Importance of long-term research in classical biological control: an analytical review of a release against the cabbage seedpod weevil in North America

D. R. Gillespie[1], P. G. Mason[2], L. M. Dosdall[3], P. Bouchard[2] and G. A. P. Gibson[2]
[1]Agriculture and Agri-Food Canada, Research Centre, Agassiz, British Columbia; [2]Agriculture and Agri-Food Canada, Research Centre, Ottawa, Ontario; [3]Department of Agricultural, Food and Nutritional Science, University of Alberta, Edmonton, Alberta, Canada

Abstract: Cabbage seedpod weevil, *Ceutorhynchus obstrictus* (Marsham) (Col., Curculionidae), is an invasive alien pest that is spreading in North America. To aid with planning for introductions of European parasitoids in North America, we examined the status of the only classical biological control release against this pest in North America, which in 1949 introduced *Mesopolobus morys*, *Stenomalina gracilis* and *Trichomalus perfectus* (Hym., Pteromalidae). Weevils and parasitoids were reared in 2005 from mass collections of seedpods of *Brassica napus*, *Brassica rapa* and *Raphanus raphanistrum* (Brassicaceae) from 18 sites in the Fraser Valley, near Vancouver, British Columbia, Canada. Of the three European parasitoid species that were originally released, only *S. gracilis* was found. The predominant hymenopterous parasitoid species were *Trichomalus lucidus*, *S. gracilis*, *Mesopolobus moryoides* (Pteromalidae), *Necremnus tidius* (Eulophidae) and *Eupelmus vesicularis* (Eupelmidae). These constituted over 97% of the parasitoids reared, although overall parasitism was low. Only *M. moryoides* is clearly North American in distribution; other than *S. gracilis*, the remaining species were either accidentally introduced or are Holarctic in distribution. Based on these results, re-releases of *M. morys* and *T. perfectus* in North America should be considered as part of a classical biological control programme. However, redistribution of *S. gracilis* is not recommended at present because of potential conflicts with biological control programmes against weeds. Ongoing re-examination of classical biological control programmes can further our understanding of failure of release programmes, particularly when re-examination can be made in the light of improved taxonomy and systematics of the target and agent species.

1 Introduction

Biological control has provided important solutions to invasions of alien insect pest species in agricultural and forest ecosystems since formal programmes were implemented more than 100 years ago. The ecological basis of classical biological control is to reconstruct the natural enemy complexes of non-indigenous plant or arthropod species that have become pests in regions where they have been accidentally introduced (Mills 1994). Despite the many successes in biological control, a great number of releases have failed in one way or another (Turnbull and Chant 1961; Beirne 1975; Van Driesche and Bellows 1996). Long-term studies of the fate of classical biological control releases are almost universally recommended as a way to record and understand both the successes and failures, but such studies are rarely accomplished in practice. In the absence of such long-term studies, retrospective analyses can be useful to better understand the reasons why failures have occurred and so improve future chances for success in biological control (Hopper 2001).

Cabbage seedpod weevil, *Ceutorhynchus obstrictus* (Marsham) [*C. assimilis* (Paykull); see Colonnelli 1990, 1993], an invasive species of European origin, is a serious pest of canola and rapeseed (*Brassica napus* L. and *Brassica rapa* L.) in North America (McCaffrey 1992; Buntin et al. 1995; Cárcamo et al. 2001; Dosdall et al. 2002; Mason et al. 2004). Economic losses result from adult feeding on flower buds (bud-blasting) and larvae feeding within seedpods (McCaffrey et al. 1986; Buntin and Raymer 1994). The weevil was first recorded in North America in 1931 at the port city of Vancouver, British Columbia (McLeod 1962), and has since spread to other parts of western and eastern North America (Baker 1936; Hagen 1946; Crowell 1952; Walz 1957; Anonymous 1977; Dolinski 1979; Boyd and Lentz 1994; Buntin et al. 1995; Brodeur et al. 2001; Cárcamo et al. 2001; Dosdall et al. 2002;

Mason et al. 2004). It was not discovered in Alberta until 1995, but based on surveys conducted from 1997 to 2000, Dosdall et al. (2002) determined that it was dispersing at the rate of approximately 55 km per year. As a result, they predicted that *C. obstrictus* will eventually establish itself throughout the entire canola-growing region of western Canada. Furthermore, Olfert and Weiss (2006) predicted that, with increases in temperature because of climate change, the risks associated with *C. obstrictus* will become more severe in areas it presently occupies, and it will be able to establish in new localities. Consequently, *Brassica* industries, particularly those producing seed crops, will increasingly risk damage by this pest. The only control measure currently available to producers is the application of broad-spectrum chemical insecticides (Dosdall et al. 2001). In Europe, where the North American weevil populations originated (Laffin et al. 2005), natural enemies provide control (Murchie 1996; Williams 2003). Thus, management strategies that include classical biological control should be pursued in North America.

The only attempt at classical biological control of *C. obstrictus* in North America was the release of three species of pteromalid larval ectoparasitoids in British Columbia, Canada in 1949. These species were reported as *Habrocytus* sp. (*Pteromalus* sp.), *Trichomalus fasciatus* (Thomson) [*Trichomalus lucidus* (Walker)] and *Xenocrepis pura* Mayr [*Mesopolobus morys* (Walker)] (Hym., Pteromalidae) (Anonymous 1949). It was not until over 50 years later that voucher material of the introduced species was critically re-examined to substantiate their identity. The identification of *M. morys* was confirmed but it was determined that *T. lucidus* and *Habrocytus* sp. were misidentifications of *Trichomalus perfectus* (Walker) and *Stenomalina gracilis* (Walker) (Pteromalidae), respectively (Gibson et al. 2006a).

Several studies have reported parasitoids reared from *C. obstrictus* in North America (Baker 1936; Gahan 1941; Breakey et al. 1944; Doucette 1944, 1948; Hanson et al. 1948; McLeod 1953; Walz 1957; Harmon and McCaffrey 1997; Buntin 1998). Reported parasitoids include *Microctonus melanopus* Ruthe (Hym., Braconidae), and specimens identified as *T. perfectus* and *M. morys*. All three of these species are important regulators of *C. obstrictus* populations in Europe (Crowell 1952; Bonnemaison 1957; Jourdheuil 1960; Laborius 1972; Lerin 1987; Büchi 1991, 1993; Murchie 1996; Williams 2003). In North America, parasitism levels associated with these species were generally very low and it was assumed that biological control by *T. perfectus* and *M. morys* was not effective (Harmon and McCaffrey 1997; Buntin 1998; Fox et al. 2004). However, examination of the voucher material of chalcid parasitoids associated with *C. obstrictus* in North America by Gibson et al. (2005, 2006a,b) showed that specimens cited as *T. perfectus* and *M. morys* were misidentifications of *T. lucidus* and *Mesopolobus moryoides* Gibson, respectively. Low levels of parasitism in North American weevil populations could then be explained by the absence of the two parasitoid species most responsible for population regulation of *C. obstrictus* in Europe.

The discovery that *T. perfectus* and *M. morys* had in fact been released in British Columbia in 1949 (Gibson et al. 2006a), but had never been reared from surveys in western and south-eastern United States (Gibson et al. 2005, 2006b), indicated the need for a new survey to determine whether or not either species had established and is now present in British Columbia. *Trichomalus perfectus*, *M. morys* and *S. gracilis* were released in British Columbia near Dewdney and Sardis in the lower Fraser Valley (McLeod 1951). Definitive information concerning their presence or absence in British Columbia would most likely be obtained through surveys in the area where they were first introduced. If either or both species could not be found, then introductions could be considered (Kuhlmann et al. 2002). If either or both species were present, then populations could be redistributed into areas where *C. obstrictus* has more recently dispersed and is causing extensive economic damage.

The classical biological control release against *C. obstrictus* was regarded as a 'partial success' by McLeod (1962) and Munroe (1971). Evaluation of the fate of the 1949 releases has gained new urgency in the light of the extensive economic losses to western Canadian canola production that are attributable to *C. obstrictus* infestations (Dosdall et al. 2001). As part of a larger retrospective analysis of cabbage seedpod weevil biological control in North America, our objectives were to survey populations of *C. obstrictus* in the Fraser Valley in order to clarify the presence of *T. perfectus* and *M. morys* in British Columbia and to document the host plant and parasitoid associations that have evolved over the 70 years since *C. obstrictus* was introduced.

2 Materials and Methods

Collections were made among Brassicaceae plants at 18 sites in the Fraser Valley of British Columbia (table 1, fig. 1). Adult weevils collected from sweep-net samples made at the 18 sites were sorted and stored in 70% ethanol. We were unable to make collections at all sites on each sample date because of disruptions from mowing and other agricultural operations. Timing of attack by weevils and parasitoids was estimated from eight sites (sites 3, 7, 8, 10, 17, 22, 25, 27) where it was possible to make collections throughout the period when weevils were present. Site 3 was located at a rail crossing where *B. napus* was growing in gravel on the edge of the tracks and also among the grass, weeds and European blackberry (*Rubus fruticosus* L.) (Rosaceae) that dominated the nearby vegetation. Site 7 had *B. rapa* and *B. napus* plants on the border of a former field of Brussels sprouts (*Brassica oleraceae* L.). The fence next to the field was overgrown with *R. fruticosus*. Site 8 had *Raphanus raphanistrum* L. (wild radish) plants growing on a waste-disposal site in a field next to a dairy farm. The waste-disposal area was surrounded by weedy grasses. Sites 10 and 17 consisted of *B. napus* plants growing among weedy grass next to a former broccoli (*B. oleraceae*) field. Site 22 had *R. raphanistrum* plants growing among grass next to a red raspberry (*Rubus idaeus* L.) field. Site 25 had *R. raphanistrum* plants growing on a dike edge among mixed-production farm fields. Site 27 had *B. rapa* plants growing among grass on a waste dump in a fallow field. Although some sites were very close to the original

Table 1. *Localities and plant species (Brassicaceae) surveyed for* Ceutorhynchus obstrictus *and parasitoids in the Fraser Valley, British Columbia, in 2005*

Locality	Species	Latitude	Longitude	Number of collections	Site no.
Chilliwack	*Sinapis arvensis* L.	49°12.134′N	121°47.685′W	2	2
Chilliwack	*Brassica napus* L.	49°10.740′N	121°48.226′W	7	3
Chilliwack	*B. rapa*	49°09.345′N	121°57.345′W	2	4
Abbotsford	*B. rapa + B. napus*	49°03.102′N	122°11.353′W	7	7
Abbotsford	*Raphanus raphanistrum* L.	49°00.979′N	122°11.614′W	7	8
Abbotsford	*B. napus*	49°03.359′N	122°08.291′W	7	10
Abbotsford	*B. rapa + B. napus*	49°05.495′N	122°16.234′W	3	15
Abbotsford	*B. rapa*	49°06.230′N	122°17.896′W	7	17
Agassiz	*R. raphanistrum*	49°14.950′N	121°46.113′W	2	20
Abbotsford	*R. raphanistrum*	49°00.398′N	122°20.940′W	7	22
Langley	*B. napus + B. rapa*	49°00.506′N	122°33.513′W	2	23
Surrey	*R. raphanistrum*	49°01.880′N	122°41.414′W	2	24
Delta	*R. raphanistrum*	49°05.188′N	122°56.696′W	7	25
Delta	*B. rapa*	49°05.465′N	123°09.863′W	7	27
Chilliwack	*R. raphanistrum*	49°09.048′N	121°56.622′W	2	29
Abbotsford	*B. napus*	49°03.346′N	122°10.212′W	2	43
Abbotsford	*R. raphanistrum*	49°02.847′N	122°11.922′W	2	44
Agassiz	*B. napus*	49°14.434′N	121°45.289′W	2	41
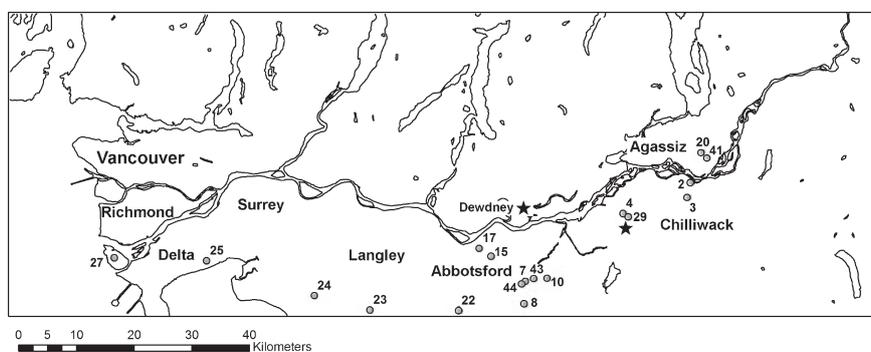
Fig. 1. *Map of the Fraser Valley, British Columbia, showing the locations of sample survey sites (circles) and the two original release localities for parasitoids of* Ceutorhynchus obstrictus *according to Biological Control Investigations Unit (1949), McLeod (1951) and Gibson et al. (2006a) (stars)*

release localities for parasitoids in British Columbia (fig. 1), we did not make collections from plants at the original release sites. The Sardis site was destroyed by urban development, and host plants of *C. obstrictus* were not available in Dewdney.

Sites were visited periodically between late May and mid-August 2005. On each sample date, 1000–3000 pods were collected by removing branches containing approximately 100–250 pods from randomly selected *B. napus*, *B. rapa* and *R. raphanistrum* plants. The branches were brought to the laboratory where 50–100 mature pods were removed from each collection and dissected to determine prevalence of weevil eggs, larvae and ectoparasitoids. We did not attempt to rear ectoparasitoid larvae that were found during dissections because our dissection method often damaged the host and/or parasitoid larva. The remaining pods were placed in 23 × 31 × 16 cm cardboard emergence boxes containing about 2 cm of lightly moistened horticultural peat moss as a pupation substrate. A 4-cm-diameter hole in the end of the box allowed insects to exit into plastic collection containers. These boxes were placed on shelves in a lighted room at 22 ± 1°C. Collection containers were inspected daily until no insects emerged from the boxes for 20 consecutive days. Insects that emerged were collected into vials containing 70% ethyl alcohol, and weevils and parasitoids were enumerated. Parasitoids were identified by G.A.P. Gibson, and weevils by

P. Bouchard. Voucher specimens of weevils and parasitoids were deposited in the Canadian National Collection of Insects and Arachnids, Ottawa, Ontario. Site coding reported herein is consistent with labels on these specimens.

The relative abundance of the five most common parasitoid species, at sites with *B. rapa* and/or *B. napus* or with *R. raphanistrum*, was analysed by a multivariate ANOVA (JMP, SAS Institute 2003).

3 Results

Only *C. obstrictus* was recovered in sweep-net samples throughout the season. Parasitoids were found attacking *C. obstrictus* at all the sites surveyed, although adult weevils only emerged successfully from collections at 16 of the 18 sites. Five species of parasitoids – *T. lucidus*, *M. moryoides*, *S. gracilis*, *Necremnus tidius* (Walker) (Hym., Eulophidae) and *Eupelmus vesicularis* (Retzius) – constituted over 97% of the parasitoid specimens reared, and, with the exception of the last, occurred at half or more of the sites (table 2). Another 27 specimens of seven taxa were also identified but constituted

Table 2. *Numbers of Brassicaceae seedpods collected and* Ceutorhynchus obstrictus *adults and parasitoid species, in order of prevalence, reared from 18 sites in the Fraser Valley, British Columbia in 2005*

	Total	♂	♀	Number of sites
Seedpods	84 536			18
C. obstrictus adults	5725			16
Parasitoids	1120			18
Trichomalus lucidus (Walker)	548	287	261	15
Stenomalina gracilis (Walker)	327	108	221	13
Mesopolobus moryoides Gibson	120	72	48	12
Necremnus tidius (Walker)	81	40	41	9
Eupelmus vesicularis (Retzius)	20	0	20	4
Other species	27			

incidental records at two or fewer sites. Although we attempted to remove potential host species other than *C. obstrictus* from our collections, small numbers of adults of the diamond back moth, *Plutella xylostella* (Lep., Plutellidae), as well as aphids (Hem., Aphidoidea), thrips (Thysanoptera) and flies (Diptera) emerged from some collections. Therefore, some of the less common parasitoids may have been associated with these or other unrealized insect contaminants of the mass-reared pods rather than with *C. obstrictus*. Nine specimens of a *Eurytoma* sp. (Hym., Eurytomidae) were reared from two sites. A *Eurytoma* sp. has also been previously reported from *C. obstrictus* in North America (see Gibson et al. 2006b for references) and the species from British Columbia is probably the same as the one identified as *Eurytoma tylodermatis* Ashmead in Gibson et al. (2006b). *Eurytoma tylodermatis* act as either primary or hyperparasitoids (Bugbee 1967). Literature host records for *E. tylodermatis* are largely unreliable because of taxonomic problems in identifying species of *Eurytoma* accurately, but they include species in several genera of Curculionidae and Braconidae (Noyes 2002). Species of *Baryscapus* (eight specimens reared from two sites) have a wide host range, but are often hyperparasitoids (Noyes 2002). Consequently, our record from *C. obstrictus* is dubious and it is more likely that it was present as a hyperparasitoid of parasitoids of *P. xylostella*. Also dubious are our records of *Gonotocerus* sp. (Mymaridae) and *Halticoptera* sp. (Pteromalidae) because both are incidental parasitoids (three specimens of each) and neither has been reported previously as associated with *C. obstrictus*. Mymaridae are primary endoparsitoids of insect eggs and host records indicate Cicadellidae (Hemiptera) as the hosts for most species of *Gonotocerus* (Huber 1986). Many *Halticoptera* are parasitioids of Diptera, particularly Agromyzidae and Tephritidae (Noyes 2002), and it seems probable that these were present as parasitoids of some fly. Three specimens of *Mesopolobus* sp. were reared, and these represent at least one species. All of these genera require a species revision for North America before accurate species identifications are possible. One specimen of *Conura albifrons* Walsh (Hym., Chalcididae) was reared. Dosdall et al.

(2006) previously reported rearing this species from mass-collected *B. napus* seedpods in Alberta. Gaines and Kok (1995) reared it as a hyperparasitoid of a braconid pupal endoparasitoid of Lepidoptera in *Brassica* crops in eastern North America. Most literature host records indicate that *C. albifrons* is a hyperparasitoid of various Lepidoptera, although Noyes (2002) also listed it as a hyperparasitoid of three species of *Hypera* Gemar (Col., Curculionidae).

In all collections, *C. obstrictus* larvae were present in dissected pods throughout the survey period, from late May to early August but larvae were most abundant in June and early July (fig. 2a). The incidence of parasitism based on dissections was in the range of 2–4%, and was greatest in August (fig. 2b). The product of average numbers of weevils per pod at these sites and the numbers of pods collected, suggested that emergence of adult weevils in emergence boxes was a very small fraction of the numbers present in the collected pods (table 3). At all eight of these sites, the parasitoid community was dominated by either *T. lucidus* or *S. gracilis*.

Analysis of data from the eight localities where weevils and parasitoids were most abundant indicated that host plant species had a significant effect on the species composition of the four dominant parasitoids (table 4, Multivariate ANOVA, $F_{1,6} = 3.017$,
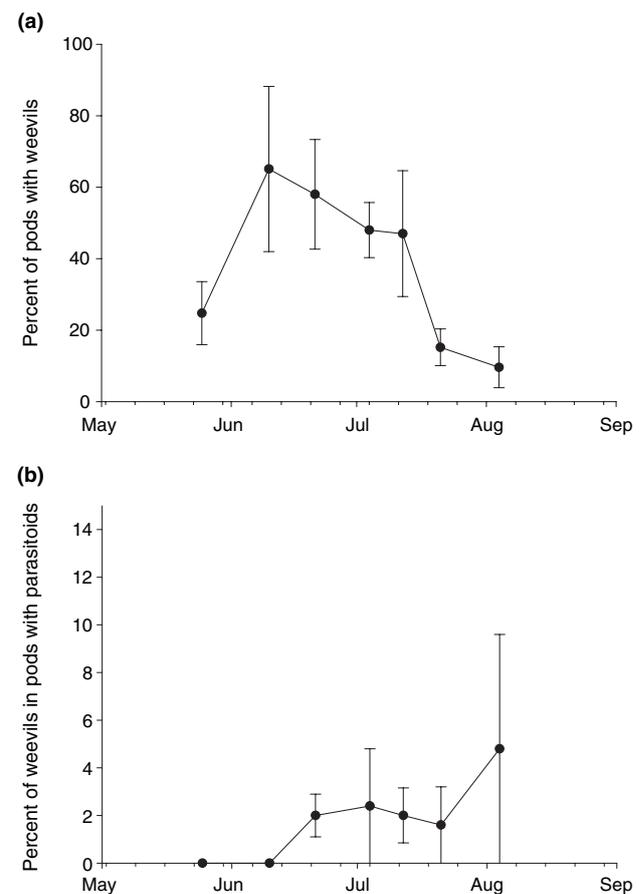

Fig. 2. *Mean ± SE (n = 8) per cent of* Ceutorhynchus obstrictus *larvae (a) and ectoparasitoids (b) that were found in samples of dissected seedpods*

Table 3. *Numbers of emerged adults of* Trichomalus lucidus, Mesopolobus moryoides, Necremnus tidius, Eupelmus vesicularis *and* Stenomalina gracilis, *as a proportion of total emergence of parasitoids from all collections*

Host plant species	Site	Average weevils per pod	Total pods	Weevil adults	Total parasitoids	T. lucidus	M. moryoides	N. tidius	E. vesicularis	S. gracilis
B. napus	3	0.24	7200	1128	54	85.2	7.4	1.9	0.0	5.6
B. rapa and *B. napus*	7	0.51	6855	450	74	66.2	2.7	6.8	0.0	24.3
B. napus	10	0.56	11845	1722	77	19.7	1.0	0.0	0.5	78.8
B. rapa	17	0.43	3445	1	62	28.6	15.6	7.8	0.0	48.1
B. rapa	27	0.4	5475	624	72	79.0	3.2	8.1	0.0	9.7
R. raphanistrum	8	0.49	11965	782	193	48.1	0.0	0.0	1.9	50.0
R. raphanistrum	22	0.24	7413	17	54	36.9	20.0	21.0	8.7	13.3
R. raphanistrum	25	0.52	10116	576	195	54.2	2.8	13.9	0.0	29.2

Table 4. *Distribution of relative parasitoid abundance (mean $\pm$ SE proportion) among populations that emerged from collections of pods of* Brassica rapa *and* Brassica napus L. (n = 5) *and* Raphanus raphanistrum L. (n = 3)

Host species	T. lucidus	M. moryoides	N. tidius	E. vesicularis	S. gracilus
B. rapa/B. napus	0.63 $\pm$ 0.101	0.06 $\pm$ 0.023	0.08 $\pm$ 0.019	0	0.23 $\pm$ 0.079
R. raphanistrum	0.35 $\pm$ 0.083	0.07 $\pm$ 0.065	0.07 $\pm$ 0.070	0.04 $\pm$ 0.025	0.47 $\pm$ 0.189
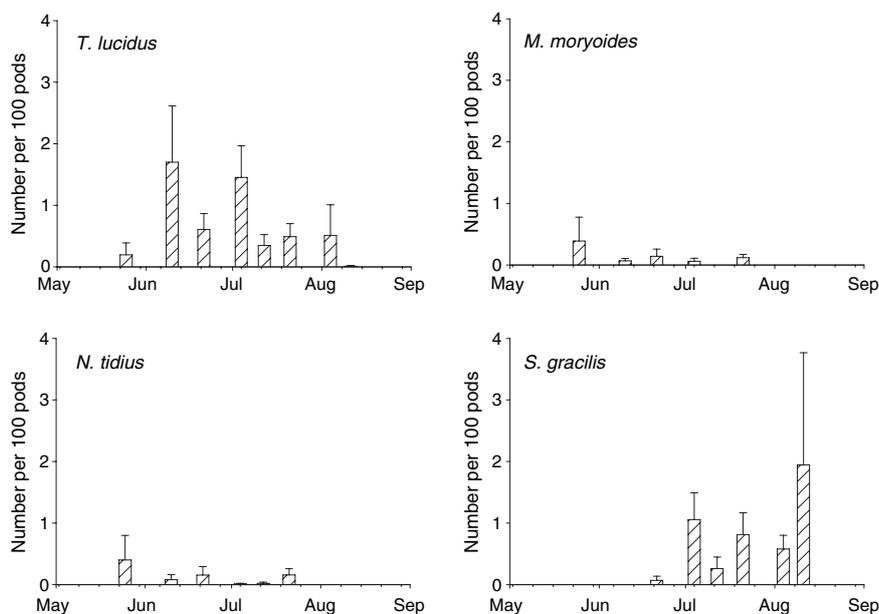
Fig. 3. *Mean number $\pm$ SE (n = 8) of* Trichomalus lucidus, Mesopolobus moryoides, Necremnus tidius *and* Stenomalina gracilis *emerging from collected cabbage seed pods at eight sites in the Fraser Valley of British Columbia*

P = 0.0031). There was a larger proportion of *S. gracilis* in the parasitoid complex on *R. raphanistrum* than on the *Brassica* spp. and a larger proportion of *T. lucidus* in the parasitoid complex on *Brassica* spp. than on *R. raphanistrum*.

There was some evidence that the times at which the parasitoids attacked hosts varied among species. *Trichomalus lucidus* emerged from seedpods collected in June, and numbers declined through July and August, whereas *S. gracilis* were most abundant in seedpods collected in July and August but were absent from pods collected in June (fig. 3). Abundance of *M. moryoides*, *N. tidius* and *E. vesicularis* was too low for phenological trends to be evident, although *M. moryoides* and *N. tidius* tended to be present earlier in the season, at the same time as *T. lucidus* (fig. 3).

4 Discussion

The survey results confirm the presence of *S. gracilis* in British Columbia, and demonstrate that the 1949 releases of *T. perfectus* and *M. morys* did not establish parasitoid populations in the Fraser Valley of British Columbia. Therefore, if warranted, introductions of *T. perfectus* and/or *M. morys* would have to originate from European populations. Release data indicate that 1063 and 208 individuals of *M. morys* and 108 and 90 individuals of *T. perfectus* were released at Dewdney and Sardis, respectively, whereas 183 individuals of *S. gracilis* were released at Sardis (Biological Control Investigations Unit 1949; McLeod 1951; Gibson et al. 2006a). The very low numbers (< 200) of *T. perfectus* liberated may explain the failure of this species to establish, perhaps due to an Allee effect (see Hopper

and Roush 1993). McLeod (1951, 1962) concludes that *S. gracilis* was established in North America prior to his 1949 liberations; however, subsequent analysis (Gibson et al. 2006a) demonstrates this conclusion to be untrue. It seems probable that this species established from the relatively small numbers liberated. In contrast, reasonably large numbers of *M. morys* were released (McLeod 1953), and did not establish. These results emphasize the importance of biological studies of parasitoid species in the area of origin prior to release, to determine seasonal timing, alternative host requirements and other essential details of natural history.

Five parasitoid species were conclusively associated with *C. obstrictus* (table 2). Overall, parasitism was between 2% and 4% based on pod dissections (fig. 2b). The five most abundant species, *T. lucidus*, *M. moryoides*, *N. tidius*, *E. vesicularis* and *S. gracilis*, are known parasitoids of *Ceutorhynchus* spp. and constituted 97% of the parasitoid complex. *Trichomalus lucidus*, the most abundant species (49%), has a Holarctic distribution, though it is uncertain whether this is natural or whether the species was accidentally introduced into North America (Gibson et al. 2005). In Europe, *T. lucidus* has been recorded as a parasitoid of *Ceutorhynchus pallidactylus* (Marsham) (Ulber 2003). The next most abundant species, *S. gracilis* (29%), has a Palaearctic distribution. This species was found to also be present in British Columbia, probably due to the establishment of a European population released there in 1949 (Gibson et al. 2006a). In Europe, *S. gracilis* is a minor component of the *C. obstrictus* parasitoid complex (Murchie 1996, cited in Williams 2003) but it can be abundant on other *Ceutorhynchus* spp. (Muller et al. 2004). *Necremnus tidius* (9%) occurs in both Europe and North America, but *M. moryoides* (12%) is known only from North America (Gibson et al. 2005). *Eupelmus vesicularis* (2%) has been recorded from a taxonomically diverse group of hosts in Europe and North America as either a primary or hyperparasitoid (Floate et al. 2000; Ellis 2002; Noyes 2002; Hayman et al. 2003; Bullock et al. 2004). It was previously reared from *C. obstrictus* in North America (Hanson et al. 1948; McLeod 1953) and Europe (Dmoch 1975), but it is unknown if those rearings or ours were as a primary parasitoid of *C. obstrictus* or as a hyperparasitoid through one of the other reared parasitoids.

It is significant that, more than 70 years after *C. obstrictus* was first reported in British Columbia, very few native North American parasitoids have utilized it as a host. In other areas, several native species have been found on *C. obstrictus* but none has become a factor limiting *C. obstrictus* populations (Gibson et al. 2005, 2006b). This lack of adaptation of native parasitoids has positive implications for the integrity of weed biological control programmes using exotic ceutorhynchine weevils, in that native parasitoids may be unlikely to impede the effectiveness of the weevil biological control agents.

Because *S. gracilis* has established successfully in British Columbia, there are no legal restrictions to prevent it from being redistributed to other provinces in Canada for biological control of *C. obstrictus*. However, in spite of the extensive economic damage now being caused to western Canadian canola crops by the weevil, release of *S. gracilis* is not recommended at this time. In Europe, *S. gracilis* is a minor component of the parasitoid fauna of *C. obstrictus*, with *T. perfectus* and *M. morys* responsible for much higher levels of weevil parasitism (Williams 2003; Muller et al. 2004). In addition, *S. gracilis* is a significant parasitoid of *Microplontus edentulus* in Europe, sometimes causing parasitism levels as high as 67% (Muller et al. 2004). *Microplontus edentulus* has been released in western Canada for biological control of the weed, scentless chamomile (*Matricaria perforata* Merat) (McClay et al. 2002b), and *S. gracilis* could negatively impact its effectiveness. Furthermore, Dosdall et al. (2006) have found that in southern Alberta, endemic parasitoid populations attacking *C. obstrictus*, primarily *T. lucidus*, *N. tidius* and *Chlorocytus* sp., increased approximately 50-fold from 2002 to 2004. Levels of parasitism in southern Alberta increased further in 2005 (L. M. Dosdall, unpublished data), and the possibility of competitive interference by *S. gracilis* with these native parasitoid species must be investigated before deliberate redistribution of *S. gracilis* outside British Columbia.

The proportion of *S. gracilis* in the parasitoid community was lower on *Brassica* spp. host plants than on *R. raphanistrum* host plants (table 4). This could be due to differences in timing of pod formation in the two plants, or to other, as yet unknown, plant traits. *Raphanus raphanistrum* is an annual or winter annual that is very abundant in cultivated fields in the Fraser Valley (Mulligan 2002). It has an indeterminate growth habit and the sequentially emerging flowers result in a long, continuous fruiting period (Warwick and Francis 2005). Thus, pods are available for colonization by *C. obstrictus* and parasitoids for an extended period. In contrast, flowering and fruiting of weedy *B. napus* and *B. rapa* populations may be more compressed because domestic varieties tend to be bred for synchronization of seed production. Thus, these plant species would be available for colonization by *C. obstrictus* and parasitoids for a shorter period. Associations of parasitoids of *C.obstrictus* with host plants should be a component of future study, to help clarify this issue.

The earlier description of the classical biological control attempt against cabbage seedpod weevil in 1949 as a 'partial success' by McLeod (1962) appears to be inaccurate in the light of results from this survey because the two species most responsible for biological control in Europe failed to establish themselves. The reasons for this failure are not evident from our study, and future investigations should address this question.

The high infestation rates of pods (fig. 2) demonstrate that *C. obstrictus* remains a significant pest in the Fraser Valley of British Columbia. Based on dissections, more than 50% of *B. rapa*, *B. napus* and *R. raphanistrum* seedpods were occupied by *C. obstrictus* larvae. Although neither cabbage seed nor canola production are significant industries in the Fraser Valley, the abundance of *C. obstrictus* would be a serious constraint to production. Elsewhere in North

America, infestations in canola are causing significant economic losses, and endemic parasitoid populations are not controlling populations below an economic injury threshold (Cárcamo et al. 2001). In Europe, the impact of *M. melanopus*, an endoparasitoid of adults, and the larval ectoparasitoids *T. perfectus* and *M. morys* on *C. obstrictus* populations has been documented in several studies (e.g. Crowell 1952; Bonnemaison 1957; Jourdheuil 1960; Laborius 1972; Lerin 1987; Büchi 1991, 1993; Murchie 1996; Williams 2003). The most important parasitoid is *T. perfectus* and estimates of its levels of parasitism in Europe range from 10% to 44% (Laborius 1972), 20% to 40% (Crowell 1952), 38% to 80% (Büchi 1991), and up to 95% (Lerin 1987). Therefore, despite the presence of an established parasitoid complex in North America, biological control of *C. obstrictus* with the introduction of one or both of *T. perfectus* and *T. morys* should be pursued as part of comprehensive integrated pest management strategy, after consideration of host ranges of these species.

Several Ceutorhynchinae species, including *Mogulones crucifer* (Pallas) [*Mogulones cruciger* (Herbst)], *Hadroplontus litura* (Fabricius), and *Microplontus edentulus* (Schultze), have been released for biological control of weeds in British Columbia and other locations in North America (De Clerck-Floate and Schwarzlaender 2002; McClay et al. 2002a,b). Introduction of parasitoids, or their redistribution to control the cabbage seedpod weevil in oilseed crops in North America, must consider potential conflicts with related weevil species that have been introduced for weed biological control (Kuhlmann et al. 2006). Populations of weed biological control agents could be negatively affected if agents released for biological control of *C. obstrictus* are not specific to the target host. Consequently, knowledge of host plant–weevil–parasitoid associations is necessary.

In summary, we examined the outcomes of a classical biological control introduction against *C. obstrictus*. We showed that, contrary to previous reports (McLeod 1962), of the three European parasitoid species that were introduced into British Columbia, only *S. gracilis* appears to have established. More than 50 years after release of parasitoids and 70 years since introduction of the weevil, parasitism rates are low, and the diversity of the complex is restricted to a few native and Holarctic species. This assessment of parasitoid status, supported by sound systematic knowledge of the agents, helped to clarify our understanding of the apparent failure of the classical biological control releases of parasitoids against the cabbage seedpod weevil. This work is integral to a comprehensive retrospective analysis of the biological control of cabbage seedpod weevil in North America.

Acknowledgements

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Author's address: D.R. Gillespie, Agriculture and Agri-Food Canada, Research Centre, P.O. Box 1000, Agassiz, Canada. V0M 1A0. E-mail: gillespied@agr.gc.ca