anecdotal evidence exists on the amounts of food carabids consume (see Hengeveld 1980c). A number of species have been shown to take multiples of their body weights in food daily (Scherney 1959). *Philonthus decorus* larvae

were found to require only 6 winter moth pupae in order to successfully mature to adults (Kowalski 1976). Varley (1970) estimated that the mean annual consumption rates of *Philonthus*, *Abax* and *Pterostichus* per m^2 at Whytham Wood totaled 92Kcal, while the total winter moth production was only 8Kcal. Therefore, only when winter moth were very numerous would it provide more than a small portion of food for predators. The ecological effects of carabids as a group of predators is difficult to assess due to a lack of information on the amount of each prey category consumed within a defined period of time, and on the temporal and spatial variation of this pattern of prey consumption (see Hengeveld 1980c).

I suggest that beetle larvae have an important role in the predation of winter moth pupae. Beetle larvae as predators have not been addressed in great detail in previous studies of winter moth predation, and larval feeding in general has received little attention in the literature, probably because larval instars are difficult to identify and are subterranean (Hengeveld 1980b). There have been no successful analyses of the gut contents of carabid larvae. Carnivory is however, suggested to predominate. Larvae of *P. madidus*, *P. nigrata* and *Nebria complata* require live prey to develop. Similarly animal material may be necessary for the survival of *Amara* spp. larvae (Thiele 1977). Larvae of *H. affinus* have been shown to be predaceous as well as phytophagous (Brigg 1965). Beetle larvae may have more specialized diets than adults, *Abax* larvae for example, are specialized on worms. However, extreme specialization like this is probably an exception (Thiele 1977).

The high occurrence of beetle larvae in baited subsoil traps in this study is notable. Larvae of a number of different species were captured, these included a number of carabids and staphylinids. *Pterostichus* spp. larvae were most common and have been observed feeding on winter moth pupae in beetle exclosure cages. All species that were caught in subsoil traps were brevimandibular suggesting a polyphagous habit (Thiele 1977). Because of the subterranean nature of both the winter moth and the beetle larvae, and because of the higher numbers in baited subsoil traps, olfactory stimuli are most likely used by larvae in

locating prey. It is likely that these larvae are causing most of the mortality on the pupae. Larvae of *Carabus* spp. were frequently caught in pitfall traps. These were surface active and feed on pupae in the arena studies. Because of this epigeal habit, they are unlikely to attack subsoil pupae. Larvae of 14 different species were captured in pitfall traps, the majority of these were caught at site BBII. Of these 14 different species, 5 were longimadibular. This morphological trait suggests that they are predators of snails (Greene 1975). *Carabus* spp. larvae are brevimandibular.

Predation of pupae in 1mm mesh exclusion cages varied from 15 - 40% (depending on the site in question). This is low, but the mesh used in the subsoil exclosures probably excluded some of the larger subsoil beetle larvae. Roland's (1986a) use of 2mm mesh would have allowed most larvae to enter his beetle exclusion cages, and there was significant mortality on the pupae. Larger larvae may be more important in the total predation. Kowalski (1976) noted that larger larvae of *P. decorus* were more successful in attacking winter moth pupae than were smaller earlier instars. Roland's (1986a) beetle removal plots also implicate beetle larvae as important predators. In his plots he reduced the numbers of carabids by 10 - 100 times, staphylinids by 10 - 30 times, but beetle larvae by only 3 times. There was no significant difference in predation of pupae in either the removal or control plots. This could suggest that beetle larvae were the most important component of the predator complex to begin with. It is very difficult to estimate densities of subsoil larvae and their responses to winter moth densities have never been addressed. One might expect that when winter moth densities are high there is increased survival of the larvae and thus increased numbers of adults in the following season. However, many species undergo dispersal flights as immature adults (i.e. *H. affinus* see Holliday and Hagley 1978) and dispersal in general by carabids is efficient (Rivard 1965).

Ants were abundant at the bog sites studied in Richmond. Both these sites had very high levels of predation (predation was 100% at both sites in 1990). Ants were also a

noticeable feature of the insect community at site BBI. Since ants are not successfully sampled by pitfall trapping (Williams 1958), it is difficult to compare densities or abundances of ants between sites or years. In 1991 and 1992, I made a survey of ant colonies. At the birch sites only three *Formica* sp. colonies were located (1 at RNP and 2 at BI). At BBII only one *Formica* sp. colony was located. BBI had two colonies of *Formica* sp. and numerous colonies of *Myrmica* sp.. Because of the dry ground at this site and the emergence of ants from cracks in the soil, it was difficult to distinguish the boundaries of *Myrmica* sp. colonies. In 1990, 20 wooden boards were left on the ground at site BBI over winter. In 1991, colonies had established beneath 18 of them. The occurrence of these ants in subsoil traps is not surprising then since they were generally abundant. *Myrmica* sp. were found feeding on winter moth pupae, but with some difficulty. The larger *Formica* sp. are probably more successful, but were not observed. The foraging trails of each *Formica* sp. colony were observed in 1991. There was no apparent confinement of the trails to areas of higher winter moth densities. In the incidence where trails left a high winter moth density area to a lower one, i.e. from BBI to an insecticide sprayed commercial blueberry field, the foraging trails were noticeably longer, but more study is required. *Formica* spp. are probably more important as predators of prepupae and larvae. The impact of ants on pupae has received little attention in the literature (see Campbell and Torgensen 1964, Torgensen *et al.* 1983, Kelly and Régnière 1985, Eskafi and Kolbe 1990). However, ant predation on larvae and their use in biological control have frequently been addressed (Ives 1984, Harris 1984, Finnegan and Smirnoff 1984 and see references in Ito and Higashi 1991).

A large number of small mammals mainly shrews and voles were caught in pitfall traps, at the Richmond sites. Analysis of their gut contents was not carried out since they were generally partially decayed by the time the traps were emptied. Shrews are known to be predators of a number of subsoil pupae (Buckner 1966, McLeod 1966, Hanski and Parvianen 1985, Kelly and Régnière 1985) including pupae of the winter moth (Frank

1967a, East 1974, Buckner 1969). Buckner (1969) suggested that shrews are responsible for most of the pupal predation of winter moth at Whytham Wood, but East (1974) has rejected this idea. Few of the outplanted pupae in this study showed signs of predation by small mammals. I suggest that small mammals were responsible for a very small portion of the predation, particularly at blueberry sites.

Small mammals are perhaps more important in their affects on the beetle populations (Parmenter and MacMahon 1988, Grüm 1979) and are expected to impact a greater influence in winter, since there are fewer alternative food items for them at that time (Buckner 1969, Frank 1967b, Kowalski 1976). This influence of winter active small mammals on populations of beetles has been implicated in the lack of a delayed density dependent numerical response of generalist invertebrate predators to winter moth densities. There is a strong preference for heterogeneous habitats among small mammals (Parmenter and MacMahon 1983). This was observed at Richmond also, with six times as many small mammals caught at birch sites. The effects are therefore expected to be greater at birch sites since these had the highest numbers of small mammals. Unlike the situation in Britain, high densities of *C. albicans* pupae in the soil at the birch sites and at Roland's oak site might have been expected to reduce predation pressure on invertebrate predators and allow a delayed numerical response, but this has not been observed. Furthermore, beetle populations in orchards at Vancouver Island (Roland 1986a) and at blueberry sites in this study have not presented any evidence to suggest delayed numerical responses in spite of few small mammals.

Cyzenis-Predator interactions

There have been suggestions for a number of different response types of generalist predators to winter moth pupal densities. In Nova Scotian apple orchards, Pearsall (1993 in Press) has demonstrated an aggregated functional response of predators to winter moth

pupal densities. This has also been suggested by East (1974) for *P. madidus*. Roland (1986a) found pupal predation to be spatially density dependent, but discounted aggregated or numerical responses among carabids or staphylinids to changing winter moth pupal densities. Aggregated responses are difficult to interpret. Hagley and Allan (1988) found a significant relationship between numbers of *P. melanarius* and of fifth instar larvae of *C. pomonella* at one of three orchards which they studied in Ontario. However, at the same site there was no significant relationship between the numbers of serologically positive *P. melanarius* and larval densities. The fact that predators, particularly generalist predators, aggregate under trees with higher densities of pupae or larvae might suggest other things. In 1991, I noticed that there were more collembola and soil mites in subsoil traps that had been planted near areas of heavy defoliation at site BI. These may have been feeding from caterpillar frass or leaf material under the trees at that time, and are a significant source of food for generalist predators (see Thiele 1977 and Hengeveld 1980a).

Temporal numerical responses are subject to similar arguments. Numerical responses by generalist predators (carabids and staphylinids) to lepidopteran pupae have been noted in a number of studies (Bauer 1983 and see Hassell and May 1986) For winter moth, both delayed numerical responses (of *P. decorus*; Frank 1967b, East 1974) and current year responses of predators (*P. decorus* and *P. madidus*; Kowalski 1976, 1977) have been proposed. Buckner (1966) suggests that if small mammals are important, only a behavioural numerical response is likely to be observed. For a delay to arise in the numerical response, the reproductive output or survival of predators must be affected. Abundance of food can affect reproductive processes. Murdoch (1966) for example, found *Agonum fuliginosum* to have a delayed reproduction when food was scarce. However, cases like this are rarely noted and a review by Hengeveld (1980a) indicates that the effects of food availability on the sizes and stability of carabid populations needs considerably more attention.

In this study predation of pupae appeared to be temporally density dependent at all sites except BBI, where deviations from the trend occurred only in 1992. There was no delay in the predation at any site. Interestingly, levels of predation were very similar in spite of very different abundances and assemblages of predatory beetles. Only two years of data are available on the abundances of predators at the sites. At three of the four sites, there were increases in the total numbers of predaceous beetles in 1992, when winter moth pupal densities were lower. Looking only at the most important predators however, i.e. *Amara* spp., *H. affinus* and *Pterostichus* spp. there have been general declines in abundance, (*P. melanarius* is the only exception). If these declines are the result of declines in winter moth pupae, then it may be affected through the larvae. Little is known about the seasonal occurrence of larvae of the native *Amara* spp.. Indications are that they hibernate as adults, with the larvae present from early spring until August: similarly *H. affinus* larvae are present from June till August (Lindroth 1961 - 1969, Holliday and Hagley 1978). All the *Pterostichus* spp. present at Richmond overwinter as larvae and emerge as adults in the early spring (although the occurrence of two maxima separated by a minimum abundance of beetles in late July and early August, suggest that there may be larvae present until July or August). Larvae of each species could therefore have increased survival either due to the presence of winter moth or *C. albicans* pupae (*Amara* and *Harpalus*) or due to *C. albicans* pupae alone (*Pterostichus*). Most of the predation of winter moth at Richmond occurred before August. Similar observations have been made in Nova Scotia (Pearsall 1992) and in Britain (East 1974). This was when beetle activity (both adult and larval) was at a peak. Roland's (1986a, 1988) suggestion that the increase in the period of availability of pupae in the soil due to the presence of *C. albicans*, leads to a numerical response (his first mechanism), is therefore only possible for *Pterostichus* spp. and only at birch sites.

In this study tethered C. *albicans* pupae were more highly predated than tethered winter moth pupae. This occurred at both blueberry and birch sites, although at BBI the differences were negligible. Interestingly the appearance of predation differed at each site.

At RNP, both large and small sized *C. albicans* were more heavily predated. At BI only small *C. albicans* were significantly more heavily predated than winter moth. Similarly, at BBII *C. albicans* pupae were significantly more predated, but at BBI there was no difference in the predation levels on *C. albicans* or moth pupae. This suggests that the predators at the sites, even within the same habitat types (i.e. blueberry or birch), are different. In no case did *C. albicans* have lower predation. This differs from Roland's (1986a, 1988) observations on Vancouver Island, and discounts the possibility of his second mechanism (greater parasitism of unparasitized pupae) operating at Richmond.

Differences in the predation rates of different sized *C. albicans* at BI is notable, and suggests that some pupae may be more vulnerable to predation due to a smaller size. In an unparasitised population of winter moth only about 20% of the pupae are under 0.02g, at low population densities this is expected to be even less (see Table 3.9). At Richmond, Vancouver Island and Nova Scotia where levels of parasitism were high, the percentage of available pupae that are below 0.02g rises to about 60%. Since the smaller pupae were most highly predated, I suggests that some predators may be capable of handling only these and not the larger pupae. These predators may include the early instars of beetle larvae. A considerably higher proportion of smaller more manageable pupae, as in situations with high levels of parasitism, may therefore, allow increased survival of early instar beetle larvae, or of the larvae of smaller beetles i.e. *Agonum* or *Bembidion* spp.. Unfortunately, very little is known about the feeding behaviours of beetle larvae, and I have not investigated the toughness of pupal integuments. The pupal integuments of small *C. albicans* pupae (< 0.01g) did appear to break more easily than those of similar sized winter moth. Opening the cocoons to examine the condition of the pupae inside may have introduced a bias to the study. The cocoon has a protective role and many predators which feed on pupae in this study may not normally be able to penetrate the cocoon. Furthermore, *C. albicans* pupae are enclosed in the integument of the host winter moth pupae. On examining the pupae this integument was normally removed. Although the host pupal

integument is very fragile, there again is a suggestion that it may have been easier for the predators to attack the *C. albicans* pupae in this study.

Roland (1986a) tended to discount larvae as having a role in the predation of winter moth pupae on Vancouver Island, since pitfall trapping had revealed that larvae were abundant only when both the winter moth and *C. albicans* pupae were absent from the soil. Surface active beetle larvae also diminished in pitfall traps at the time of winter moth pupation at Richmond. However, the traps did not account for subsoil larvae which were an active component of predation as revealed by subsoil traps at that time. Therefore, increased availability of food for larvae may give rise to increased survival and thus increased numbers of adults in the subsequent generation. However, this would not necessarily lead to increased adult abundances or the manifestation of a delayed numerical response if the adults are actively dispersing.

Roland's (1986a) findings that predation of the *C. albicans* pupae was reduced in the absence of beetles and regressions of weekly pupal predation rates against the different components of the predator community from this study, suggest that an alternate interaction could occur. It is possible that the adult beetles may be favoured by the presence of *C. albicans* pupae. In this study, only three of the regressions were positive, *C. albicans* predation against all beetles at BBII and at BI, and winter moth pupal predation against beetle larvae at BBII. In general however, regressions of beetle abundance showed positive relations against predation, but there were no trends for *C. albicans* predation, and also beetles in arenas appeared to favour winter moth pupae. It is not clear which component of the predator population (i.e. adults or larvae) benefits most from the presence of *C. albicans* pupae. What these data do indicate, however, is that different components of the predator complex are responsible for predation on different components of the pupal complex. A third mechanism therefore by which *C. albicans* pupae may have increased predation could be by making food available for both adult and larval predators, and thus

increasing total survival or reducing dispersal from the area. This mechanism is somewhat similar to Roland's (1986a, 1988) first mechanism except that the effects of *C. albicans* in the pupal complex act at the same time as the increased availability of food due to winter moth pupae. The availability of pupae over winter may or may not be necessary to bring about an effect.

The occurrence of *C. albicans* pupae in the soil may not have been the only factor bringing about increased predation. On both Vancouver Island and in Nova Scotia, pupal predation began to rise before levels of parasitism were very high. However, rises in parasitism and predation, were largely synchronous at both locations. It is possible that the constant proportions of favorable pupae allowed populations to build up over time. But declines in the winter moth populations occurred in very different habitats with different levels of parasitism at the same time (Roland 1988, Embree 1991). This would tend to suggest that something in addition to predators or parasites brings about the declines. At both Vancouver Island and Nova Scotia in the years previous to the increases in both parasitism and predation, there were high levels of larval mortality (that is 1959 at Nova Scotia and 1983 at Vancouver Island) presumably, to a large extent due to starvation. Since high larval mortality has been associated with increased mortality of pupae (death due to unknown causes), and predation is higher on dead pupae, this high larval mortality may have also initiated predation increases. Dead pupae could therefore, either have supported adult beetles and reduced their dispersal, or increased survival of beetle larvae, building up a numerical response. *Cyzenis albicans* may have only played a role in maintaining predator populations after larval mortality decreased or may have accentuated the effects of high levels of dead pupae in the population. High larval mortality in 1957, may not have had an effect because *C. albicans* was still at low levels. This fourth mechanism therefore incorporates larval mortality into the system, with *C. albicans* only playing a role in accentuating the effects.

As was mentioned in Chapter 2, the Richmond situation is very different from those of Vancouver Island and Nova Scotia. The parasitoids probably arrived in Richmond at the same time as the winter moth. A post-introductory outbreak occurred about 1986 to 1988, and parasitoids soon went into increase. Levels of parasitism were already high in 1989, but levels of parasitism have never reached the levels observed on oak in Nova Scotia or on Vancouver Island. The decline began in 1990. There was no lag of four years between *C. albicans* occurrence and winter moth decline, as had occurred in the other two situations. The drastic population decline in 1992 was largely attributed to larval mortality (numbers of females in 1990 and 1991 have been estimated to be about the same). I found predation to be temporally density dependent, and found weak evidence for numerical responses of beetle predators, with a number of beetle species declining in 1992 under lower winter moth pupal densities. There was no inverse density dependent increase in predation as occurred on both Vancouver Island and Nova Scotia. I suggest that these differences can be explained by looking only at the response of predators to parasitoids. In Nova Scotia, Vancouver Island and Richmond this was density dependent, and may be due to those life stages that utilize the *C. albicans* pupae surviving better or dispersing less (depending on the stage in question) and allowing that stage which predates winter moth to build up. There are still a number of problems with this idea because it is not known what is causing the mortality. Arena studies are not helpful due to altered behaviours of insects in the arenas and cages (see Hand and Keaster 1967). Serological studies are the only way to have reasonable certainty of what eats pupae in the field. Serological studies are becoming frequently more common in such studies. These too have their problems and knowledge of the background phenomenon which influence the detection of prey items is far from satisfactory (Lövei *et al.* 1985). The use of pitfall traps in this and other studies has given dubious results and does not give any information about larval stages (Greenslade 1964, Holliday and Hagley 1978). It is unlikely that a single species of predator would be responsible for the mortality and it is not important which predators are involved.

The mechanisms by which *C. albicans* may have caused increased predation of winter moth pupae appear to be more complicated than Roland (1986a, 1988) had originally proposed. Roland's first mechanism, in which an increased period of availability of pupae in the soil, due to the presence of *C. albicans*, allows a numerical response, now appears unlikely. There was a weak indication of a numerical response among some predators in Richmond, but in general predators were most abundant in the year of decline. Predator activity was also severely reduced for most of the winter months. This suggests that the availability of *C. albicans* pupae overwinter is probably not important in allowing a numerical build-up of predators. If *C. albicans* were important in this respect, then it would be most likely to affect the *Pterostichus* spp., since these were active throughout the year. At the birch sites there was an indication of a numerical response among *Pterostichus.*

Roland's (1986a, 1988) second mechanism suggests that winter moth pupae are preferentially predated from the pupal complex. This causes increased predation pressure on the remaining winter moth pupae and allows better survival of the fly parasitoid. This mechanism can be discounted in Richmond since examination of predation on tethered pupae indicated that it is the *C. albicans* pupae that are more heavily predated. I have proposed two further mechanisms. The first suggests that predation on the winter moth pupae is by a different life stage(s) of the predators than that predating the *C. albicans* pupae. Therefore, a numerical response may be allowed since food is available for all life stages. A second proposed mechanism incorporates the occurrence of dead pupae in the pupal complex. Dead pupae are most highly predated so that large numbers of dead pupae in the soil allow a build-up of predators. The presence of *C. albicans* in the pupal complex maintains the predator population at a high level until outbreak decline. This latter mechanism might allow predator build-up to occur in areas with different levels of parasitism of winter moth, but is still dependent on parasitism.

CHAPTER 4
GENERAL DISCUSSION

It has recently become clear that the successful biological control of winter moth in Canada by its parasitoid *C. albicans* has not been due simply to the parasitoid-host interactions, but that other factors including generalist predators have played an essential role (see Table 4.1). In North America, outbreaks of winter moth have predominantly been of the post-introduction type, suggesting that natural enemies are essential in maintaining population equilibrium. These natural enemies include viral diseases and parasitoids, but generalist predators are not capable of inhibiting the occurrence of outbreaks after introduction. Tenow (1972) indicated that a maritime type climate is important for outbreaks of winter moth to occur. All the regions in North America where outbreaks have occurred have mild winters (see also Chapter 1 under 'winter moth'). Winter temperatures that fall below -33°C inhibit outbreaks (Wylie 1960b). Tenow (1972) however, gives no indication of the causes of outbreaks.

Outbreak decline

Winter moth outbreak declines can be attributed to a variety of factors, but three main factors predominate (see Table 4.2).

Parasitism: Varley *et al.* (1973) maintained that winter moth populations in England were regulated by generalist predators of the pupae, and that winter mortality determined the levels of the population each year. Parasitism in Britain was deemed unimportant in winter moth population regulation. Unfortunately, the period through which they conducted life

Table 4.1. Synopsis of characteristics of winter moth outbreaks and the factors attributed to their declines.

CHARACTERISTIC	POPULATION	SOURCE
Outbreaks with parasitoids present	Europe Nova Scotia Richmond	Tenow 1972 Embree 1991 This study
Inverse density dependent increases in predation	Nova Scotia Victoria	Embree 1966 Roland 1988
Increases in predation before increases in parasitism	Nova Scotia Victoria Richmond	Embree 1966 Roland 1988 This study
Reduced fecundity after heavy defoliation in the previous year	Hokkaido Victoria (apple) Richmond	Kukuzawa *et al.* 1979 Roland and Myers 1987 This study
Foliage quality important	Whytham wood Hokkaido	Varley *et al.* 1973 Kikuzawa *et al.* 1979
Decline in parasitism after an initial high	Nova Scotia Victoria Richmond	Embree 1966 Roland 1988 This study
Declines with low levels of parasitism	Oregon	Kimberling *et al.* 1986
High larval mortality before the population crash	Nova Scotia Victoria Richmond	Embree 1965 Roland 1988 This study
Pupal predation as the main regulator	Whytham wood Nova Scotia (apple) Victoria Richmond	Varley *et al.* 1973 McPhee *et al.* 1988 Pearsall 1992 Roland 1988 This study
Parasitism as the main regulator	Nova Scotia	Embree 1966
Simultaneous declines in sites with different host plants	Nova Scotia Victoria Oregon Richmond	Embree 1966 Roland 1988 Kimberling *et al.* 1986 This study

Table 4.2. Information on outbreak of winter moth from seven studies, with information on the success of *Cyzenis albicans* in parasitizing the populations.

Winter moth population	Native/ introduced	host plants	duration of outbreak	*Cyzenis* released	Highest levels of parasitism reached	Colapse attributed to	source
Whytham Wood	native	*Quercus robar*	no outbreak between 1950 and 1970: Minor outbreaks from 1957 to 1958 and in1966	native	0-22%	Pupal predation	Varley *et al.* 1973
Hokkaido	native	*Alnus inokumae*	1975-1976	?	?	Food shortage	Kikuzawa *et al.* 1979
Scotland	native	*Picea sitchensis*	1981-?	native	?	?	Stoakley 1985
Nova Scotia	introduced	*Quercus rubra* & *Malus spp.*	1950's-1962	1954-1961	61%	Parasitism	Embree 1966
Victoria	introduced	*Quercus garyana* & *Malnus spp.*	1970's-1982	1979-1982	84%	Parasitism and pupal predation	Roland 1988
Oregon	introduced	*Corylus avellana, Malus silvestris* & *Prunus cerasifera*	?-1983	1982	<4%	unknown	Kimberling *et al.* 1986
Richmond	introduced	*Betula papyfolia* & *Vaccinium corymbosum*	1988-1992	not released	55%	Pupal predation and larval mortality	This study

table analyses at Whytham Wood does not appear to have incorporated an outbreak[1] , in fact the year in which they commenced the life table studies was a year of population decline from the highest levels recorded at Whytham Wood (see Appendix 7). Densities of winter moth larvae in 1949 (500 L/m^2) were about five times higher than those of 1950 (112L/m^2). Minor outbreaks occurred in 1957 and 1964. In the early 1970's there was an outbreak at Wistman's Wood, a site adjacent to Whytham Wood, in Oxford. Because levels of parasitism were not recorded at Wistman's wood and because of the lack of a major outbreak at Whytham between 1950 and 1968, we do not know how *Cyzenis* responds to outbreaking densities of winter moth in Europe. Tenow (1972) noted that declines from outbreak in the Scandes are often associated with high levels of parasitism. Therefore, the basic premise that parasitism is low in Britain can be disputed; the fact is we do not know what parasitism is like during outbreaks there. Embree (1966) suggested that the introduction of *C. albicans* and *A. flaveolatum* brought about a decline in Nova Scotia. Parasites however, do not appear to be of sole importance. This is apparent from declines observed in different regions with different levels of parasitism, including simultaneous declines in 1982-1983 in Victoria and Oregon with about 70% and 4% parasitism respectfully (see Table 4.2). Furthermore, there have been simultaneous declines on different host plants within the same regions, in spite of differences in the oviposition responses of *C. albicans* on these plants with resulting differential success of parasitism.

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1 What constitutes an outbreak? The arbitrary nature of this term may cause some problems. A brief review of the densities reported as outbreaks indicate great variability among studies (see Table 4.3). Much of this variation may be due to the great variety of host plants on which outbreaks develop. The best measure of density is the number of larvae per bud, leaf cluster or shoot (leaf clusters and shoots having developed from a single bud). In these terms outbreak densities are dependent on the host plant, for example Kikuzawa *et al.* (1979) present 0.3L/bud as an outbreak density on alder, while on oak 5L/cluster is an outbreak (Embree 1966). The numbers of pupae/m^2 is a more satisfactory measure for comparing across studies, since it has a two dimensional nature, is easily recorded, and has significant biological meaning. Also Roland (1986a) has shown that larval density may vary temporally while pupal density remains more stable as a result of compensatory mortality.

Table 4.3. History of outbreaks of the winter moth from seven regions, with indications of the levels of parasitism (mainly due to *Cyzenis*) and soil mortality presented as percentages and k-values. Corresponding densities of winter moth are also indicated. 'H' indicates highest levels, 'L' indicates lowest levels and 'O' indicates outbreak populations. An asterix indicates that values for pupal predation are presented rather than soil mortality.

% Parasitism	K_3	% soil mortality	K_5	Year	Densities L/Cluster	L/M^2	P/M^2	Location	Source
?	?	33	0.176	1976 (O)	O.3L/bud	240 (1976) 17 (1977)	9	Japan	Kikuzawa *et al.* 1979
0 (L) 22.38 (H)	0 (L) 0.11 (H)	39.74 (L) 86.51 (H)	0.22 (L) 0.87 (H)	1950-1968		6.3 492	0.27 81.3	England	Varley *et al.* 1973
1.14-8.8 (O)	0.005-0.04 (O)	81.8-86.51 (O)	0.74-0.87 (O)	1964-1966(O)		269 (H)	78.4		
?	?	98.42 (1974) 99.81 (1975)	1.80 (1974) 2.71 (1975)	1973-1975 (O)		1465-1845	176-296	England	Wigley 1976
?	?	?	?	1988	4L/shoot			Scotland	Hunter *et al.* 1991
4 (H)	0.018 (H)	?	?	1980-1983 (P)	2.5L/cluster 1980			Oregon	Kimberling *et al.* 1986
61.1 (oak)(H)	0.41 (H)	94 (H)	1.2 (H)	1954-1962 (P)	5L/cluster			Nova Scotia	Embree (reanalysed by Roland 1988)
84 1985(oak)(H) 65 1984(apple)(H)	0.796 (H) 0.46 (H)	96 (H) 85.87 (H)	1.40 1987(oak) 0.85 1984 (apple)	1983-1985 (P)	3.36L/cluster (oak)1983 8.96 L/cluster (apple) 1983			Victoria B.C.	Roland 1992 and 1986a
<16 (Agrypon) (H) <10 (Cyzenis)		96.84 (H) 29.21 (L)	1.5 (H) 0.15 (L)	1967-1980	0.05-1.4L/cluster			Nova Scotia	McPhee *et al.* 1988
0-18.6	0-0.089	98.4-74.5 95.8-47.8*	1.795-0.59 1.376-0.282*	1991	0.17-4L/cluster		7.4-347.7	Nova Scotia	Pearsall 1992
36.28 (blueberry) 55.18 (birch)	0.196 0.349	96.25* 98.75*	1.426* 1.902*	1989-1992 (P)	0.36L/cluster 1991 0.74L/cluster 1991		72.41 378.2	Richmond B.C.	This Study

Foliage quality: The importance of foliage quality in bringing about population declines has frequently been omitted from studies of outbreaking winter moth populations. This is in spite of a realization of the importance of synchronies between bud-burst and larval eclosion (Feeny 1970, Holliday 1977, Hunter 1990, Watt 1987). In this study, an early spring may have caused asynchronies between the winter moth egg hatch and a number of its host plants. High incidences of "death due to unknown causes" as well as low female fecundities suggest that there may have been asynchronies or some nutrient deficiencies that reduced the vigour of caterpillars and moths. Hunter *et al.* (1991) looking at an outbreaking population on Sitka spruce in Scotland, found no evidence to suggest that nutrient deficiencies of trees or the timing of bud-burst had any role in determining the course of winter moth outbreaks there. Kikuzawa *et al.* (1979) on the other hand suggest that it was reduced quantity of food, and thus a reduction in fecundity that was responsible for the 1977 crash on alder in Japan. Simultaneous declines under different levels of parasitism with different host plants occurred on both the east and west coasts of Canada (Roland 1988, Embree 1991). This suggests that weather effects may be important. Weather patterns can have effects on the quality of host plants for the moth, and on synchronization of bud burst and larval eclosion. These in turn might appear as increases in larval mortality, increases in soil mortality, and reduced fecundities. High levels of larval mortality in Nova Scotia and Victoria before population declines, may indicate that climatic conditions had affected these populations in a similar manner to Richmond in 1992. Therefore, climatic conditions may have been very important in the success of the biological control program. Which particular aspect of weather has not been elucidated. Climatic data should be examined from all three regions, both before and during the winter moth declines. However, in this study, while winter moth were declining in the Richmond area where outbreaks initially occurred in the mid-1980's, populations on the edge of the northern spread into Vancouver were still very high. This argues that the history of the population has a dominant effect and may over ride any weather related influences.

Pupal predation: Predation of winter moth pupae by generalist predators is now at the forefront of mechanisms implicated in the control of winter moth outbreaks, and the maintenance of winter moth populations at equilibrium densities (MacPhee *et al.* 1988, Pearsall 1992, Roland 1992). Data on soil mortality from a number of studies, are more complete than those of parasitism or other factors (see Table 4.3). Wigley's (1976) data from England, suggest that soil mortality was as high as 99.81% in 1975, a figure higher than any recorded at Whytham Wood. Table 4.3 indicates that pupal predation is generally high among all high density populations of winter moth studied. It appears therefore, that soil mortality can not be ruled out as important in the control of outbreaking populations. An exception is that of the 1976 outbreak in Japan, but at that site pupal densities were very low, ca. $9/m^2$. In Canada, ground predators have been the main causal factor in bringing about the initial declines of the winter moth populations, and have also played a vital role in maintaining the populations at low densities after the initial suppression (Roland 1992).

Cyzenis-generalist predator link

It has been proposed that the presence of *C. albicans* was essential in bringing about winter moth regulation by predators (Roland 1986a, 1988). Therefore, a proper evaluation of this case of biological control requires an understanding of a three-way interaction, namely that of, winter moth, *Cyzenis* and the generalist predators. The winter moth-*Cyzenis* interaction has been the subject of a number of papers (Embree 1965, 1966, Embree and Sisojevic 1965, Hassell 1966, 1980). However, the winter moth-generalist predator and especially the *Cyzenis*-generalist predator interactions have received considerably less attention. Roland (1988) has suggested a link between ground predators and *Cyzenis* parasitism such that the parasitoid may have been responsible for initially increasing pupal predation. This was based on the observation that in both Nova Scotia and

on Vancouver Island there was a similar occurrence of events, in spite of the implementation of biological control after very different periods of high winter moth density (see Chapter 1, Chapter 2 and Roland 1988). Roland proposed three mechanisms by which *Cyzenis* could have caused increases in predation. The first mechanism suggests that a longer availability of pupae in the soil due to the presence of *Cyzenis* pupae over the winter and early spring, allows a numerical build-up of predators. A second mechanism suggests that a preference for healthy pupae make winter moth pupae more susceptible to predation when parasites are present in the population. Finally, a third mechanism suggests that parasitoids act as vectors of disease and cause increased soil mortality by infecting prepupae. Results from this study indicate that all three of these mechanisms are unlikely to have occurred in Richmond. Based on observations of differential predation on winter moth and *Cyzenis* pupae, and the indication that different components (larvae or adults of the same species) of the predator complex differentially take moth and fly pupae, I have presented a further mechanism. I suggest that the important predators of winter moth pupae require *Cyzenis* pupae for a population build-up, due to the inability of some stage of the life cycle to consume healthy winter moth pupae. Given the complexity of predator assemblages involved and the very different assemblages at different sites, it may be that all of these mechanisms have acted to increase predation, but the mechanisms may differ between sites. At sites with low levels of parasitism, factors other than predation may have played a more important role. At these sites, little is known of the impact of predation (see Table 4.3).

Very similar species of moth endemic to North America often occur at the same sites as winter moth. In North America there are two native *Opheroptera* species. The most important is *O. bruceata* (Hulst) which has a northern distribution. The other *O.danbyi* (Hulst) is endemic to the Pacific Northwest with a more limited distribution (Miller and Cronhardt 1982, Troubridge and Fitzpatrick 1993). Two allopatric subspecies of *O.*

bruceata (*O. bruceata occidentalis* [Hulst] and *O. bruceata bruceata* [Hulst]) can be distinguished (Troubridge and Fitzpatrick 1993). American authors treat *O. bruceata occidentalis* as a separate species, *O. occidentalis* (see Miller 1982, Miller and Cronhardt 1982). *Operophtera bruceata* and *O.brumata* appear very closely related, and are known to interbreed in regions of overlapping distribution (Underhill *et al.* 1987, Hale 1989, Troubridge and Fitzpatrick 1993), although the extent of this in the wild is unknown (see Fitzpatrick *et al.* 1991). Compared to winter moth, *O. bruceata* emerges later in the fall, has a one to two week earlier larval eclosion, and has only four instars (Brown 1962, Kimberling *et al.* 1986). Males are attracted to the same synthetic pheromone as winter moth males (Underhill *et al.* 1987). They differ in the levels of parasitism, virus, etc., observed among their populations (Pivnick *et al.* 1988), and they have different species of parasites though they share a number of common genera (Wylie 1960a, Sechser 1970a, 1970b). All the *Operophtera* species are highly polyphagous. Brown (1962) lists 17 plants from which *O. bruceata* feed, these included plants from the genera, *Populus, Salix, Acer, Fagus, Malus, Prunus, Betula, Lornicera, Alnus, Amelanchier, Ribes, Rosa,* and *Holodiscus*. Millar and Cronhardt (1982) list 19 plants on which *O. bruceata occidentalis* larvae have been found, these included both coniferous and deciduous species such as *Corylus, Crataegus, Fraxinus, Oemleria, Physocarpus, Pseudotsuga, Quercus, Rubus, Tsuga,* and *Symphoricarpos*. A number of these plants are shared hosts with winter moth.

Given the similarities of these species, they should be expected to display similar dynamics. In the Scandes, Tenow (1972) showed similarities in the periodicities and occurrences of outbreaks of winter moth, *O. fagata* and a similar species, *Oporina autumnata* Bkh., and indicated that mild winters greatly influence the dynamics of these species, since outbreaks generally coincided with mild winters. Bruce's spanworm undergoes outbreak in Canada. These outbreaks last from 1-5 years, and have a periodicity of about 7 years. Decline has been attributed to viral disease (1964 and 1973 in Quebec)

and to high numbers of ground beetles (in 1976 in Cumberland Co. Nova Scotia) (Canadian Department of Forestry 1964, 1974, 1976). Embree (1965) found that mortality occurring between pupal and adult stages of Bruce's spanworm was density dependent. He estimated mortality at between 15 and 49% (although he suggested that this may be low due to experimental procedures). It is therefore apparent that generalist predators may be regulating Bruce's spanworm also.

It seems likely that these ground predators would readily have moved from taking spanworm pupae to taking winter moth pupae. Why then was the increase in predation delayed until after *Cyzenis* became established? It is most probable that these predators have been eating the winter moth pupae since the early stages of introduction. However, it is a noted feature of generalist predation that it is not capable of preventing outbreaks from occurring (Hance 1987). For some reason the winter moth population must have become uncoupled from the spanworm population and went into post-introduction outbreak. This reason may be the absence of parasitoids or disease among winter moth.

Roland (1992) evaluated the effects of reduced levels of the observed parasitism each year on the rate of population change (Rt) at Victoria. He demonstrated that for the winter moth on Vancouver Island strong regulation by predators allows levels of parasitism to vary greatly without the eruption of the winter moth population. However, if parasitism were to fall below certain very small levels (less than 0.4% of the observed values each year), then the populations would erupt to prebiological control levels. This might explain why there was successful biological control over large areas of Nova Scotia and British Columbia at the same time, in spite of great spatial variations in the levels of parasitism attained at the sites. The observed increases in predation during the decline phase, are necessary before predation assumes the regulatory process.

In Richmond populations, predation and parasitism were high. The populations have not been monitored for long enough to suggest whether pupal predation may be temporally density dependent. Pupal predators may regulate the population. However, it was larval mortality in 1992 that caused the greatest stage specific mortality. This suggests that although regulating the moth, at high moth densities the predators are less efficient. The link between parasitism and predation, and between weather and predation, may be that these factors had driven winter moth populations to levels low enough that the pupal predators could again gain efficient control of the population. The dramatic increases observed between 1989 and 1990 at Richmond indicate that there may also be some factor causing increased levels of predation before the predators gain control. The absence of a link might simply have extended the period over which the predator control was gained or *A. flaveolatum* would have played a more important role, since it could drive the populations to a very low density, where *Cyzenis* alone would have allowed higher equilibria to have developed.

Continued control of winter moth

Since the introductions of *Cyzenis* and the eventual winter moth declines, the situation in Canada has become much like that of Britain. Following the post-introduction outbreak the moth is apparently regulated by generalist predators (Roland 1992). Among these, carabid beetles and beetle larvae appear to be very important. Levels of winter moth pupal predation at Richmond were found not to differ in spite of different habitats and different complexes of predators. Continued control of winter moth should therefore concentrate on avoidance of interference and maintenance of suitable habitat for invertebrate predators.

Introduced carabids have become an important faunal component of North American cultivated land. On Vancouver Island and in Nova Scotia, the most abundant beetles and those implicated in winter moth predation, were all introduced from Europe. In Richmond, native species predominated in abundance at birch sites, but the majority of the most common species were introduced. In blueberry fields, introduced beetles were again a notable feature with *P. melanarius* and *H. affinus* noted as possibly the most important predators. These two featured commonly in pest management of unsprayed and sprayed orchards in Ontario, where *P. melanarius* is noted as the most common carabid (Rivard 1974, Hagley 1975, Hagley and Allen 1988). In general introduced species are becoming a notable feature of North American cultivated lands. Finlayson and Campbell (1976) studying agricultural land in the Lower Fraser Valley found *Bembidion lampros* (Hrbst.) a small generalized European beetle to be the most abundant species on crop and fallow land. Other numerous species included *Harpalus affinus, Calathus fuscipes* (Goeze) and *Clivinia fosser* (L.) all introduced from Europe. Introduced carabids were most numerous on cultivated land and introduced staphylinids were an important component of grasslands (Finlayson and Campbell 1976). Introduced species therefore appear to do well in habitat that has been affected by man's activities. Similar findings have been made for other groups (i.e. dung beetles), and it has been suggested that European species have had a greater time to adapt to cultivation, while north American species are mainly forest specialists (Spence and Spence 1988, Hanski 1992). The *Amara* species are also a common feature of cultivated land and have been noted as common in all the above mentioned studies (except Roland's). *Amara* were very common at blueberry site I (BBI), the site most approaching a commercial blueberry site at Richmond. These are native species (though *A. erratica* (Dfsch.) an introduced species was common in eastern Canada) favoured by dry habitat (Lindroth 1961-1969).

Roland (1992) has suggested that the reason for the successful biological control of winter moth on oak and not on apple may have to do with the use of pesticides in orchards. Similarly, Bruce's spanworm is a problem in orchards where pesticides are frequently used (McMullan 1973, Angenilli and Logan 1985). Pearsall (1992) found high levels of winter moth pupal predation in unsprayed orchards in Nova Scotia. She (1992) did not estimate predation of winter moth pupae in commercial (insecticide sprayed) orchards. However, these had similar abundances of beetles to unsprayed orchards. The compositions of beetles at the orchards were very different. In commercial orchards *Harpalus rufipes* and *Pterostichus coracina* were the dominant species, while in unsprayed orchards *Carabus* spp. were generally more abundant. A number of insecticides do adversely affect beetle abundances, but many authors suggest that carabids undergo rapid recolonization following spraying (Rivard 1974, Roland 1986a, Brust *et al.* 1986, Underwood 1989, Pearsall 1992). Unfortunately, each of these studies only used pitfall traps as a way of estimating beetle abundances. In orchards beetles are likely to disperse more rapidly due to less ground vegetation and so have a greater chance of being trapped. Lack of other insects (i.e. Collembola) and other food sources, especially worms and slugs may inhibit beetles from staying on sprayed land, and this could prevent constant buildup of beetle numbers.

In general organo-phosphates and pyrethroids have been recommended against winter moth (Sanford and Herbert 1966, Tonks *et al.* 1978, AliNiazee 1986, Hardman and Gaul 1990, Sheppard *et al.* 1990). In eastern Canada the use of pyrethroids has lead to problems with the European red mite, and so use of Bt has been proposed. The success of Bt has been limited so that mixtures with conventional pesticides are now recommended (Sanford and Herbert 1966, Hardman and Gaul 1990). Simply allowing pupal predators to build up is not feasible for commercial orchards, blueberry plots, etc. because:

i) winter moth is generally not the sole pest. Leaf rollers were a noted feature of Richmond blueberries. Other pests are not necessarily reduced by predators and so generally some insecticide is necessary.

ii) Since winter moth larvae attack early buds, damage is often severe. Therefore, biological control is not feasible for winter moth on orchards and particularly on blueberry; and

iii) Some of the invertebrate predators may actually damage the crop plants, particularly herbivores such as *H. affinus* and *Amara* spp., though all carabids are noted as consuming vegetation to some degree (Briggs 1957, 1966, Thiele 1977).

There is however a clear need for a greater emphasis on IPM. A frequent use of pesticides leads to a depletion of ground beetles and to a dependence on pesticides. The situation in forest systems is different. There the control of winter moth has been very successful, with winter moth populations now behaving like populations in endemic situations. Small outbreaks have occurred in Nova Scotia (Embree 1991), but these are not likely to cause continued long term defoliation episodes as occurred in prebiological control situations. In urban environments where predator populations are expected to be lower, winter moth may be prone to more frequent outbreaks. In Europe, for example, winter moth has remained as an important garden pest in urban environments (Speight 1979). In such situations *C. albicans* and *A. flaveolatum* may assume a more important role in the control.

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APPENDIX 1: LARVAL DISPERSAL AND PREFERENCE FOR APICAL BUDS.

In 1992, experiments were conducted to examine the dispersal behaviour of winter moth neonates on stage II blueberry buds. I wanted to examine whether dispersal was dependent on i) larval density, ii) bud size and iii) the position of the buds on the branch.

Adult moths were collected during the winter of 1991 from stocking traps and from pupae maintained in the laboratory. Adults were mated and oviposited on sponge (as in Hale 1989). Eggs were kept in an outside shed until they turned brown, and then were held in a refrigerator at 4°C until required. Blueberry twigs were collected and pruned so that only 4 flower buds remained on each twig. Bud length and width were measured and multiplied to give an index of bud volume. Twigs were held in cardboard containers as shown in figure 1. Winter moth neonates which had hatched during the previous night, were applied with a paintbrush, at equal spacing along the twig. Four densities were set up: 2, 5, 10 and 20 per twig (N=5). Twigs were ranked according to their bud sizes and the treatments were arranged so that bud sizes were as equal as possible. Wind was simulated with an electric fan, and the experiment was set up as a Latin square design. The numbers of larvae in the tanglefoot were recorded at irregular intervals over 7 days. A similar experiment was set up in the field at BBI. Twigs were chosen and pruned as above. Tanglefoot was applied at the base of each twig to restrict larval movement. Densities of 5, 10 and 20 neonates were applied (N=12). Half of the twigs were clipped after 6 hours and the rest were collected 24 hours later.

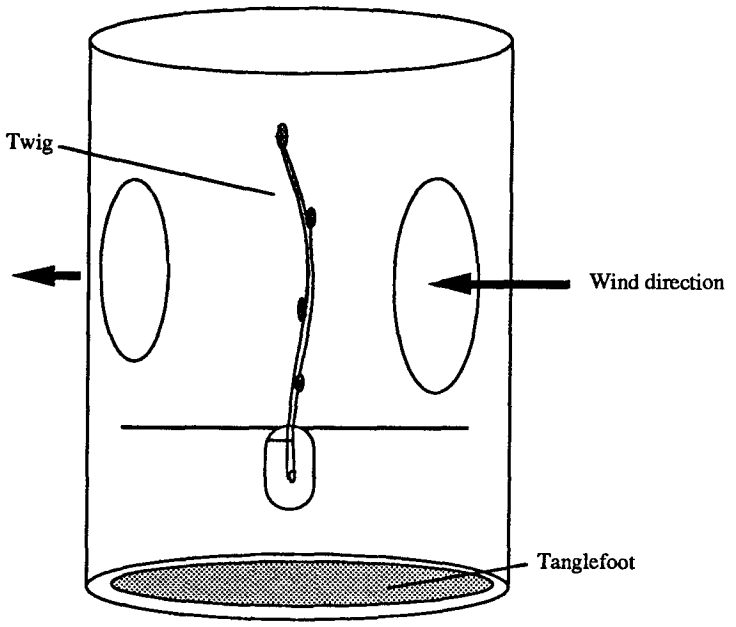


Figure 1. Dispersal chamber.

Results indicated that larval dispersal was not density dependent either in the field or in the laboratory experiment. Most of the dispersal in the field occurred within the first six hours (Fig. 2). There was much less dispersal in the laboratory than in the field. In the laboratory, dispersal commenced earlier from high density branches, but the proportion dispersing did not vary among treatments. The dispersal rate tended to be greatest from twigs with smaller buds. Apical buds are larger than subapicals (1-way ANOVA, $P>0.001$ [N=59]). First and second buds were not different (Tukey test, $P=0.999$), and third and fourth buds were not different (Tukey test, $P=0.538$). However, third and fourth buds were smaller than firsts and seconds (Tukey test, $P>0.02$). Twigs collected from the field

experiment were examined, the numbers of larvae remaining in the buds were recorded and tested with a $\chi 2$ analysis. Significantly more larvae were found on the two apical buds than on the remaining buds at each density (Table 1).

Table 1. Chi-squared analysis of larval distribution on blueberry buds, at three larval densities. Bud position refers to the position of the buds on individual twigs, buds numbered 1 are the apical buds, 2 are subapicals, etc.. ** = P> 0.005, *** = P>0.001.

Density	Bud position				N	$\chi 2$	DF
	1	2	3	4			
20	23	18	10	8	59	9.9**	3
10	23	12	2	4	41	26.6***	3
5	10	11	2	1	24	13.7**	3
pooled	66	49	14	17	146	52.4***	3

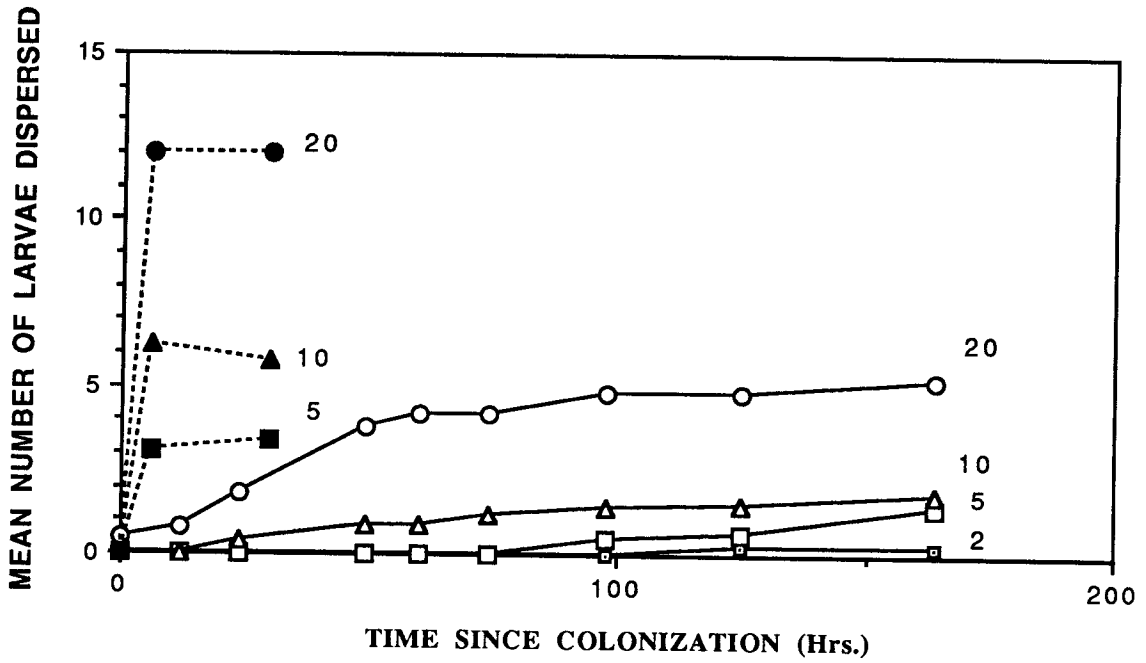


Figure 1. Larval dispersal from stage II blueberry buds under laboratory (solid line) and field (dashed lines) conditions. Numbers indicate larval densities per twig. Note that the proportions of larvae dispersed from each treatment are similar. For the laboratory experiment this is about 20% while for the field experiments it is about 50%.

APPENDIX 2: WINTER MOTH INSTARS

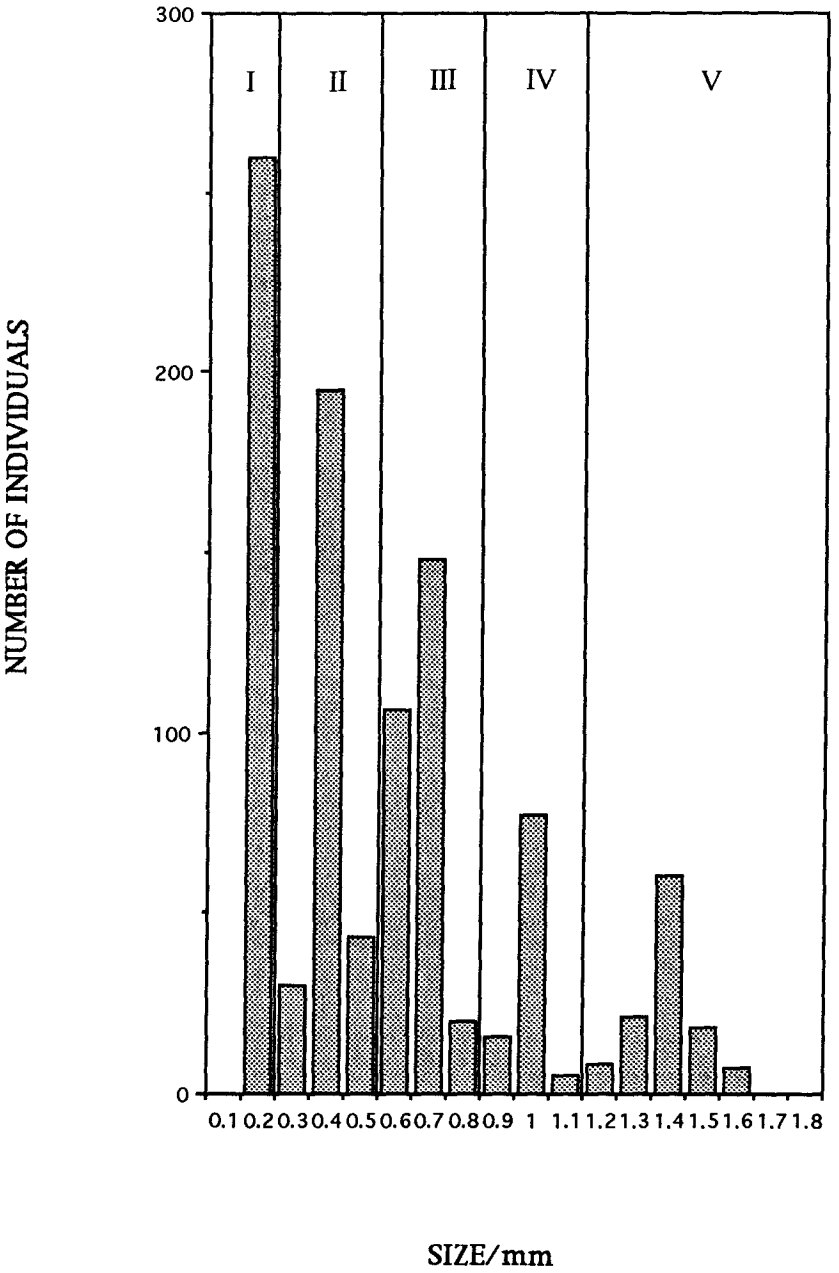


Figure 1. Distribution of head capsule widths among larvae collected at Richmond Nature Park in 1992. Five instars can be distinguished as indicated with roman numerals.

APPENDIX 3: PARASITISM AND PUPAL DEATH OF WINTER MOTH.

K-values for parasitism and death due to unknown reasons have been presented in the text, for ease of comparison with other published studies. The following tables present parasitism and death due to unknown factors as percentages of prepupae.

Table 1 Levels of Parasitism at four field sites in Richmond, between 1989 and 1992. Standard errors are presented in brackets and are not available for 1989.

SITE	1989	1990	1991	1992
BI	43	23.68 (5.36)	53.53 (4.87)	38.31 (5.83)
RNP	38	18.73 (2.29)	55.18 (7.44)	36.69 (7.06)
BBI	3	12.43 (7.21)	13.79 (9.21)	50 (25)
BBII	18	23.73 (3.03)	36.28 (9.71)	0

Table 2 Incidence of mortality due to unknown factors among pupae at four field sites in Richmond, between 1989 and 1992. Standard errors are presented in brackets and are not available for 1989.

SITE	1989	1990	1991	1992
BI	10.23	15.11 (5.41)	8.13 (1.52)	19.75 (4.92)
RNP	7.77	28.02 (2.72)	8.6 (2.45)	36.69 (7.06)
BBI	21.05	18.11 (8.30)	0	50 (25)
BBII	3.92	13.36 (18.35)	1.78 (0.99)	41.6 (18.31)

APPENDIX 4: WINTER MOTH DISEASE

Winter moth [*Operophtera brumata* (L.)] of every life-stage were taken from wild populations at Richmond and reared in the laboratory in 1991 and 1992. Caterpillars were reared in individual cups and fed ample quantities of fresh birch, apple or blueberry foliage. Larvae were carefully observed for the incidence of viral death. Of 628 larvae reared in 1991 and 1021 in 1992, there was no indication of viral disease. All larvae which had died in the laboratory and a number of extra larvae taken from the field (56 in 1991 and 339 in 1992) were smeared and stained. At blueberry site I (BBI) in 1991, 18 fifth instar larvae collected on May 9th showed symptoms of disease. These individuals had severe constriction of the first abdominal segments, with the second, third and fourth abdominal segments also constricted. Larvae were sluggish and stopped feeding before death. All 18 larvae died and were smeared and stained (for details of staining see text Chapter 2).

Fourteen of the larvae had dark staining ovoid bodies of 2 to 4 μm. Most of these were microsporidia. However, the larger bodies may have been cytoplasmic polyhedrosis virus (CPV). In 1991, 69 adults and 120 eggs and in 1992, 27 adults and 28 pupae were stained and smeared, but microsporidia, cytoplasmic polyhedris virus (CPV) and nuclear polyhedrosis virus (NPV) were not observed.

In 1992, an experiment was carried out to examine the cross-infection of *O. brumata* and *O. bruceata* NPV. Viruses were supplied by Dr. J. Cunningham, Forest insect and disease laboratory, Saulte St. Marie, Ontario. Larvae from four instars were collected from Richmond on April 29th and infected with *O. brumata* NPV and *O. bruceata* NPV on May 1st. Larvae were inoculated as follows: 400 PIB (+) *O. brumata* NPV per individual and high doses of *O. bruceata* NPV (the actual PIB counts for the *O. bruceata* NPV culture was not estimated). Larvae of Bruce's spanworm [*O. bruceata* (Hulst)] were collected from the Okanagan on May 6th and infected on May 10th with high doses of *O. bruceata* NPV. Larvae were fed virus on 5mm diameter birch leaf discs. Results of this cross- infection experiment are presented in Table 1. Mortality of the primary hosts was high for both species (90-100% for winter moth and 78.6% for spanworm). The *O. bruceata* NPV was not a pure culture and there was a high incidence of CPV among the dead spanworm larvae. Only two (10%) early instar winter moth larvae treated with *O. brumata* NPV showed signs of infection. Both died on the 23rd of May and in each case these had both CPV and NPV infections. Naturally occurring CPV, has not been recorded from winter moth, CPV reduces fecundity and causes deformities of adult winter moth, and cross-infection among Lepidopteran species is apparently high. Eleven major CPV's have been distinguished, several of which are capable of infecting more than one host (see Wigley 1976). These results indicate that there could be a low incidence of disease among the Richmond population. Viral cross-infection from *O. bruceata* is possible, but is probably very limited due to the high amounts of innoculum required and the resistance of the late instars.

TABLE 1. Results of 1991 cross-infection experiments. 'N' indicates the numbers of larvae used in each treatment, 'S' is the number of larvae which survived to pupation, '+V' indicates the number of larvae which were positively identified as having NPV infection. A number of larvae which died for reasons other than viral infection. Possible explanations for their deaths are presented ('Other'). 'Wm' = winter moth, 'bs' = spanworm.

NPV	*O. brumata*				*O. bruceata*				Control			
Sp. Instar	N	S	+V	Other	N	S	+V	Other	N	S	+V	Other
wm 2	35	0	32	?	20	8	2	failed pupae/ dessica -tion	19	9	0	
3/4	10	1	9		10	5	0	?	14	12	0	
5	10	0	10		5	0	0	failed pupae	5	0	0	failed pupae
bs 5					14	3	11		14	4	0	pupal death

APPENDIX 5: PITFALL TRAP CATCHES AT RICHMOND.

Table 1. Species trapped at Richmond in 1991 and 1992. Generalist invertebrate predators and beetle larvae are not included in this table.

SPECIES	Total number caught									
	BBI		BBII		RNP		RNPII	BI		BII
	1991	1992	1991	1992	1991	1992	1992	1991	1992	1992
Ground-beetles										
specialists										
Callisthenes wilkerii									1	
Carabus granulatus		3	7	21			5	8	37	81
C.nemoralis		11	15	5			1		5	11
Laevitus ferruginosis									2	1
Loricera decempunctata			2	2	4	2	13	1	10	12
Notiophilus sp.				4			6		12	
Dyschinius sp. 1		8		44			12		10	5
Dyschinius sp. 2									1	2
Scaphinotus marginatus			8	60	1	23	88	25	104	106
Carrion feeders										
Nicrophora spp.	1	2	15	1	38	69	73	116	99	51
Catharis rufa			2			3	5	6	40	157
Hydrophilidae										
Sp. 1			11		15		2	108	32	15
Cercyon spp.									4	
Staphylinidae										
S. 1		1					85		2	3
S. 2 (*Philonthus* sp.)						2	104	27	46	38
S. 3 (*Philonthus* sp.)		1		12		3	9		3	31
S. 4 (*Philonthus* sp.)				1		1	2			
S. 5 (*Philonthus* sp.)							5			
S. 6		2		3			3		2	4
S. 7						1				
S. 8										
S. 9 (*Tachinus* sp.)							3			
S. 10							2		1	
S. 11 (*Philonthus* sp.)							1	3		1
S. 12							7			
S. 13 (*Tachinus* sp.)										3
S. 14 (*Tachinus* sp.)								18		
S. 15 (*Queduis* sp.)								1		
Ants										
Myrmica sp.	265	103							2	2
Formica sp.	57	60	5		3		2			
Dermaptera	2	9						2	2	
Small Mammals	5	1	9		14	13	6	45	2	7

APPENDIX 6: GROUND-BEETLE INFORMATION.

Table 1. Biological information on ground-beetles from this study (taken from Lindroth 1961-1969 and Agriculture Canada 1991).

Species	Habitat	BB	B	Over-wintering stage	Body length	Pupal predator	Native
Amara aurata Dejean 1828	Found in dry areas with little vegetation.	*		?	5.6 - 7mm	*	*
A. litteralis Mannerheim 1843	In open moderately dry country with rich and incoherent vegetation. Usually pronounced weed character favoured by human activities.	*		Hibernate as adults	6.2 - 9.3mm	*	*
A. laevipennus Kirby 1837	In open dry country with grass or meadow vegetation. Usually on sandy moraine.	*		Hibernate as adults	5.8 - 7.1mm	?	*
Calathus fuscipes (Goeze)	Found on open ground with meadow or weed vegetation, synathropic.	*		Hibernate as larvae.	10 - 15mm	?	
Callisthenes wilkerii LeConte 1852	Xerophilous in dry open country sometimes in meadows and thin forests.		*	?	15 - 18mm	?	*
Carabus granulatus Linné 1758	Open light deciduous woods, usually near water, often on cultivated ground where soil is moist.	*	*	Hibernate as adults.	16 - 24mm	*	
C. nemoralis Müller 1764	Restricted to cultivated ground.	*	*	Hibernate as adults.	21 - 26mm	*	
Harpalus affinus (Schrank) 1781	Open dry country - favoured by human activities.	*		Hibernate as adults.	8.5 - 12mm	*	
H. rufipes (DeGeer) 1774	Open dry country especially cultivated fields (mainly seed eater).	*		Hibernate as adults and larvae	10 - 16.7mm	*	
Pterostichus algidus Leconte 1852	Less pronounced forest species, also occurs in open country with rich vegetation.		*	Hibernate as larvae.	12 - 16mm	*	*
P. herculaneus Mannerheim 1843	In dense but often dry conifer or mixed forests.		*	Hibernate as larvae.	13.5 - 17mm	*	*
P. melanarius (Illiger) 1798	In light forests and open meadows, favours cultivated land and waste places.	*	*	Hibernate mainly as larvae.	12 - 19mm	*	
Scaphinotus marginatus (Fischer) 1822	Eurytopic, in southern regions mainly in forests, in particular near the margins of brooks.		*	Hibernate as larvae.	11.5 - 19mm	?	*

Table 1. cont.

Leistus ferruginosus Mannerheim 1843	On moderately moist half-shaded ground, usually near running water.	*	?	7.8 - 9.3mm	?	*
Loricera decempunctata Eschscholtz 1833	In the vicinity of water.	*	Hibernate as adults	6.7 - 8.1mm		*
Notiophilus sp.	Forest xerophilus.	*	varies	6 - 8mm	?	?
Bembidion sp.	Mostly hygrophilus	*	?	6 - 8mm		?
Agonum sp.	Mostly hygrophilus	*	?	5 - 8mm	?	?

APPENDIX 7: WINTER MOTH POPULATION TRENDS

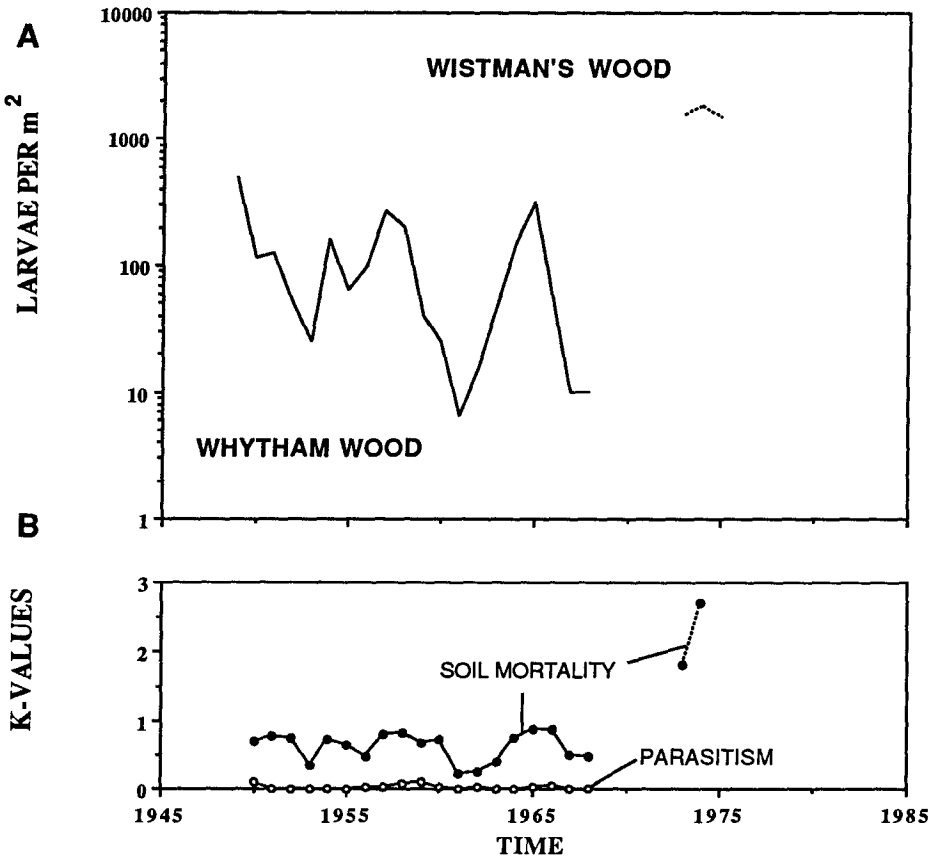
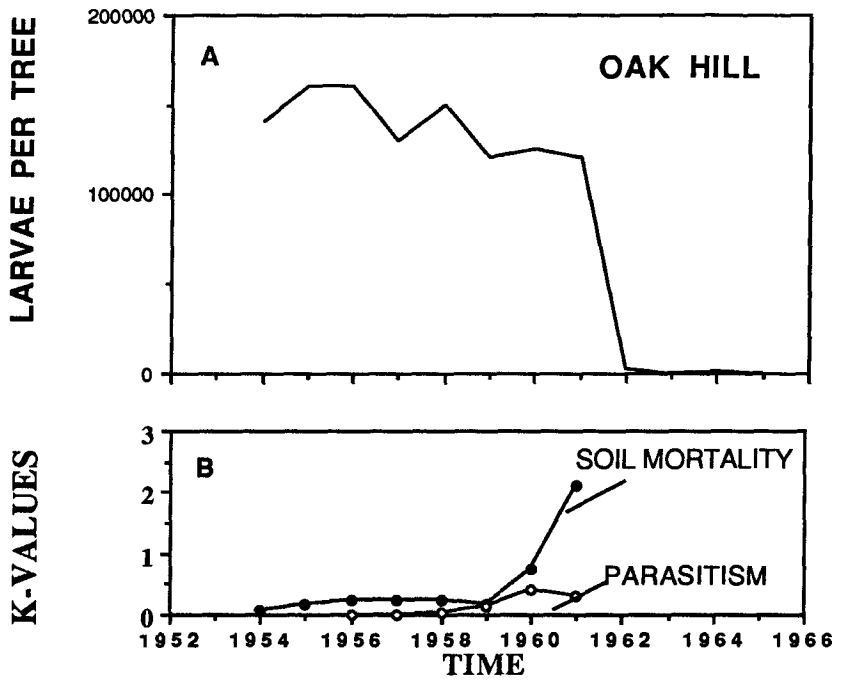


Figure 1. Winter moth population data from two oak woods in England. 'A' indicates the population densities of winter moth at Whytham Wood and Wistman's Wood. 'B' indicates the mortality due to parasitism by *Cyzenis albicans* (open circles) and mortality due to soil mortality (closed circles). (Data are taken from Varley, Gradwell & Hassell 1973 and Wigley 1976).

Figure 2. Winter moth population trends in Nova Scotia. Population trends at Oak Hill are shown in Part 1, with trends at Shefield orchard in Part 2. population densities (A) and mortality due to *C. albicans* parasitism (open circles) and soil mortality (closed circles) (B) are shown for each site. (Data are taken from Embree 1966, Roland 1988 and McPhee *et al.* 1988).

1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200000
100000
0
A
OAK HILL
K-VALUES
3
2
1
0
B
SOIL MORTALITY
PARASITISM
1952
1954
1956
1958
1960
1962
1964
1966
TIME

2

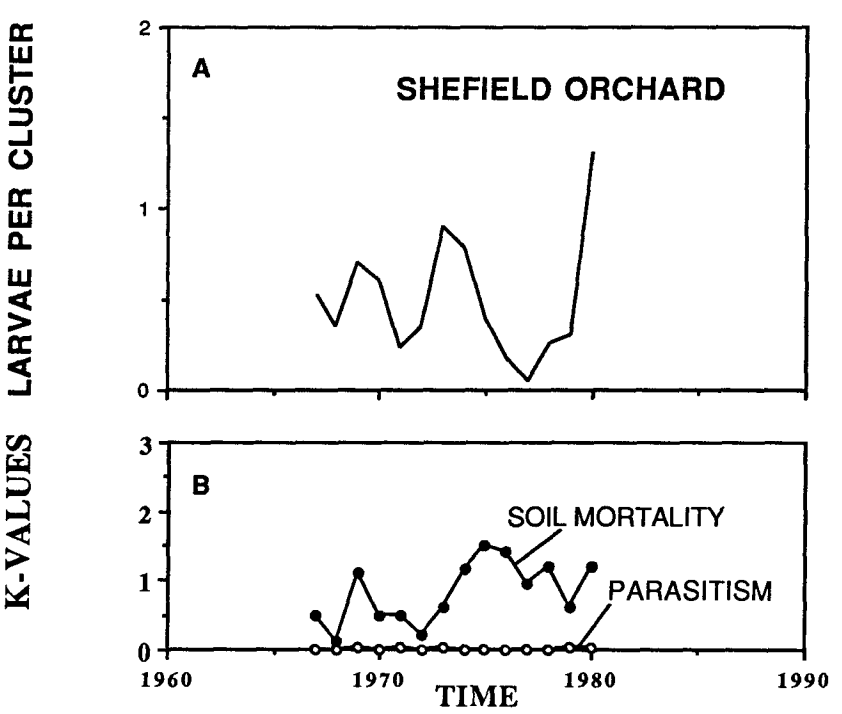
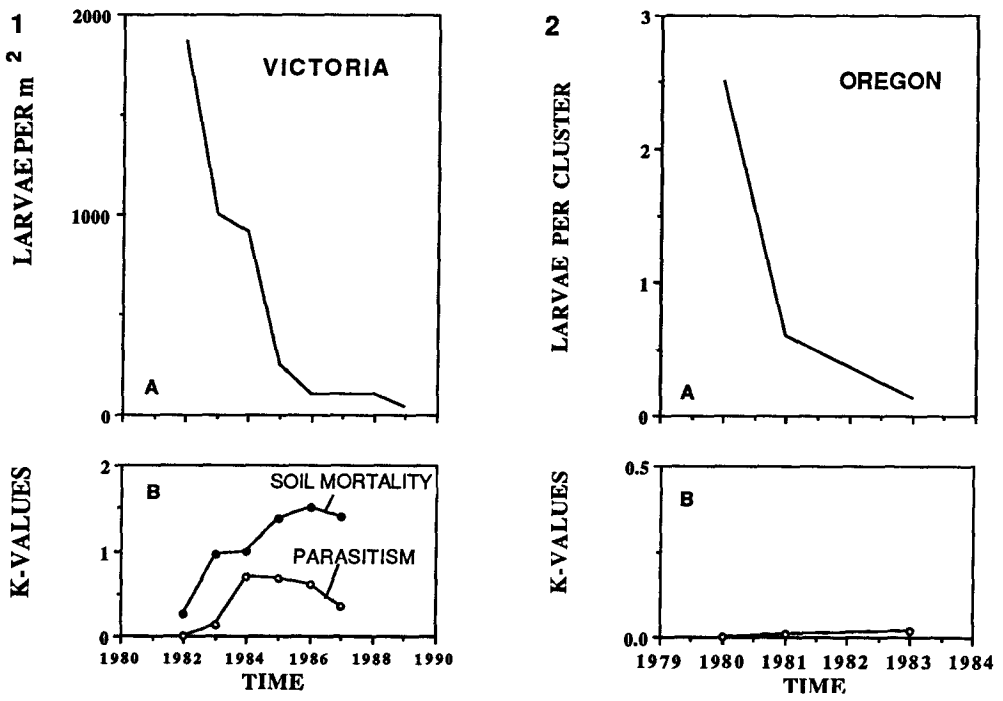
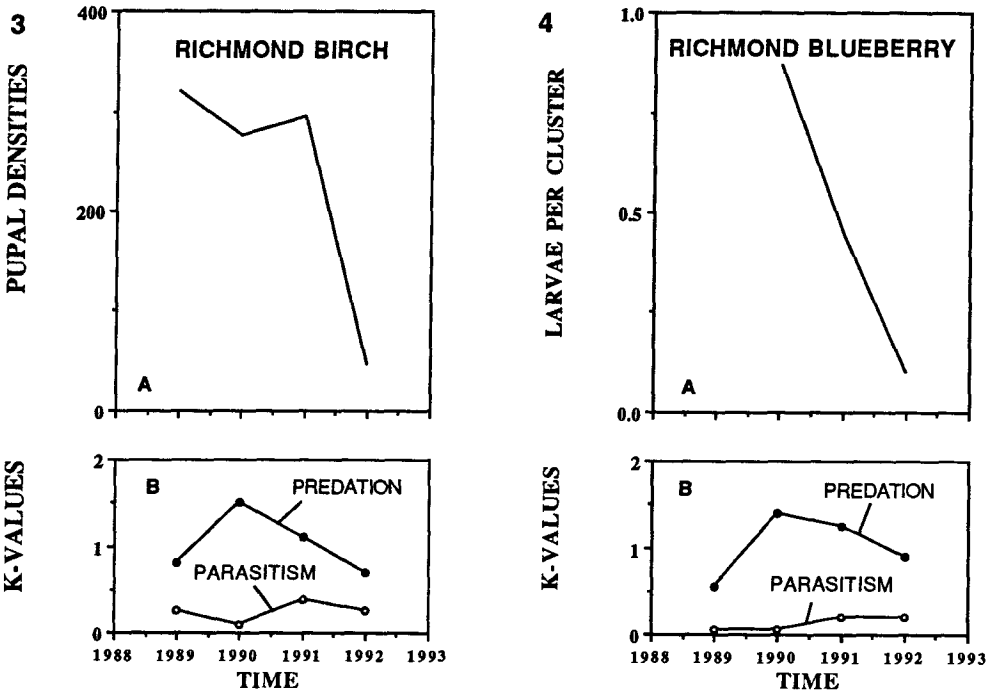

LARVAE PER CLUSTER
2
1
0
A
SHEFIELD ORCHARD
K-VALUES
3
2
1
0
B
SOIL MORTALITY
PARASITISM
1960
1970
1980
1990
TIME

Figure 3. Winter moth population trends in western North America. Population trends are shown at: 1) Victoria and 2) Oregon and at Richmond on 3) birch and 4) blueberry. Population densities are presented (A) with an indication of parasitism by *C. albicans* (open circles) and pupal predation or soil mortality (closed circles) at the sites (B). Data on pupal predation is not available from Oregon and parasitism did not exceed a K-value of 0.02. (Data is taken from Kimberling *et al.* 1986, Roland 1988 and 1992, Sheppard *et al.* 1990, a personal communication from the Winter Moth Committee of British Columbia and from this study.


1
LARVAE PER m 2
2000
1000
0
VICTORIA
A
K-VALUES
2
1
0
B
SOIL MORTALITY
PARASITISM
1980 1982 1984 1986 1988 1990
TIME
2
LARVAE PER CLUSTER
3
2
1
0
OREGON
A
K-VALUES
0.5
0.0
B
1979 1980 1981 1982 1983 1984
TIME


3
PUPAL DENSITIES
400
200
0
RICHMOND BIRCH
A
K-VALUES
2
1
0
B
PREDATION
PARASITISM
1988 1989 1990 1991 1992 1993
TIME
4
LARVAE PER CLUSTER
1.0
0.5
0.0
RICHMOND BLUEBERRY
A
K-VALUES
2
1
0
B
PREDATION
PARASITISM
1988 1989 1990 1991 1992 1993
TIME