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DISTRIBUTION OF *COTESIA RUBECULA* (HYMENOPTERA: BRACONIDAE) AND ITS DISPLACEMENT OF *COTESIA GLOMERATA* IN EASTERN NORTH AMERICA

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Abstract

A survey was conducted from May to Oct of 2011 of the parasitoid community of the imported cabbageworm, *Pieris rapae* (Lepidoptera: Pieridae), in cole crops in part of the eastern United States and southeastern Canada. The findings of our survey indicate that *Cotesia rubecula* (Hymenoptera: Braconidae) now occurs as far west as North Dakota and has become the dominant parasitoid of *P. rapae* in the northeastern and north central United States and adjacent parts of southeastern Canada, where it has displaced the previously common parasitoid *Cotesia glomerata* (Hymenoptera: Braconidae). *Cotesia glomerata* remains the dominant parasitoid in the mid-Atlantic states, from Virginia to North Carolina and westward to southern Illinois, below latitude N 38° 48'. This pattern suggests that the released populations of *C. rubecula* presently have a lower latitudinal limit south of which they are not adapted.

Key Words: imported cabbageworm, *Cotesia glomerata*, parasitoid displacement, latitudinal adaptation

Resumen

Se realizó un sondeo de la comunidad de parasitoides del gusano importado del repollo, *Pieris rapae* (Lepidoptera: Pieridae), en los cultivos de crucíferas en una parte del este de los Estados Unidos y del sureste de Canadá desde mayo hasta octubre del 2011. Se encontró que *Cotesia rubecula* (Hymenoptera: Braconidae), ahora se ha extendido hasta el oeste de Dakota del Norte y se ha convertido en el parasitoide dominante de *P. rapae* en el noreste y el norte central de los Estados Unidos y en los partes adyacentes del sureste de Canadá, donde ha desplazado al parasitoide anteriormente común, *Cotesia glomerata* (Hymenoptera: Braconidae). *Cotesia glomerata* sigue siendo el parasitoide dominante en los estados del Atlántico medio, desde Virginia hasta Carolina del Norte y hacia el oeste hasta el sur de Illinois, bajo la latitud N 38° 48'. Nosotros interpretamos este patrón que indica que las poblaciones liberadas de *C. rubecula* en la actualidad tiene un límite inferior de latitud mas al sur del que están adaptados.

The parasitoid *Cotesia glomerata* (L.) (Hymenoptera: Braconidae) was introduced to the United States as a biological control agent against the invasive vegetable pest *Pieris rapae* (L.) (Lepidoptera: Pieridae) in 1884 near Washington, District of Columbia (Clausen 1978). *Cotesia glomerata* is a gregarious endoparasitoid of several species of pierid butterflies. Although *C. glomerata* established, it was unable to reduce damage from *P. rapae* larval feeding to a level acceptable to vegetable growers. *Cotesia glomerata* kills *P. rapae* larvae at the end of the fifth instar, after most larval feeding has occurred. In fact, larvae parasitized by *C. glomerata* consume significantly more food during their development than unparasitized ones (Rahman 1970). Thus *C. glomerata* pest control benefit is limited to intergenerational reduction in *P. rapae* density, which has not been sufficient to reduce *P. rapae* to non-pest status in the United States. Also, *Cotesia glomerata* is not host specific, and has non-target impacts on native pierid butterflies, including *Pieris oleracea* Harris (formerly *Pieris napi oleracea*) (Benson et al. 2003).

Cotesia rubecula (Marshall) (Hymenoptera: Braconidae) is a solitary host specific endoparasitoid of *P. rapae* that attacks first and second instars. *Cotesia rubecula* not only attacks *P. rapae* at a high rate (e.g., Van Driesche 2008), but also reduces feeding damage on a per larva basis (Le Masurier & Waage 1993). *Cotesia rubecula* is successful at reducing feeding damage because it kills *P. rapae* in the fourth instar, before most larval feeding occurs. Also, because *C. rubecula* is host specific, it rarely attacks native pierids in the field (Van Driesche et al. 2004).

There have been several introductions of *C. rubecula* into North America since the 1960s. A population of *C. rubecula* that was not deliberately introduced was detected on Vancouver Island, British Columbia in 1963 (Wilkinson 1966). By the 1980s, this strain had spread as far south as Oregon and displaced *C. glomerata* there, but did not do so below latitude 44°35' (Biever 1992). The Vancouver strain of *C. rubecula* was later released in Ontario, Missouri, New Jersey, and South Carolina in the 1960s (Puttler et al. 1970; Williamson 1971, 1972). The Vancouver strain of *C. rubecula* established in Ontario (Corrigan 1982), but failed to establish in more southern areas, including Missouri (Parker & Pinnell 1972).

It was suggested that this strain failed to establish more southern areas because its diapause requirements were not met (Nealis 1985). To overcome this problem, a strain of *C. rubecula* from the former Yugoslavia was introduced in the 1980s to Ontario, Missouri, and Virginia (McDonald & Kok 1992). In 1988, the Yugoslavian strain of *C. rubecula* was recovered in Virginia, but it did not persist. This may have been due either to its diapause requirements not being met or the negative effects of hyperparasitism (McDonald & Kok 1992; Gaines & Kok 1999). In a third attempt to find a climatically adapted population, *C. rubecula* was collected in Shenyang, China, in 1988,and this strain was released in 17 locations in southern New England (Van Driesche & Nunn 2002), where it established and spread. In the early 1990's, individuals from both the former Yugoslavian and Chinese populations were released in Minnesota and *C. rubecula* recoveries were made beginning in 2000 (Wold-Burkness et al. 2005; Lee & Heimpel 2005).

Before the release of *C. rubecula* in New England, the dominant parasitoid of *P. rapae* was *C. glomerata* (Van Driesche & Bellows 1988). By 2002, *C. rubecula* was widely distributed in southern New England, and had become the dominant parasitoid of *P. rapae* (Van Driesche & Nunn 2002). In western Massachusetts, Ontario, and the western United States *C. rubecula* has outcompeted and displaced *C. glomerata* (Corrigan 1982; Biever 1992; Van Driesche 2008).

The purpose of this study was to assess the current geographical distribution of *C. rubecula* and *C. glomerata* in the northeastern and north central parts of the United States and adjacent parts of Canada in order to determine if *C. rubecula* has displaced *C. glomerata* at this scale as it has done locally in New England. We hypothesized there would be a southern limit to the spread of *C. rubecula* due to an incompatibility between local seasonal day length patterns and diapause cue sensitivity of the parasitoid, as suggested by Nealis (1985). We also hypothesized that *C. rubecula* would displace *C. glomerata* over some larger spatial scale given that it has done so in New England, Ontario, Washington, and Oregon (Corrigan 1982; Biever 1992; Van Driesche 2008).

Materials and Methods

Samples of *P. rapae* and *Cotesia* parasitoids were collected from May to late Sep 2011 in 14 states and 2 Canadian provinces, from New England to North Dakota, southward to North Carolina and northward to New Brunswick and Quebec. Samples were collected from various types of cole crops at organic vegetable farms or private gardens. All *P. rapae* larvae from first to fifth instars, as well as pupae, and cocoons of both species of *Cotesia* parasitoids (emerged or not) were collected. Collectors were provided with pictures and descriptions of these life stages. Up to 1 h was spent examining crop plants, collecting all of the above life stages until 30 or more "individuals" (one *C. glomerata* cocoon mass was considered one individual, as it came from one host larva) had been collected. Actual sample numbers per site ranged from 5-103 individuals, depending on local *P. rapae* density. First and second instar *P. rapae* larvae may be underrepresented in the survey samples due to their small size. Insects in samples were counted by species and life stage, and all *P. rapae* larvae were dissected to determine the level of parasitism by each parasitoid species. The only parasitoids observed in dissection were *C. glomerata* and *C. rubecula*. All dissections were done by the senior author. The immature stages, including eggs, of these 2 species can be readily separated in dissection by several characteristics. Visible mandibles and an anal hook are present in first instars of *C. rubecula*, but not in those of *C. glomerata* (Van Driesche 2008). Also, the number of parasitoid larvae per host is diagnostic (*C. rubecula* is solitary; *C. glomerata* is gregarious). No parasitoid eggs were seen in this survey although they can be distinguished by size, shape, and number (Van Driesche & Nunn 2002).

In total, 32 samples of *P. rapae* larvae or pupae and parasitoid cocoons were examined, comprising 1571 individuals. Sample percent parasitism

Table 1. Rates of parasitism in 2011 by *Cotesia* wasps (Hymentoptera: Braconidae) of *Pieris rapae* from organic vegetable farms in the Eastern United States and Canada.

			% parasitized, 95% CI, (n)		
State/Province[2]	Date	Coordinates	*C. rubecula*	*C. glomerata*	Crop[1]
Newark, DE	15 Jun	N 39° 41'; W 75° 44'	70.7 ± 0.14 (41)	19.5 ± 0.12 (41)	B, Cau.
Champaign, IL	15 Jun	N 40° 4.5'; W 88° 12'	0.9 ± 0.02 (103)	5.8 ± 0.05 (103)	C, Cau., K
Lexington, KY	20 Jul	N 38°7'; W 84° 30'	0 ± 0 (65)	5 ± 0.05(65)	Ko
Midway, KY	7 Sept	N 38° 11'; W 84° 42'	0 ± 0 (32)	0 ± 0 (32)	C
Westhampton, MA	12 Aug	N 42° 57'; W 72° 46'	41 ± 0.15 (41)	0 ± 0 (41)	C
Northampton, MA	24 Aug	N 42° 19'; W 72° 38'	53 ± 0.16 (38)	0 ± 0 (38)	B, C, K
Ashfield, MA	18 Aug	N 42° 18'; W 72° 45'	5.9 ± 0.11 (17)	0 ± 0 (17)	Misc.
Westhampton, MA	19 Aug	N 42° 31'; W 72° 47'	0 ± 0 (31)	0 ± 0 (31)	Misc.
Upper Marlboro, MD	8 Jun	N 38° 49'; W 76° 45'	0 ± 0 (67)	52 ± 0.12 (67)	K
East Lansing, MI	13 Jul	N 42° 42'; W 84° 29'	70.6 ± 0.13 (51)	0 ± 0 (51)	C
East Lansing, MI	13 Jul	N 42° 42'; W 84° 29'	13.6 ± 0.07 (103)	0.9 ± 0.02 (103)	C
St. Paul, MN	11 Jul	N 44° 56'; W 93° 5'	14 ± 0.10 (50)	0 ± 0 (50)	B, C, K,
St. Paul, MN	31 Aug	N 44° 56'; W 93° 5'	60 ± 0.30 (10)	0 ± 0 (10)	B, C
Northampton, NB	27 Jun	N 46° 3'; W 67° 33'	88.9 ± 0.21 (9)	0 ± 0 (9)	B
Pittsboro, NC	2 Jun	N 35° 42'; W 79° 17'	0 ± 0 (36)	19.4 ± 0.13 (36)	C, Co, K
Chapel Hill, NC	2 Jun	N 35° 51'; W 79° 12'	0 ± 0(29)	10.3 ± 0.11 (29)	C, Co, K
Harwood, ND	14 Sept	N 47° 25'; W 96° 50'	8.6 ± 0.07 (70)	0 ± 0 (70)	B, C
Geneva, NY	10 Aug	N 42° 52'; W 77° 50'	0 ± 0 (103)	0 ± 0 (103)	C
Fairville, NY	29 Sept	N 43° 7'; W 77° 4'	13 ± 0.09 (55)	0 ± 0 (55)	Cau.
Fairville, NY	29 Sept	N 43° 7'; W 77° 4'	44 ± 0.12 (71)	0 ± 0 (71)	Misc.
Terre Hill, PA	20 May	N 40° 9'; W 76° 3'	4.1 ± (97)	0 ± 0 (97)	Misc.
Hustontown, PA	31 Aug	N 40° 2'; W 78° 1'	0 ± 0 (44)	2.3 ± 0.04 (44)	Br
Montreal, QC	14 Sept	N 45° 30'; W 73° 36'	59 ± (66)	0 ± 0 (66)	Misc.
Charlestown, RI	2 Aug	N 41° 21'; W 71° 42'	60 ± 0.18 (30)	3 ± 0.04 (30)	Co, K
South Kingston, RI	2 Aug	N 41° 28'; W 71° 31'	41.9 ± 0 (31)	0 ± 0 (31)	C, Co
Birdsnest, VA	15 May	N 37° 25'; W 75° 51'	0 ± 0 (32)	3.1 ± 0.06 (32)	C, Co
Birdsnest, VA	30 May	N 37° 13'; W 75° 59'	0 ± 0 (40)	42.5 ± 0.15 (40)	C, Co
Blacksburg, VA	15 Jun	N 37° 13'; W 80° 24'	0 ± 0 (51)	62.7 ± 0.13 (51)	CC, K, RC
So. Burlington, VT	2 Aug	N 44° 38'; W 72° 52'	100 ± 0 (18)	0 ± 0 (18)	C, K
Burlington, VT	2 Aug	N 44° 26'; W 73° 9'	100 ± 0 (5)	0 ± 0 (5)	C, K
Cambridge, VT	8 Aug	N 44° 28'; W 73° 13'	100 ± 0 (41)	0 ± 0 (41)	C, Co.
Madison, WI	3 Aug	N 43° 4'; W 89° 24'	5.3 ± 0.05 (94)	0 ± (94)	Misc.
Total			20.6 ± 0.02 (1571)	7.3 ± 0.01 (1571)	

[1]Crop key. B-broccoli, Br-brussel sprouts, C-cabbage, CC-Chinese cabbage, Cau-cauliflower, Co-collards, K- kale, Ko- kohlrabi. RC-red cabbage, Misc.-miscellaneous cole crops.

[2]State/Province abbreviations key. DE-Delaware, IL-Illinois, KY-Kentucky, MA-Massachusetts, MD-Maryland, MI-Michigan, MN-Minnesota, NB-New Brunswick, NC-North Carolina, ND-North Dakota, NY-New York, PA-Pennsylvania, QC- Québec, RI-Rhode Island, VA-Virginia, VT-Vermont, WI-Wisconsin.

rates for each species were calculated at each location and mapped to look for geographical patterns. Average parasitism rates per species across all sites with any parasitism were also calculated. The percentages were arcsine transformed to better meet the assumption of normality, and then compared with a t test. Hyperparasitism was not examined in this study.

Results

Summed across all 32 samples collected in the survey, 1571 individuals, were obtained and examined (Table 1). From that pool of samples, the only parasitoids recovered were *C. rubecula* and *C. glomerata*. *Cotesia rubecula* was present at 22 of the 32 sample sites (Table 1) and parasitized 20.6 ± 0.02% (95% CI) of the 1571 individuals examined. *Cotesia glomerata* was present at 12 sites and parasitized 7.3 ± 0.01% (95%CI) of the 1571 individuals. When parasitism was calculated based only on sites where a given parasitoid actually occurred, we found an average parasitism rate of 47 ± 0.03 % (95% CI, n = 1041) for *C. rubecula* and 25 ± 0.03 % (95% CI, n = 641) for *C. glomerata* (t-value: 2.748, df: 31, P = 0.0049).

Spatially, *C. rubecula* and *C. glomerata* were largely exclusive in the distribution of their recoveries (Fig. 1). Only at 4 out of the 32 sites sampled was parasitism by both *C. rubecula* and *C. glomerata* detected. These 3 of these 4 sites (exclusive of the Charlestown, Rhode Island site) ere on the border of what appears to be a latitudinal point of separation of the regions that each parasitoid now occupies. *Cotesia rubecula* recoveries were highly concentrated in the north, while *C. glomerata* was dominant farther south. *Cotesia rubecula* was not found below latitude N 38° 48', and is the only parasitoid found in our samples above latitude N 40° 2'. Within the area surveyed, no westward limit was detected for the distribution of *C. rubecula* (i.e., it was present in the most western of our sample locations [North Dakota]).

Discussion

The *Cotesia* spp. distribution patterns observed in our survey (Fig. 1) are not explained by

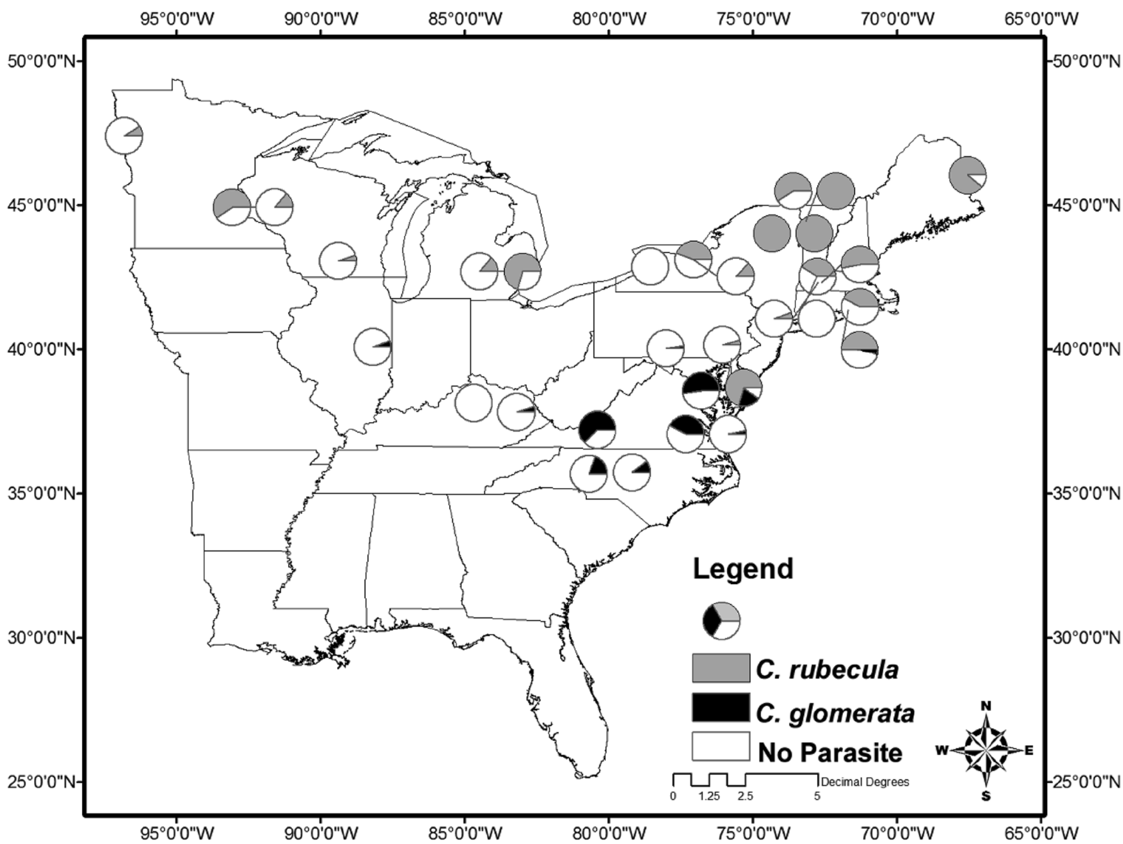

Fig. 1. Observed pattern of *Cotesia* parasitism of *Pieris rapae* in parts of the eastern United States and southeastern Canada in 2011. Parasitism by *Cotesia rubecula* is shown in gray and *Cotesia glomerata* in black. The percentage of unparasitized larvae is shown in white.

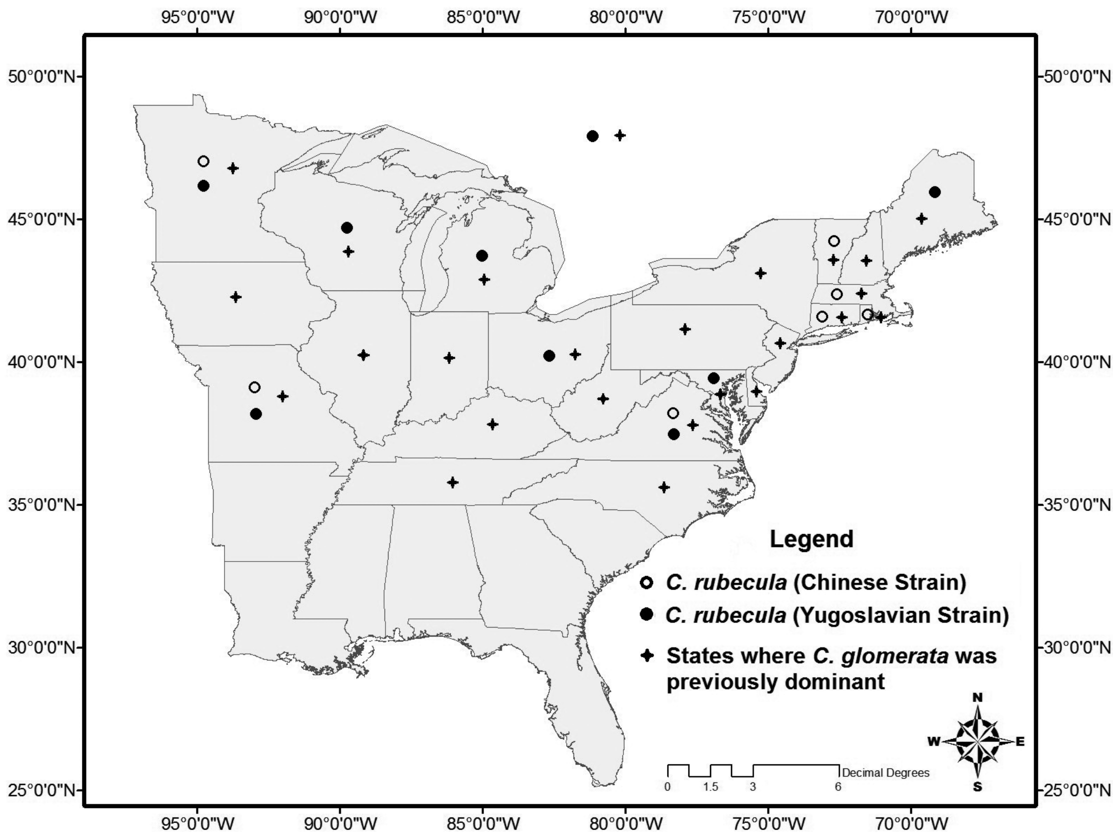

Fig. 2. USA States and Canadian Provinces where the *Pieris rapae* parasitoid, *Cotesia glomerata*, was previously (pre-1990) dominant (crosses), and where releases of the Chinese strain of *Cotesia rubecula* (open circles) or the Yugoslavian strain (black circles) were made.

the history of these species. *Cotesia glomerata*, now largely absent in the northern portion of our survey area, was once widely present there (Fig. 2) and likely still occurs there at very low levels (e.g., in Massachusetts, Van Driesche 2008). Similarly, the absence of *C. rubecula* in the southern portion of our survey area is not due to failure to release the parasitoid there, since releases were made in both Virginia and Missouri (Fig. 2). The absence of *C. rubecula* in the southern portion of our survey area is consistent with previous studies on the diapause needs of this species (Nealis 1985). Diapause in *C. rubecula* is induced by short day length. Cool temperatures during diapause are believed to preserve the insect's fat supply and coordinate post-diapause development (Nealis 1985). Nealis (1985) further suggested that the mechanism for poor establishment of some populations of *C. rubecula* in southern locations was the premature induction of diapause, caused by short daylength, before seasonal temperatures had declined. Temperatures above 15 °C on average have been hypothesized to be lethal to diapausing prepupae of *C. rubecula* (Nealis 1985). Another potential explanation for the failure of *C. rubecula* to establish in some areas of the United States is the effect on *C. rubecula* densities of high rates of mortality to its immature stages due to hyperparasitism, as observed in Virginia (McDonald & Kok 1992; Gaines & Kok 1998); however, there is no evidence in the literature that hyperparasitism rates in southern states are higher than in other areas. We did not examine hyperoparasitism rates in our survey.

The absence of *C. glomerata* in samples from the northern portion of our survey area, where it was formerly widespread, is likely related to competitive displacement by *C. rubecula*. The phenomenon of parasitoid displacement has been well documented in other systems (e.g., DeBach & Sundby 1963; Le Brun et al. 2009). Our study suggests that such displacement of *C. glomerata* by *C. rubecula* has occurred at this larger spatial scale, as was previously observed for these species at the state/province level in Massachusetts (Van Driesche 2008), Quebec (Godin & Boivin 1998), and Oregon and Washington (Biever 1992). *Cotesia rubecula* is now widespread in the northeastern and north central United States and parts of southeastern Canada. The lack of such displacement in Europe, where both *Cotesia* species coexist, is likely due to the presence of the specific host of *C. glomerata*, *Pieris brassicae* L. and which is not attacked by *C. rubecula*.

The increase in prevalence and dominance of *C. rubecula* provides benefits both by increasing the level of control of the imported cabbageworm (*P. rapae*) and lessening the damage to non-target native pierids from *C. glomerata*. The displacement of *C. glomerata* in the northern United States by the more host-specific *C. rubecula* should allow some native pierids such as *P. oleracea* (Benson et al. 2003; Van Driesche et al. 2004) and *Pontia protodice* Boisduval and Leconte (Dave Wagner, University of Connecticut, pers. comm.), whose ranges collapsed in some regions due to attack by *C. glomerata*, to recolonize areas from which they were extirpated, providing a benefit to protection of native biodiversity.

Also vegetable producers will benefit from this change in parasitoid species. *Cotesia rubecula*, which is now the dominant parasitoid of *P. rapae* in the northern part of our survey area, causes high levels of mortality to *P. rapae* (47 ± 0.03%). and kills individual larvae before most of their feeding occurs. Although we cannot say with certainty which strain of *C. rubecula* is now found at particular sites, the introduction of *C. rubecula* in North America appears to be at least a partially successful biological control program that has met its objectives.

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