

AN ABSTRACT OF THE THESIS OF

Glenn R. Kohler for the degree of Master of Science in Forest Science presented on March 19, 2007.

Title: Predators Associated with Hemlock Woolly Adelgid (Hemiptera: Adelgidae) Infested Western Hemlock in the Pacific Northwest.

Abstract approved:

Darrell W. Ross

The hemlock woolly adelgid, *Adelges tsugae*, is causing widespread mortality of eastern hemlock, *Tsuga canadensis*, in the eastern United States. In the West, *A. tsugae* causes negligible damage to western hemlock, *Tsuga heterophylla*. Host tolerance traits and presence of endemic predators may be contributing to the relative tolerance of western hemlock to *A. tsugae*. Field surveys of the predator community associated with *A. tsugae* infestations on 116 *T. heterophylla* at 16 locations in Oregon and Washington were conducted every four to six weeks from March 2005 through November 2006. Predators collected from *A. tsugae* infested *T. heterophylla* represent 55 species in 14 families, listed in order of abundance: Derodontidae, Chamaemyiidae, Hemerobiidae, Coccinellidae, Cantharidae, Reduviidae, Miridae, Syrphidae, Chrysopidae, Coniopterygidae, Staphylinidae, Anthocoridae, Nabidae, and Raphidiidae. *Laricobius nigrinus* (Derodontidae), *Leucopis argenticollis*, and *Leucopis atrifacies* (Chamaemyiidae) are the most abundant predators; together

comprising 59% of predator specimens recovered. The abundance of derodontid larvae, *L. nigrinus* adults, chamaemyiid larvae, and *L. argenticollis* adults was found to be positively correlated to *A. tsugae* density. The remaining 52 species represent a diverse complex of predators potentially attacking *A. tsugae*. However, many are known to feed on non-adelgid prey. Predators were most abundant when the two generations of *A. tsugae* eggs were present. The phenology of immature and adult predators suggests temporal partitioning of prey across all seasons. Fifteen predator species were either reared from larvae to adult on a diet of *A. tsugae* in the laboratory or were observed feeding on *A. tsugae*. *L. argenticollis* and *L. atrifacies* were reared on *A. tsugae* in the laboratory and host records show them to feed exclusively on Adelgidae. Both species should be investigated as candidates for *A. tsugae* biological control in eastern North America.

©Copyright by Glenn R. Kohler
March 19, 2007
All Rights Reserved

Predators Associated with Hemlock Woolly Adelgid (Hemiptera: Adelgidae) Infested
Western Hemlock in the Pacific Northwest.

by
Glenn R. Kohler

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Presented March 19, 2007
Commencement June 2007

Master of Science thesis of Glenn R. Kohler presented on March 19, 2007.

APPROVED:

Major Professor, representing Forest Science

Head of the Department of Forest Science

Dean of the Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Glenn R. Kohler, Author

ACKNOWLEDGEMENTS

This research was funded in part by the USDA Forest Service, Forest Health Technology Enterprise Team (FHTET), Morgantown, WV.

My committee members Peter B. McEvoy, Darrell W. Ross, and Kimberly F. Wallin provided essential direction and feedback for this project. The late Vernon Stiefel provided untiring assistance in identifying specimens and processing thousands of samples. I also have Dr. Stiefel to thank for a large part of my taxonomic education. I would also like to thank Chris Marshall, Sujaya Rao, and the staff and supporters of the Oregon State Arthropod Collection.

For their cooperation in establishing and maintaining field sites, I thank Dan Cress, Jim Hargrove, Jessica Joseph, Joyce Mobley, Dan Moeller, Dave Overhulser, Rick Quam, Karen Ripley, Arlene Roux, Bill Schlatter, Stewart Smith, Thurston Title Company, Kathy van Pelp, Don Wallace, Bob Wells, RJ Wentworth, Beth Willhite, and Don Wright.

I would like to thank the following taxonomists for identifying insect specimens: Brian Brown, Matt Buffington, Don Chandler, Raymond Gagne, Steve Gaimari, Steven Heydon, Steve Krauth, Paris Lambdin, John Lattin, John Luhman, Alfred Newton, Joseph McHugh, Norm Penny, Alistair Ramsdale, Roy Snelling, Catherine Tauber, Margaret Thayer, Christian Thompson, Natalia Vandenberg, Robert Wharton, Terry Wheeler, Matt Yoder, and Dan Young.

Lisa Ganio and Bruce McCune provided invaluable statistical and community structure analysis expertise.

ACKNOWLEDGEMENTS (Continued).

And finally, special thanks to my supportive wife, Libi Sundermann, and our son, Hayes Kohler, for keeping me smiling through it all.

TABLE OF CONTENTS

	<u>Page</u>
Chapter 1: Introduction and Literature Review	1
<i>Adelges tsugae</i> in North America	2
Biology of <i>A. tsugae</i>	4
Effects of <i>A. tsugae</i> on host trees	7
<i>A. tsugae</i> impact to eastern hemlock ecosystems.....	9
Integrated <i>A. tsugae</i> management alternatives.....	10
Use of predators for adelgid biological control.....	13
Predators of the Adelgidae	14
Current progress of <i>A. tsugae</i> biological control efforts in the eastern United States	24
Balsam woolly adelgid biological control	33
<i>Pineus</i> spp. biological control	35
Conclusion and research objectives	35
Chapter 2: Predators Associated with Hemlock Woolly Adelgid (Hemiptera: Adelgidae) Infested Western Hemlock in the Pacific Northwest.	37
Introduction	40
Materials and Methods.....	45
Results	53
Discussion	75
References Cited	83
Chapter 3: Conclusion.....	89

TABLE OF CONTENTS (Continued).

	<u>Page</u>
Bibliography.....	94
APPENDICES	107
Appendix A. Pacific Northwest locations not included in the survey where hemlock woolly adelgid infestations were observed during 2005 through 2006.	108
Appendix B. Abundance of adult predatory species identified from <i>Adelges tsugae</i> infested <i>Tsuga heterophylla</i> in the Pacific Northwest, January 2005 through November 2006.	109
Appendix C. Abundance of predatory species identified from infestations of <i>Adelges piceae</i> and <i>Adelges cooleyi</i> in the Pacific Northwest, June 2005 through October 2006.	114
Appendix D. Adult Hymenoptera identified from <i>Tsuga heterophylla</i> beat samples in the Pacific Northwest, January 2005 through November 2006.	116

LIST OF FIGURES

<u>Figure</u>	<u>Page</u>
1. Abundance of predatory Hemiptera (A) and Neuroptera (B) sampled from <i>A. tsugae</i> infested western hemlock in the Salem area of northwest Oregon over one year beginning fall 2005.....	60
2. Abundance of predatory Hemiptera (A) and Neuroptera (B) sampled from <i>A. tsugae</i> infested western hemlock in the Portland area of northwest Oregon over one year beginning fall 2005.....	61
3. Abundance of predatory Hemiptera (A) and Neuroptera (B) sampled from <i>A. tsugae</i> infested western hemlock in western Washington over one year beginning fall 2005.	62
4. Abundance of predatory Coleoptera (A) and Diptera (B) sampled from <i>A. tsugae</i> infested western hemlock in the Salem area of northwest Oregon over one year beginning fall 2005.....	63
5. Abundance of predatory Coleoptera (A) and Diptera (B) sampled from <i>A. tsugae</i> infested western hemlock in the Portland area of northwest Oregon over one year beginning fall 2005.....	64
6. Abundance of predatory Coleoptera (A) and Diptera (B) sampled from <i>A. tsugae</i> infested western hemlock in western Washington over one year beginning fall 2005.	65
7. Three dimensional nonmetric multidimensional scaling (NMS) ordination joint plot of sample units in species space with ordination rotated to load variance of hemlock woolly adelgid (HWA) population score on axis 2 (r^2 -value = 0.77).....	71
8. Response curves for six two-dimensional models of abundance predicted by hemlock woolly adelgid (HWA) population score from per sample abundance data pooled by location across one year, December 2005 through November 2006. Models generated by Gaussian local-mean nonparametric multiplicative regression (LM-NPMR).....	74

LIST OF TABLES

<u>Table</u>	<u>Page</u>
1. Attributes of <i>Tsuga heterophylla</i> at sixteen Pacific Northwest U.S. locations surveyed for predators of <i>Adelges tsugae</i>	51
2. Abundance of adult and immature predators collected from <i>Adelges tsugae</i> infested <i>Tsuga heterophylla</i> in the Pacific Northwest, January 2005 through November 2006.	54
3. Comparison of predator abundance among <i>Adelges tsugae</i> infested and uninfested <i>Tsuga heterophylla</i> at five locations in the Pacific Northwest. Mean per sample abundance data are pooled across location and time from December 2005 through November 2006.	56

DEDICATION

To Dr. Vernon L. Stiefel

1961 – 2006

Chapter 1: Introduction and Literature Review

Adelges tsugae in North America

The hemlock woolly adelgid, *Adelges tsugae* Annand, was introduced from Asia to the eastern U.S., where it is a pest of eastern hemlock, *Tsuga canadensis* (L.) Carrière; and Carolina hemlock, *Tsuga caroliniana* Engelmann. As of 2004, *A. tsugae* has infested at least one fifth of the *T. canadensis* natural range in eastern North America. Counties reporting *A. tsugae* infestation cover an area of the Appalachians and surrounding regions from northeastern Georgia to southwestern Maine, and as far east as coastal Massachusetts. It is thought the combination of bivoltine life cycle, wind dispersal, susceptible host trees, and few natural enemies contributes to the rapid spread of *A. tsugae* in the eastern U.S. (McClure 1989, 1990; Cheah et al. 2004). *A. tsugae* spreads at a rate of approximately 15.6 km per year in the southern part of its eastern U.S. range; however, expansion in the northern part is slowed to approximately 8.1 km per year where mean minimum temperatures are below -26° C (Shields and Cheah 2005; Evans and Gregoire 2006). Early symptoms of infestation, needle drop and reduced shoot growth, are followed in two to four years by limb dieback, increased exposure to blow down, and secondary attack by insects and diseases (Cheah et al. 2004). *T. canadensis* mortality can occur between four and ten years following initial infestation (McClure et al. 2001). The only natural check on the northward expansion of *A. tsugae* range may be minimum winter temperatures below -26° C, which have been shown to increase *A. tsugae* mortality and slow its rate of spread (Skinner et al. 2003; Shields and Cheah 2005; Evans and Gregoire 2006).

An exotic from Asia, *A. tsugae* is an innocuous pest of Japanese hemlocks [*Tsuga diversifolia* (Maxim.) Masters and *Tsuga sieboldii* Carrière] and Chinese hemlocks [*Tsuga chinensis* (Franchet) E. Pritzel, *Tsuga forrestii* Downie, and *Tsuga dumosa* (D. Don) Eichler] in their native range and only reaches high population densities on ornamental or stressed trees. *A. tsugae* has also been recorded on *T. dumosa* in India (McClure et al. 2001; Del Tredici and Kitajima 2004; Havill et al. 2006). In eastern North America, *A. tsugae* was first reported near Richmond, Virginia in 1951 (Stoetzel 2002a). The strain of *A. tsugae* in eastern North America is thought to have been introduced from Japan, possibly originating from a single introduction. All *A. tsugae* in the eastern U.S. are genetically similar, belonging to a single haplotype which is also found on *T. sieboldii* at low elevations in Japan (Havill et al. 2006).

A. tsugae is also found in western North America, from northern California to southeastern Alaska and as far east as Montana (Havill et al. 2006). Its hosts in this region are western hemlock, *Tsuga heterophylla* (Raf.) Sargent, and mountain hemlock, *Tsuga mertensiana* (Bong.) Carrière (Annand 1924; McClure 1992b). Also originating from Japan, western *A. tsugae* are more genetically variable than those in eastern North America; belonging to at least six different haplotypes. This evidence, in addition to genetically tolerant host trees and the presence of a specialized predator, suggests an introduction to western North America that occurred long before the first *A. tsugae* specimen was collected from Washington in 1907 (Havill et al. 2006).

Biology of *A. tsugae*

During the 1980s and 1990s, when *A. tsugae* was gaining pest status in the eastern U.S., thorough studies of its biology were conducted by Mark S. McClure. Most of what is known about *A. tsugae* biology is based on observations of infested *T. canadensis* in eastern North America and *Tsuga* species in Japan. Apart from phenological observations by Zilahi-Balogh et al. (2003a), no biological or morphological studies exist for *A. tsugae* in western North America.

Living within cottony flocculence at the base of hemlock leaves, *A. tsugae* is a minute (0.4-1.4 mm length) sucking insect that remains stationary for most its life. As nymphs and adults, *A. tsugae* feed on xylem ray parenchyma cells through a stylet bundle up to three times the length of its body (Young et al. 1995). Feeding during early spring and late fall allows *A. tsugae* to access the highest quantity of nutrients produced by the hemlocks, which in turn supports heavy oviposition. There are two generations per year, with oviposition occurring in late winter (progreiens eggs) and early summer (sistens eggs). A mobile crawler emerges from the egg and seeks out an unoccupied leaf base where it settles, inserts its stylet, and molts to a first instar nymph. In early spring and summer the crawler stage can disperse to new trees via wind, nursery trade, birds, mammals, or humans. Dispersal by wind can carry them at least 1,350 meters (McClure 1990; Ward et al. 2004). The settled nymphs begin producing the waxy secretions that will eventually grow to be an ovisac for the adult. The first instar nymph of the sistens generation will undergo a two to four month

aestival diapause during late summer. When the nymphs end aestivation in late fall, feeding begins and continues through the winter at suitable temperatures.

A major difference between eastern and western North American populations is the timing of adult sistens maturation. In British Columbia sistens mature as early as October, while in Connecticut they mature in February; the difference is likely due to a warmer winter climate in coastal B.C. (McClure 1989; Zilahi-Balogh et al. 2003a). However, progrediens eggs are laid nearly simultaneously on both coasts, as early as January in B.C. and February in Connecticut. The biology of *A. tsugae* in the West is not fully understood, particularly the behavior of adults prior to oviposition. The progrediens generation will feed throughout the spring and early summer (McClure 1989; McClure et al. 2001).

A. tsugae females are highly fecund, each sistens female oviposits between 50 and 175 eggs, and the progrediens female between 25 and 125 eggs (McClure et al. 2001). There is no sexual reproduction of *A. tsugae* in North America, all individuals are reproduced parthenogenetically. In its native Asian range and in eastern North America, eggs laid in late winter will either mature as apterous progrediens adults or alate sexuparae. The sexuparae fly to an alternate host, a spruce (*Picea* spp.), where they produce a small number of eggs; these will become the sexual generation, known as sexuales. In eastern North America, sexuales do not survive past the first instar; presumably because none of twelve *Picea* species present are suitable for their development. The abundance of sexuparae produced is density dependant, increasing with overall *A. tsugae* density. In spite of the annual loss of the entire sexuparae

progeny, *A. tsugae* populations grow rapidly in eastern North America. Only in Asia do spruce species exist that will support the sexuales to maturity, allowing sexual reproduction to occur (McClure 1989).

No alate sexuparae were recorded in a two year survey of *A. tsugae* on *T. heterophylla* in British Columbia by Zilahi-Balogh et al. (2003a); or in Oregon by Annand (1924). Zilahi-Balogh et al. (2003a) observed similar *A. tsugae* densities and reduction in host tree health that induced production of sexuparae in Connecticut and Virginia. This dramatic biological difference between eastern and western *A. tsugae* populations and the recent evidence of genetic variation among the geographic and host tree groupings of *A. tsugae* by Havill et al. (2006) warrant future studies of possible biological and morphological differences among the various lineages.

The minimum threshold for development of *A. tsugae* progrediens collected from *T. canadensis* is quite low at 3.9° C (Salom et al. 2002). Some individuals can survive up to 8 hours at -30° C, although the critical limit to cold tolerance is nearer to -25° C (Skinner et al. 2003). The cold hardiness of *A. tsugae* varies with geographical location, and the duration of *A. tsugae* developmental stages is affected by temperature (Salom et al. 2002; Skinner et al. 2003). Shields and Cheah (2005) found a positive correlation between *A. tsugae* mortality and latitude and a negative correlation between *A. tsugae* mortality and minimum recorded temperature. They reported average *A. tsugae* mortality as high as 93% in New York and New England.

Effects of *A. tsugae* on host trees

A. tsugae can utilize all nine species of hemlock as hosts, but feeding causes the highest mortality to *T. canadensis* and *T. caroliniana*. All sizes and ages of *T. canadensis* are susceptible (McClure 1991). Late winter and early spring feeding reduces or prevents new growth and can severely affect bud break, even at low *A. tsugae* densities (McClure 1987; McClure 1991). *A. tsugae* preferentially attacks the youngest twigs, causing desiccation, discoloration, and eventually needle drop. Branch dieback begins in the lower branches and advances upward (McClure 1991; McClure et al. 2001). Feeding in xylem ray parenchyma cells depletes hemlock storage reserves (Young et al. 1995). There are two possible mechanisms of mortality in *T. canadensis*. First, salivary toxins may build up during stylet bundle reinsertion following each molt because successive saliva sheaths remain in the intercellular space. Second, reduction in stored nutrients may negatively affect host tree response to environmental stressors (Young et al. 1995). *T. canadensis* stands in poor growing conditions, such as xeric soil, quickly succumb to *A. tsugae* damage and mortality can reach as high as 99% (Jenkins et al. 1999, Orwig et al. 2002). However, under unusually moist conditions favorable to hemlock growth, some eastern hemlocks have recovered from *A. tsugae* damage (McClure et al. 2001; Cheah et al. 2005).

As with Asian hemlock species, *A. tsugae* infestations appear to cause negligible damage to the relatively tolerant *T. heterophylla* and *T. mertensiana*, rarely causing tree mortality in healthy stands (McClure 1992b). However, *A. tsugae* can reach high densities on orchard and ornamental western hemlock, occasionally causing

injury and mortality (Furniss and Carolin 1977; McClure 1987, 1992b). These off-site trees grow in conditions which are known to increase susceptibility to *A. tsugae* attack; including compacted soil, xeric soil, deliberate stressing for seed production, or regular nitrogen fertilization (McClure 1987, 1992a, 1992b; Orwig et al. 2002; Zilahi-Balogh et al. 2003a). In early research, McClure (1992b) found little or no bud injury to *A. tsugae* infested *T. heterophylla*, *Tsuga mertensiana*, and *T. diversifolia* compared to 85% bud mortality on *T. canadensis*, supporting the hypothesis of genetic tolerance to *A. tsugae* in Asian and western North American hemlock species. Montgomery et al. (2005) found genetic variation for terpenoids, compounds known to deter feeding by Aphidoidea, among seven hemlock species. The lowest levels of terpenoids were found in *T. canadensis* and *T. caroliniana*, species which were shown to be the most susceptible to *A. tsugae*. However, terpenoids have not been shown to be the cause of hemlock tolerance to *A. tsugae*.

The tolerance of *T. heterophylla* to *A. tsugae* was rated “questionable” in a review of the literature by Del Tredici and Kitajima (2004). The significantly lower levels of infestation on *T. heterophylla* and *T. chinensis* when compared to *T. canadensis* reported by McClure (1992b) and Del Tredici and Kitajima (2004), respectively, were based on comparisons of seedlings. When comparing mature trees, Montgomery et al. (2005) found *T. chinensis* to be the most tolerant and *T. heterophylla* to be the least tolerant of the five western and Asian species. The level of *A. tsugae* tolerance varies by species, clone, and environmental conditions (McClure 1987, 1992a, 1992b; Orwig et al. 2002; Zilahi-Balogh et al. 2003a; K.F.

Wallin, personal communication, December 20, 2005). To guide breeding efforts, future research should investigate interactions of tolerance to *A. tsugae* with age class and environment in all *Tsuga* species.

A. tsugae impact to eastern hemlock ecosystems

Eastern hemlock species create understory microenvironments distinct from those beneath hardwoods. The hemlock understory is characterized by low light levels, high humidity, and acidic soil with decreased nitrification. These environments can stunt the growth of some understory plants and simultaneously promote growth of shade tolerant species, such as hemlock itself. In otherwise homogeneous deciduous stands, hemlocks increase landscape diversity by providing patches of coniferous habitat (Orwig and Foster 1998; Evans 2002). The long-term effects of eastern hemlock decline are unknown. *A. tsugae* kills juvenile eastern hemlocks as well as seed producing canopy trees, compromising advance regeneration (Orwig et al. 2002). With no similarly functioning replacement species, removal of eastern hemlock can cause dramatic changes in microenvironment and soil conditions; possibly leading to very different plant community dynamics and diversity (Orwig and Foster 1998).

T. canadensis mortality has resulted in increased nitrogen mineralization, nitrification, gap light levels, soil temperature, and seedling cover (Jenkins et al. 1999, Yorks et al. 2003). Nitrogen leaching from soil water can increase nitrogen limitation in recovering sites and can create water pollution, especially near affected riparian hemlock stands. Nitrogen limitation can be mitigated in stands where hemlock is

quickly replaced by species such as beech, which have similar N-cycling properties (Jenkins et al. 1999).

The loss of eastern hemlock species in riparian ecosystems has resulted in increased light levels in streams and increased summer stream temperatures. These conditions may lead to algal blooms, more extensive dry streambeds, and reduced numbers of native fish species. There are 37% more stream macroinvertebrate taxa in hemlock streams than in hardwood streams; some of which may be dependant on conditions created by hemlock overstory and debris. The loss of invertebrates via stream drying and altered water conditions may negatively affect higher level consumers (Evans 2002).

More than 130 vertebrate species have been recorded in mature eastern hemlock stands. Many of these species may benefit from year-round shelter, shade, and thermal insulation provided by an evergreen canopy (Ward et. al 2004). At least three bird species are almost exclusively associated with healthy eastern hemlock stands. On the other hand, several bird species were found at higher densities in defoliated hemlock stands (Tingley et al. 2002). It may be some time before the long term effects of eastern hemlock decline on fauna are known.

Integrated *A. tsugae* management alternatives

Devastation of hemlocks in the eastern U.S. is attributable to a combination of host-tree susceptibility and absence of natural enemies (Cheah and McClure 1996). Conversely, genetic host tolerance to *A. tsugae* and presence of endemic adelgid

predators or pathogens may be contributing to the relative tolerance of western hemlock (Cheah and McClure 1996). Heritable traits play a role in the tolerance of Asian and western North American hemlock species to *A. tsugae* (McClure 1992b; Del Tredici and Kitajima 2004; Montgomery et al. 2005). Breeding for host tolerance to *A. tsugae* in eastern hemlocks is being investigated and may provide management options in the future. Cross-pollination testing by Bentz et al. (2002) yielded 59 *T. caroliniana* × *T. chinensis* hybrids; however they encountered cross-incompatibility between *T. canadensis* and three Asian *Tsuga* species.

While impractical on a stand scale, immediate control for threatened ornamental and high-value trees can be achieved by application of horticultural oils, insecticidal soaps, or pesticides. The systemic insecticide, imidacloprid, is the most effective chemical treatment for *A. tsugae* infestation (McClure 1992a; Webb et al. 2003). However, some insecticide treatments may result in an increase of normally minor hemlock pests, such as scale and spider mites (Cheah et al. 2004). In the future, it may also be possible to treat high-value trees with an antibiotic that will indirectly kill *A. tsugae*. *A. tsugae* carries a bacterial endosymbiont in its gut that is essential to survival. Antibiotic treatments aimed to kill these bacteria and in turn *A. tsugae* are being investigated (Shields and Hirth 2005).

It is known that drought stress increases the susceptibility of hemlock to *A. tsugae*, thus an effective silvicultural control for high-value stands is to irrigate during drought periods (McClure et al. 2001). Attempts to increase tree vigor by fertilization should be avoided because nitrogen fertilization may actually increase susceptibility to

A. tsugae attack (McClure 1992a). Rehabilitation planting of native conifer species or *A. tsugae* tolerant western and Asian hemlocks to replace dead ornamental eastern hemlocks in the eastern U.S. is another silvicultural option. Salvage harvesting of damaged eastern hemlocks is an increasingly common management practice (Ward et al. 2004). However, logging should be carefully planned to avoid negative ecological impacts greater than those caused by *A. tsugae* (Kizlinski et al. 2002).

Limited cultural control can be achieved by avoiding transport of materials between infested and non-infested sites (Ward et al. 2004; Blumenthal and Werner 2005). Birdfeeders can also be removed from hemlocks to prevent transport of crawlers on birds. These types of controls are probably futile in contiguous stands because crawlers can also move by wind (McClure 1990).

It appears that minimum winter temperatures below -26° C may limit the spread of *A. tsugae*, giving managers in affected areas an advantage in controlling *A. tsugae* damage (Shields and Cheah 2005; Evans and Gregoire 2006). However, effective management tactics have limitations. For example, breeding for host tolerance to *A. tsugae* will take time to implement. Insecticide applications are limited to high-value trees and carry financial and environmental costs. It is believed that predators play a role in regulating *A. tsugae* in western North America and Asia. Therefore, a large part of current research on strategies to minimize tree mortality on a stand-level scale is focused on developing a biological control program for *A. tsugae* (McClure 1992b; Ward et al. 2004; Cheah et al. 2004).

Use of predators for adelgid biological control

After 115 years of biological control efforts, many researchers agree that to control an insect pest, the ideal biological control agent would be a host-specific parasitoid (Kimberling 2004). The adelgids pose a unique challenge because there are no known parasites of any adelgid species (Balch et al. 1958; Clausen 1978; Schooley et al. 1984). The remaining control agents must either be predators or entomopathogens. A classical biological control program, using repeated releases to establish imported natural predators, to manage *A. tsugae* has been under way in the eastern U.S. since 1995. In order for the program to successfully employ predators, the selection of candidate predators should adhere to established criteria meant to increase the likelihood of establishment and control. The ideal predator should be monophagous and temporally synchronized to the most vulnerable life stage of the prey (Waage and Mills 1992; van Lenteren et al. 2003; Kimberling 2004). Additional traits correlated with success include multivoltinism and oviposition that occurs on the host (Kimberling 2004).

None of the aphidophagous generalists released for biological control of adelgids worldwide has resulted in establishment or significant control. The only introduced predators shown to be responsible for curtailing adelgid outbreaks belong to two families, Anthocoridae (Hemiptera) and Chamaemyiidae (Diptera). Some introduced predators in the Coccinellidae (Coleoptera), Derodontidae (Coleoptera), and Cecidomyiidae (Diptera) families have established on adelgid hosts, however establishment has not yet resulted in large scale control (Zilahi-Balogh et al. 2002b).

Will a single biological control agent be responsible for measurable control of *A. tsugae*, or will that success involve multiple predators? The meta-analysis of biological control projects targeting insect pests performed by Denoth et al. (2002) revealed that the introduction of multiple agents does not significantly increase success over a single species introduction. However, in 40% of successful programs targeting an insect pest, multiple agents were responsible for success. Denoth et al. (2002) acknowledge that some targets may require multiple agents for control, especially if the target pest occurs over a wide range of environments where a single agent is not always present. In the case of bivoltine *A. tsugae*, vulnerable life-stages are present throughout the year, with oviposition occurring in early spring and summer. Therefore, the introduction of multiple predator species could enhance success against *A. tsugae*, provided the predators are active during different seasons to reduce interspecific competition (Zilahi-Balogh et al. 2002b; Ward et al. 2004; Flowers et al. 2006).

Predators of the Adelgidae

The following is a taxonomically arranged review of predators that have been reported feeding on species of Adelgidae around the world. It is not completely inclusive, but rather focuses on those adelgid predators that have potential for adelgid biological control or have been introduced as adelgid biological control agents.

Acari. Following surveys of four adelgid species, mites have been suggested as possible predators or indirect biological control agents. McClure (1995) observed a

ceratozetid mite, *Diapterobates humeralis* (Hermann), dislodging a high percentage of *A. tsugae* eggs from ovisacs on native hemlocks in Japan. While not a predator, the indirect negative effect of *D. humeralis* on *A. tsugae* warranted further investigation as a biological control candidate. This effort was discontinued due to difficulties in rearing the mites (Cheah and McClure 1996). Rao and Ghani (1972) also encountered difficulty rearing one of several mite species that fed on *Adelges joshii* Schneider-Orelli and Schneider and *Adelges knucheli* S.-O. and S. in the Himalayas. Mitchell (1962) made observations on six species of mites associated with the balsam woolly adelgid, *Adelges piceae* (Ratzeburg), in the Pacific Northwest (PNW). At least three mites were predators, but none were thought to be important predators of *A. piceae*.

Hemiptera: Anthocoridae. Members of the anthocorid family are the only hemipteran predators to be considered candidates for biological control of adelgids. The only introduced anthocorid to successfully establish was *Tetrupleps raoi* Ghauri, a native to Pakistan that feeds on *A. joshii* and *A. knucheli*. *T. raoi* is responsible for control of *Pineus pini* (Macquart) populations in Kenya (Aloo and Karanja 1986; Mills 1990; Zilahi-Balogh et al. 2002b). *T. raoi* was also released to control *A. piceae* in eastern Canada, but did not establish (Schooley et al. 1984). Species of native anthocorids collected in association with *A. piceae* in North America include *Tetrupleps canadensis* Provancher, *Tetrupleps latipennis* Van Duzee, and *Acomporis lepidus* (Van Duzee) (Brown and Clark 1956; Mitchell 1962; Lattin 2003).

During recent exploration in China for *A. tsugae* natural enemies, *Tetrupleps galchanoides* Ghauri, *Tetrupleps parallelus* Bu et Zheng, and *Anthocoris alpinus* Zheng were recovered from infestations on *T. chinensis* (Wang et al. 1998).

Neuroptera: Coniopterygidae. Stoetzel (2002b) observed an undetermined species of small dusty-wings, Coniopterygidae, feeding on *A. tsugae* and suggested that they may have been overlooked as *A. tsugae* biological control candidates. Coniopterygids have not been recorded in any published field surveys of adelgid predators. They are more commonly associated with scale insects (Miller et al. 2004)

Neuroptera: Hemerobiidae and Chrysopidae. The larvae of hemerobiids and chrysopids are well documented as generalist predators of Sternorrhyncha (Furniss and Carolin 1977). Most neuropterans do not specialize on prey species and are not considered to be good candidates for biological control for this reason (van Lenteren et al. 2003). In one noted exception, Fondren et al. (2004) showed that augmentative releases of *Chrysoperla rufilabris* Burmeister significantly reduced numbers of the balsam twig aphid, *Mindarus abietinus* Koch, in Michigan Christmas tree plantations.

Various species of *Hemerobius* (Hemerobiidae) and *Chrysopa* (Chrysopidae) are commonly found feeding on adelgids in field surveys, and some have been released for adelgid biological control without success. In the 1930s, *Hemerobius nitidulus* Fabricius and *Hemerobius stigma* Stephens were released as part of the *A. piceae* biological control effort in Canada and the U.S.; neither species established (Smith and Coppel 1957; Clausen 1978). Unidentified *Hemerobius* sp. and *Chrysopa*

spp. from India were released in North Carolina on *A. piceae* from 1961 to 1965; however none were able to survive on that host (Amman and Speers 1971). Another *Chrysopa* sp. from India was released in Oregon for control of *A. piceae* in 1961, but did not establish (Mitchell and Wright 1967; Clausen 1978).

Coleoptera: Derodontidae. The genus *Laricobius* is uniquely predaceous among the fungivorous derodontids; and their larvae prey exclusively on adelgids. Four species occur in North America. *Laricobius nigrinus* Fender, a native predator of *A. tsugae*, occurs in the PNW and British Columbia (Zilahi-Balogh et al. 2003b). The endemism of *L. nigrinus* was somewhat of a mystery given its high specificity to *A. tsugae*, which was thought to have been introduced to western North America in the early twentieth century (Annand 1924). However, new phylogenetic evidence produced by Havill et al. (2006) suggests that *A. tsugae* was not a recent introduction to western North America. *L. nigrinus* rarely feeds on adelgids other than *A. tsugae*; Mitchell (1962) collected *L. nigrinus* from *A. piceae* at only one location in the PNW. *L. nigrinus* was first introduced onto *A. tsugae* in the eastern U.S. in 1997, where it has successfully overwintered and reproduced in some locations (Cheah et al. 2004; Lamb et al. 2006). Another derodontid native to the PNW, *Laricobius laticollis* Fall, has been collected from *Adelges cooleyi* (Gillette) on Douglas-fir, *Pseudotsuga menziesii* (Mirbel) Franco (R.G. Mitchell, personal communication, March 22, 2007). However, no adelgid host records have been published for *L. laticollis* (Zilahi-Balogh et al. 2005).

A. piceae is the primary host of the European native, *Laricobius erichsonii* Rosenhauer, which is also known to feed on a wide variety of adelgids in Europe, including *A. cooleyi*, *Adelges nordmannianae* [= *nüsslini* C.B.] (Eckstein), and *Pineus strobi* (Hartig) (Clark and Brown 1960). From 1951 to 1969, *L. erichsonii* was introduced to both eastern and western North America for the control of *A. piceae* (Harris and Dawson 1979; Schooley et al. 1984). Recovery of *L. erichsonii* occurred up to eight years after release in eastern Canada (Schooley et al. 1984). *L. erichsonii* was the most common predator collected during monitoring of *A. piceae* infestations in British Columbia up until 1978 (Harris and Dawson 1979). No individuals of this species were recovered in the surveys of *A. piceae* conducted by Humble (1994) between 1987 and 1993. In spite of establishment, *L. erichsonii* did not provide significant control of *A. piceae* in North America (Mitchell and Wright 1967; Schooley et al. 1984).

Laricobius rubidus LeConte is native to eastern North America and primarily feeds on *P. strobi*. *L. rubidus* has also been occasionally collected from *A. piceae* and *A. tsugae* (Clark and Brown 1960; Wallace and Hain 2000; Zilahi-Balogh 2005). Zilahi-Balogh (2005) demonstrated that *L. rubidus* could complete development on a diet of *A. tsugae* in the laboratory. However, it is not being considered for augmentative biological control of *A. tsugae* due to its preference for *P. strobi*.

A recently discovered native of China, *Laricobius kangdingensis* sp. n., is a predator of *A. tsugae* in its native range. Early laboratory investigations show it to be

specific to *A. tsugae* and a possible candidate for *A. tsugae* biological control in the eastern U.S. (Gatton 2004).

Coleoptera: Coccinellidae. Lady beetles have been commonly used for biological control of Sternorrhyncha with widely varying results (Snyder and Evans 2006). North American releases of the Asian coccinellid, *Harmonia axyridis* Pallas, and the Palearctic *Coccinella septempunctata* L. for general aphid control have had some unintended negative consequences. Both species rapidly increased their geographic and host ranges in North America and are believed to have competitively excluded some native coccinellids (Elliot et al. 1996; Brown 2003). *H. axyridis* may now be considered a pest to humans. During fall migration, *H. axyridis* congregates in homes, staining walls, causing allergic reactions in some people, and even biting. *H. axyridis* also aggregates on grapes and taints flavor in wine processing (Koch 2003).

World-wide, only three species of coccinellids have established on adelgids following release for biological control; all in North America (Zilahi-Balogh et al. 2002b). *Aphidecta obliterata* (L.) and *Scymnus (Pullus) impexus* Mulsant were released up until 1968 for control of *A. piceae* in Canada and the U.S. *S. impexus* was recovered up to ten years after release in Canada (Harris and Dawson 1979). *A. obliterata* has been recovered from *A. piceae* in the West up until 1994 but provided little control. It has also reportedly been recovered from *A. tsugae* on western hemlock (Schooley et al. 1984; Humble 1994). *C. septempunctata* and a European adelgid predator, *Exochomus quadripustulatus* (L.), were also released in North

America against *A. piceae*, however, neither were subsequently recovered from *A. piceae* (Clausen 1978; Schooley et al. 1984; Zilahi-Balogh et al. 2002b).

The most recent successful establishment of a coccinellid is *Sasajiscymnus tsugae* (Sasaji and McClure), which was the first biocontrol agent to be released on *A. tsugae* in the eastern U.S. beginning in 1995. In spite of reproducing and overwintering near release sites, numbers of recovered *S. tsugae* have been lower than expected and its numerical impact on *A. tsugae* in the field is not consistent (Asaro et al. 2005; Cheah et al. 2005).

Coccinellids appear to be the most speciose predatory family associated with *A. tsugae* in Asia. One survey of *A. tsugae* predators on three *Tsuga* species in China recovered 54 species of coccinellids (Yu et al. 2000). In addition to *S. tsugae*, at least three of these Chinese lady beetles are being evaluated for efficacy against *A. tsugae* in the eastern U.S.

Diptera: Cecidomyiidae. Two genera in the gall midge family, *Aphidoletes* and *Monobremia*, are the only cecidomyiids with exclusively aphidophagous larvae; *Lestodiplosis* spp. are less likely to restrict feeding to aphids (Harris 1973).

Predaceous species of *Aphidoletes* and *Lestodiplosis* have been recovered in surveys of *A. tsugae* in the eastern U.S., *A. piceae* in the PNW, *Adelges laricis* Vallot in Switzerland, and *Pineus* spp. in Europe (Mitchell 1962; Mitchell and Maksymov 1977; Mills 1990; Wallace and Hain 2000). The use of cecidomyiids in adelgid biological control has been limited. *Lestodiplosis pini* Barnes was released in Australia against *Pineus boernerii* [= *P. laevis* (Maskell)] Annand without success

(Wilson 1960). *Aphidoletes thompsoni* (Möhn) was released on *A. piceae* in the PNW, Maine, North Carolina, and across Canada from 1957 to 1968 and was recovered in eastern and western Canada up to two years after release (Mitchell and Wright 1967; Harris and Dawson 1979; Schooley et al. 1984). As with other *A. piceae* biocontrol agents, *A. thompsoni* had no measurable impact on the adelgid.

Diptera: Syrphidae. Many species of flower or hover flies are generalist predators of Sternorrhyncha as larvae (Furniss and Carolin 1977). Species of the genera *Neocnemodon* [= *Cnemodon*], *Syrphus*, and *Metasyrphus* have been recovered from *A. piceae* in eastern Canada and the PNW; *A. laricis* and *A. cooleyi* in Europe; *A. joshii* and *A. knucheli* in India and Pakistan; and *P. pini* in England (Wilson 1938; Teucher 1955; Brown and Clark 1956; Mitchell 1962; Rao and Ghani 1972; Mitchell and Maksymov 1977). The only attempt to use syrphids for adelgid biological control was the release of an unidentified species of *Neocnemodon* on *A. piceae* in eastern Canada where it failed to establish (Smith and Coppel 1957; Clausen 1978). In addition to being generalists, the appeal of syrphids as biocontrol agents is further reduced due to vulnerability to heavy parasitism by ichneumonid, encyrtid, and pteromalid wasps (Brown and Clark 1956; Mitchell 1962; Rao and Ghani 1972).

Diptera: Chamaemyiidae. Larvae of the chamaemyiid family are specialized predators of Sternorrhyncha, including adelgids, scales, aphids, and mealybugs (McLean 1992; Gaimari and Turner 1996). Species in the genera *Cremifania*, *Neoleucopis*, and *Leucopis* are commonly found associated with Adelgidae. The genus *Neoleucopis* was formerly a subgenus of *Leucopis* until a recent revision by

Tanasijtshuk (1992). Four European species of Chamaemyiidae that were released for *A. piceae* biological control have established in Canada and the U.S. *Cremifania nigrocellulata* Czerny and *Neoleucopis* [= *Leucopis*] *obscura* (Haliday) were recovered from *A. piceae* in both eastern and western North America (Mitchell and Wright 1967; Humble 1994). *Neoleucopis* [= *Leucopis*] *atratura* (Ratzeburg) was recently recovered from *A. piceae* in British Columbia by Humble (1994), although it was not intentionally released in the West. And finally, *Leucopis hennigrata* McAlpine, which was released in both eastern and western Canada, but only established in the East (Schooley et al. 1984). The establishment of chamaemyiid predators did not, however, result in measurable control of *A. piceae* in North America (Schooley et al. 1984).

Neoleucopis obscura has also been recovered from *Pineus strobi* in the northeastern U.S.; however, it was not collected from *A. tsugae* in stands where it coexists with *P. strobi* (Montgomery and Lyon 1996). *N. obscura* was recorded as a predator of *Pineus pini* and *P. strobi* in England and was released in Australia for the control of *P. boernerii* but did not establish there (Wilson 1960). *N. obscura* was later released in Chile, where it has successfully controlled populations of *P. boernerii* (Mills 1990).

In North Carolina, three species of *Leucopis* originating from India were released on *A. piceae* between 1960 and 1969. One of these was tentatively identified by J.F. McAlpine as *Leucopis* n. sp. nr. *orbitalis* Malloch, but was later determined to be *Leucopis argenticollis* Zetterstedt by McAlpine and Tanasijtshuk (1972). There is

no evidence that any of these species established on *A. piceae*. In Europe, *L. argenticollis* is most frequently associated with *Pineus pini* and is an important predator of that pest (McAlpine and Tanasijtshuk 1972; Mills 1990). McAlpine and Tanasijtshuk (1972) include several North American adelgid host records in their redescription of *L. argenticollis* including *A. piceae* in New Brunswick, *P. strobi* in eastern North America, *Pineus pineoides* (Cholodkovsky) in Quebec, and *Pineus similis* (Gillette) in Ontario. *L. argenticollis* is also known from *Pineus* spp. in India (McAlpine and Tanasijtshuk 1972).

Leucopis atrifacies (Aldrich) was collected from *P. boernerii* in California in 1938 and released in Australia for control of that pest; however, it did not establish (Wilson 1960). Chamaemyiid specimens collected by R.G. Mitchell from *A. piceae* in Washington State during 1959 and 1960 were later determined to be *L. atrifacies* by Tanasijtshuk (2002). Both *L. atrifacies* and *L. argenticollis* were collected in large numbers from unidentified *Pineus* spp. on various pines in the San Francisco Bay area of California (Greathead 1995). The range of *L. atrifacies* is restricted to the western U.S. (Tanasijtshuk 2002).

Neoleucopis [= *Leucopis*] *tapiae* (Blanchard) was exported from England and released in New Zealand in 1932 and 1934 against *P. boernerii*. Originally thought not to have established, it was recovered in 1954 and has since been found throughout New Zealand (Zondag and Nutall 1989). In 1976-77, *N. tapiae* obtained from France were released and established on *P. pini* in Hawaii, where populations of *N. tapiae* were shown by Culliney et al. (1988) to fluctuate with *P. pini*. The authors suggest

that *N. tapiae* has maintained the adelgid pest below outbreak levels. *N. tapiae* was originally misidentified as “*L. obscura*” in the Culliney et al. (1988) publication (Greathead 1995).

Leucopis species have been collected from *A. tsugae* in limited numbers. Wallace and Hain (2000) recovered an unidentified species of immature *Leucopis* from *A. tsugae* in Virginia. Unidentified species of *Leucopis* have also been found on *A. tsugae* in its native range within China and Japan (M. Montgomery, personal communication, November 15, 2006).

Current progress of *A. tsugae* biological control efforts in the eastern United States

Three surveys of endemic predators associated *A. tsugae* populations on *T. canadensis* in Connecticut, North Carolina, and Virginia recovered at least ten species representing seven families that commonly feed on adelgids, including Hemerobiidae, Chrysopidae, Derodontidae, Coccinellidae, Cecidomyiidae, Syrphidae, and Chamaemyiidae (McClure 1987; Montgomery and Lyon 1996; Wallace and Hain 2000). Although the periods of *A. tsugae* oviposition were covered, these surveys were limited to the spring and early summer months. All studies concluded that numbers of predators were too low to have a significant impact on *A. tsugae*.

A program for biological control of *A. tsugae* utilizing non-native predators was initiated in 1995 in the eastern U.S., resulting in importation of predators from Japan, China, and Canada. Three coleopteran predators of *A. tsugae* are currently being field evaluated for efficacy against *A. tsugae* in the eastern U.S.: two coccinellid

predators, *Sasajiscymnus tsugae* from Japan and *Scymnus sinuanodulus* Yu et Yao from China, and the derodontid, *Laricobius nigrinus* from British Columbia.

Exploration for additional *A. tsugae* predators in China, Japan, and western North America is ongoing (Cheah et al. 2004).

Sasajiscymnus tsugae. Discovered in 1992 in Japan, *S. tsugae* was the first *A. tsugae* predator to be released in the U.S. in 1995. Through the following ten years, over one million have been released in at least 100 sites in 15 eastern U.S. states. Voracious larvae can eat up to 500 *A. tsugae* eggs. *S. tsugae* is bivoltine, adults and larvae are synchronized to feed on all *A. tsugae* life stages during the spring and summer (Cheah et al. 2004). While *A. tsugae* is the preferred host of *S. tsugae*, the predator will also feed on *A. piceae*, *A. cooleyi*, and *P. strobi*. The eggs of all adelgids are equally preferred (Butin et al. 2004). *S. tsugae* will even cannibalize its own eggs, which has been a challenge for laboratory rearing. In spite of early difficulties, laboratory reared colonies have been very successful. Clemson University planned to produce and release 150,000 in 2005 (Conway and Culin 2005).

Cheah et al. (2005) reported significantly increased *A. tsugae* mortality from year to year at *S. tsugae* release sites in Connecticut and New Jersey and hemlock foliar transparency measurements that were significantly lower than non-release sites. *S. tsugae* have been recovered from one to six years after release and have dispersed up to 1,000 meters from the release site. Blumenthal and Werner (2005) have also documented reproductive and overwintering success for *S. tsugae* released in Pennsylvania since 1999. Adults and larvae have been recovered up to three years

after release. To investigate the possibility of eliminating the need for laboratory rearing, Grant et al. (2005) have had some success recovering *S. tsugae* adults after egg releases in Tennessee.

Unfortunately, the number of recovered beetles in these studies is not consistently high. Both the Pennsylvania and Tennessee studies have recovered low numbers and reported a significant drop in recovery rate two years after release. Cheah et al. (2005) found a higher proportion of adult *S. tsugae* in the upper crowns of release trees. Because most surveys only cover the lower canopy, this partly explains poor recovery rates. The health of non-release hemlock stands in Connecticut and New Jersey had improved by 2004 due to more favorable environmental conditions and an unusually cold winter over 2003-2004. These conditions also negatively impacted *A. tsugae* populations and this may also have contributed to a decrease in predator populations (Cheah et al. 2005). Cheah et al. (2005) recommends re-releasing *S. tsugae* following periods of *A. tsugae* resurgence due to hemlock stress or after severe winters reduce *S. tsugae* populations.

For reasons other than population instability, *S. tsugae* may not be the ideal *A. tsugae* predator. Some studies have suggested that *S. tsugae* may not reduce *A. tsugae* numbers to the low levels expected. Butin et al. (2003) reported an increase of *A. tsugae* population in Massachusetts field caged branches containing *S. tsugae*. Asaro et al. (2005) found that *S. tsugae* had no effect on high *A. tsugae* densities in Georgia.

Scymnus sinuanodulus. One of 20 *Scymnus* species found associated with *A. tsugae* in China; *S. sinuanodulus* was imported into U.S. quarantine in 1996 to

evaluate its potential for *A. tsugae* biological control. *S. sinuanodulus* feeds in the spring, females are moderately fecund (~130 eggs/female), and oviposit singly in concealed areas. Its univoltine life cycle is somewhat synchronized with *A. tsugae* so that oviposition is concurrent in the spring, possibly an adaptation to low availability of *A. tsugae* eggs in summer. First instar *S. sinuanodulus* larvae cannot survive without access to *A. tsugae* eggs, suggesting host-specialization (Lu and Montgomery 2001).

Viability of both laboratory-reared and field-collected *S. sinuanodulus* is similar and its laboratory lifespan is longer than *S. tsugae*, making it a good candidate for mass rearing (Lu and Montgomery 2001). There are no published evaluations of *S. sinuanodulus* rearing success, but Asaro et al. (2005) states they are more challenging to mass rear than *S. tsugae*.

In Georgia, Asaro et al. (2005) are responsible for the first field release of 450 *S. sinuanodulus* in 2003-2004. The release site also happens to be the only location in the U.S. where all three *A. tsugae* biocontrol agents: *S. tsugae*, *S. sinuanodulus*, and *L. nigrinus*, have been co-released. In field caging experiments at that location, *S. sinuanodulus* had a greater impact on high density *A. tsugae* than did *S. tsugae*. *S. sinuanodulus* overwintering, establishment and recovery data has not yet been published.

***Laricobius nigrinus*.** Beginning in 1997, *L. nigrinus* was imported to Virginia from British Columbia for quarantine study. By 2005, 7,350 adults had been released in eight states from Massachusetts to Georgia (Cheah et al. 2004; Mausel et al. 2005).

Moderately fecund (~100 eggs/female) females oviposit singly into *A. tsugae* ovisacs, where wool covered larvae feed, consuming up to 250 eggs. The life cycle of *L. nigrinus* is highly synchronized to *A. tsugae*, aestivating at the same time and for the same duration as its host. *L. nigrinus* is active from October to May when the *A. tsugae* sistens generation is active and *L. nigrinus* larvae emerge during oviposition of progrediens eggs from February to May (Zilahi-Balogh et al. 2003a, 2003b). *L. nigrinus* and *A. tsugae* are also well suited climatically; the minimum temperatures for complete development of both predator and prey are within one degree Celsius (Zilahi-Balogh et al. 2003c).

L. nigrinus is host-specialized because it can only complete its development on *A. tsugae*, although it will consume other adelgids in 'no-choice' feeding trials (Zilahi-Balogh et al. 2002a). Lamb et al. (2005 and 2006) reported *A. tsugae* mortality significantly higher in field cages with *L. nigrinus* than cages without predators. Laboratory rearing of *L. nigrinus* was much improved once Lamb (2004) successfully prevented adults from emerging before prey supplies were available. Data on the impact to *A. tsugae* populations by free-released *L. nigrinus* has not yet been published.

In its native range, *L. nigrinus* adults can survive sub-zero temperatures for several days (Humble and Mavin 2005). However, the climate at release sites in the eastern U.S. can be more severe than the PNW. In laboratory testing by Humble and Mavin (2005), 40% of *L. nigrinus* adults survived at -15°C for 8 hours; a very short period climatically. The ability of *L. nigrinus* to survive and reproduce in the field has

been evaluated by several researchers in the eastern U.S. Lamb et al. (2005) reported 55% survival of *L. nigrinus* over 6 months in Virginia field cages, including winter months.

In spite of some mortality, Lamb et al. (2005) recorded an average spring production of 38 progeny per beetle in field cages. Lamb et al. (2006) recovered six F₂ adults near trees on which they had released lab reared adults 20 months previous. Small numbers of F₁ adults have been recovered by beat sampling up to two years after free-release at experimental sites in southern states: three, eighteen, and twenty-six adults from Tennessee, North Carolina, and Virginia; respectively (Mausel et al. 2005; Salom et al. 2005). To date, no recovery of *L. nigrinus* has been reported at Pennsylvania and Georgia release sites (Asaro et al. 2005; Blumenthal and Werner 2005). In literature reporting establishment of field released *L. nigrinus*, it is unclear whether released beetles were lab-reared or field-collected from the PNW. Therefore, it is difficult to determine the relative viability of the lab-reared *L. nigrinus* in eastern U.S. test sites.

Potential *A. tsugae* biological control candidates. Foreign exploration for additional *A. tsugae* predators in China, Japan, and western North America is ongoing and efforts are being accelerated (Cheah et al. 2004; Onken 2005). Newly discovered and promising foreign predators include new species of Anthocoridae, Derodontidae, and Coccinellidae; all from China. *L. kangdingensis* (Derodontidae) eggs have been successfully laboratory reared on *A. tsugae* and it has fecundity twice that of *L. nigrinus*. Unfortunately, *L. kangdingensis* appears to be adapted to a warmer climate

than that of the eastern U.S. (Gatton 2004). *Tetrableps galchanoides* (Anthocoridae) is one of three native anthocorids associated with *A. tsugae* in China. In the laboratory, *T. galchanoides* reached the adult stage on a diet of *A. tsugae* collected from *T. canadensis* in Virginia (McAvoy 2004). Another species of *Tetrableps* was released during the U.S. *A. piceae* biological control program but did not establish (Mitchell and Wright 1967).

Scymnus ningshanensis Yu et Yao, a Chinese native coccinellid very similar in appearance and biology to *S. sinuanodulus*, is also being evaluated in the U.S. as an *A. tsugae* biological control candidate. *S. ningshanensis* will feed on several species of adelgids with little preference (Butin et al. 2004). In field caging experiments by Butin et al. (2003), *S. ningshanensis* significantly reduced *A. tsugae* population and successfully reproduced 28 new adults in two months. *S. tsugae* was evaluated simultaneously under the same conditions and was a less effective predator than *S. ningshanensis*. There have been no field releases of *S. ningshanensis* to date.

Domestic exploration for new *A. tsugae* predators has been and is currently being conducted on ornamental and orchard grown western hemlocks in British Columbia, Washington, and Oregon. These surveys have yielded predator family diversity similar to other adelgid surveys, including Miridae, Reduviidae, Hemerobiidae, Chrysopidae, Cantharidae, Derodontidae, and Coccinellidae (Humble 1994; Byrkit 2004). The majority of predators are generalists, but their densities appear higher than in the eastern U.S. *L. nigrinus* is the only documented *A. tsugae* specialist found in the PNW (Zilahi-Balogh et al. 2003a). There are indications that

chamaemyiids may be attacking *A. tsugae* in the West. Michael E. Montgomery identified a species of *Leucopis* larvae occupying *A. tsugae* ovisacs on *T. heterophylla* twig samples from Vashon, Washington (K. Ripley, personal communication, Feb. 9, 2005).

Competitive interactions among *A. tsugae* predators. Flowers et al. (2005 and 2006) evaluated the competitive interactions of the specialist *A. tsugae* predators *S. tsugae* and *L. nigrinus*; and the generalist predator *Harmonia axyridis* in laboratory and field studies. *H. axyridis* is a voracious generalist and effective competitor, which has already displaced several native coccinellids. *H. axyridis* has been found on *A. tsugae* infested hemlocks in both eastern and western North America. It was included in the study to evaluate its competitive effect on new biological control agents and was also chosen as a surrogate for any endemic generalist predator that may be negatively affected by competition with biological control agents.

Competition among conspecifics resulted in the only significant negative interactions in these studies. Cannibalism of eggs was common for both specialist predators. Heterospecific groupings did not result in competitive interference; the survival of all three species was not significantly affected by other predators. The amount of predation on other predators was inversely related to *A. tsugae* population, except in the case of *H. axyridis*. *H. axyridis* was rarely consumed by *S. tsugae* or *L. nigrinus*, probably because they are highly prey-specialized. This indicates that both specialists should not impact *H. axyridis* or other generalists at release sites.

However, presence of *H. axyridis* at release sites could negatively impact both specialist predators. Although predation by *H. axyridis* on *L. nigrinus* eggs was no higher than cannibalism, *L. nigrinus* eggs are at higher risk because they are located in *A. tsugae* ovisacs. Although not significant, predation by *H. axyridis* on *S. tsugae* eggs was always higher than cannibalism. *S. tsugae* is at higher risk of competition with *H. axyridis* because both species develop in the late spring. Competitive exclusion of an *A. tsugae* specialist by *H. axyridis* is unlikely because it cannot complete its development on a diet of *A. tsugae* alone (Butin et al. 2004). Winter activity of *L. nigrinus* makes it an ideal phenological compliment and thus, an unlikely competitor to spring and summer feeding Asian coccinellid predators (Lamb et al. 2005).

L. nigrinus has the potential to displace another *Laricobius* native to the eastern U.S. that has been found associated with *A. tsugae* infestations (Wallace and Hain 2000). *Laricobius rubidus* primarily feeds on the pine bark adelgid, *Pineus strobi*, but will also complete its development on *A. tsugae* (Zilahi-Balogh et al. 2005). Numbers of *L. rubidus* collected by Wallace and Hain (2000) in the southeastern U.S. were thought to be too low to impact *A. tsugae* populations, so *L. nigrinus* will be introduced for control. Activity of the two predators overlaps in early spring and early fall. It is possible that *L. rubidus* could compete with *L. nigrinus*, but unlikely because *L. nigrinus* is a specialist. *L. rubidus* will more likely be displaced to its primary host (Zilahi-Balogh et al. 2005).

Entomopathogens of *A. tsugae*. Several virulent fungal pathogens of *A. tsugae* have been discovered and are being evaluated as control agents. These pathogens have been isolated from unhealthy populations of *A. tsugae* in the eastern U.S. and China. Two genera have proved lethal to *A. tsugae* in laboratory testing; however, field tests were inconclusive due to difficulties with spray equipment. Future field evaluations are planned (Reid et al. 2002; Costa et al. 2005). These pathogens were shown to be non-lethal to the *A. tsugae* predator *S. tsugae* (Cheah et al. 2004). *L. nigrinus* and other new predators should be subjected to similar interference testing before a pathogen based program is implemented.

Balsam woolly adelgid biological control

The balsam woolly adelgid, *Adelges piceae*, was introduced to the western U.S. from Europe before 1928, when it was discovered in California (Annand 1928). Infestations were found in 1930 on grand fir [*Abies grandis* (Dougl. ex D. Don) Lindl.] in Oregon, then in 1952 on Pacific silver fir [*Abies amabilis* (Dougl. ex Loud.) Dougl. ex Forbes] and subalpine fir [*Abies lasiocarpa* (Hook.) Nutt.] in Washington and Oregon, respectively. The USDA Forest Service and Canadian Forestry Service initiated balsam woolly adelgid biological control programs by 1957 and 1960, respectively (Mitchell 1962; Mitchell and Buffam 2001). Extensive worldwide exploration for foreign predators of *A. piceae* resulted in the release of more than 25 species in western North America and Canada, of which, eight European predators became established: *Laricobius erichsonii* (Derodontidae), *Aphidecta obliterated*,

Scymnus (Pullus) impexus (Coccinellidae), *Aphidoletes thompsoni* (Cecidomyiidae), *Cremifania nigrocellulata*, *Neoleucopis atratula*, *Neoleucopis obscura* and, *Leucopis hennigrata* (Chamaemyiidae) (Harris and Dawson 1979; Zilahi-Balogh et al. 2002b). Humble (1994) reported the current status of some of these predators in British Columbia. In Oregon and Washington, Mitchell and Wright (1967) reported five established species of imported *A. piceae* predators. No additional species have been reported to be established since then.

In spite of sustained biological control efforts, *A. piceae* populations have not been significantly impacted by introduced predators to date. In the West, populations have spread east of the Cascades into Idaho. In both eastern and western North America, *A. piceae* continues to cause fir mortality (Schooley et al. 1984; Mitchell and Buffam 2001; Cheah and Donahue 2002). The failure of biological control agents to limit *A. piceae* has been attributed to poor seasonal synchrony with the host and low tolerance of winter conditions (Montgomery and Lyon 1996; Zilahi-Balogh et al. 2002b). Alternatively, Mitchell and Buffam (2001) assert that stem infesting adelgids are likely deterred by periderm growth in the bark, an effective defensive response in tolerant hosts. In the case of many sensitive North American firs the defensive response still occurs; however, *A. piceae* feeding may cause lethal damage to the wood before adelgids reach the high densities that would attract and sustain great numbers of predators.

The *A. piceae* biological control program has been thoroughly documented and detailed publications on the phenology, biology, and range of established predators are

of great value to research on similar species that prey on *A. tsugae* in the west (Brown and Clark 1956, Smith and Coppel 1957; Smith 1958; Mitchell 1962; Mitchell and Wright 1967; Clausen 1978; Harris and Dawson 1979; Schooley et al. 1984; Humble 1994).

Pineus spp. biological control

To date, *Pineus* spp. are the only adelgids that have responded significantly to biological control. Two species of chamaemyiid flies and an anthocorid bug have been shown to reduce populations of *Pineus* pests (Zilahi-Balogh 2002b). The introduced chamaemyiid, *Neoleucopis tapiae*, has successfully controlled *P. boernerii* in New Zealand and *P. pini* in Hawaii (Culliney et al. 1988; Zondag and Nuttall 1989; Greathead 1995). Another introduced chamaemyiid, *Neoleucopis obscura*, was a successful control agent of *P. boernerii* in Chile; however, it failed to establish on the same pest in Australia (Wilson 1960; Mills 1990). The introduced anthocorid, *Tetraphleps raoi*, has reduced populations of *P. pini* in Kenya (Aloo and Karanja 1986).

Conclusion and research objectives

The only biological control programs to successfully reduce populations of adelgids are those targeting *Pineus* spp. The predatory agents responsible are members of the Chamaemyiidae (Diptera) and Anthocoridae (Hemiptera) families

(Zilahi-Balogh et al. 2002b). In the program for biological control of *A. tsugae* in the eastern U.S., only coleopteran predators have been evaluated and released. Zilahi-Balogh et al. (2002b) suggest future evaluation of natural enemies found in Asia should also include non-coleopteran orders. Cheah et al. (2004) consider both Asia and the PNW to be important areas for continued exploration for additional *A. tsugae* natural enemies. The PNW has large enough *A. tsugae* populations to support the native specialist, *Laricobius nigrinus*, an important predator in the *A. tsugae* biological control program. The PNW is also where several species of native and introduced chamaemyiids and some native anthocorids are associated with *A. piceae*.

The main objectives of this study are to 1) identify natural and introduced insect predators associated with *A. tsugae* infested western hemlocks in Oregon and Washington at regular intervals throughout two years, 2) describe phenology of predators in relation to *A. tsugae*, 3) assess correlation between abundance of predator species and prey density, and 4) record predator species reared from *A. tsugae* ovisacs or observed feeding directly on *A. tsugae*, with emphasis on identifying predators that have not previously been evaluated for *A. tsugae* feeding behavior. A secondary objective is to conduct seasonal surveys of predatory insects associated with *A. piceae* and *A. cooleyi* in the PNW for the purpose of documenting native and established predators.

Chapter 2: Predators Associated with Hemlock Woolly Adelgid (Hemiptera:
Adelgidae) Infested Western Hemlock in the Pacific Northwest.

Glenn R. Kohler, Vernon L. Stiefel, Kimberly F. Wallin, and Darrell W. Ross

Abstract

The hemlock woolly adelgid, *Adelges tsugae*, is causing widespread mortality of eastern hemlock, *Tsuga canadensis*, in the eastern United States. In the West, *A. tsugae* causes negligible damage to western hemlock, *Tsuga heterophylla*. Host tolerance traits and presence of endemic predators may be contributing to the relative tolerance of western hemlock to *A. tsugae*. Field surveys of the predator community associated with *A. tsugae* infestations on 116 *T. heterophylla* at 16 locations in Oregon and Washington were conducted every four to six weeks from March 2005 through November 2006. Predators collected from *A. tsugae* infested *T. heterophylla* represent 55 species in 14 families, listed in order of abundance: Derodontidae, Chamaemyiidae, Hemerobiidae, Coccinellidae, Cantharidae, Reduviidae, Miridae, Syrphidae, Chrysopidae, Coniopterygidae, Staphylinidae, Anthocoridae, Nabidae, and Raphidiidae. *Laricobius nigrinus* (Derodontidae), *Leucopis argenticollis*, and *Leucopis atrifacies* (Chamaemyiidae) are the most abundant predators; together comprising 59% of predator specimens recovered. The abundance of derodontid larvae, *L. nigrinus* adults, chamaemyiid larvae, and *L. argenticollis* adults was found to be positively correlated to *A. tsugae* density. The remaining 52 species represent a diverse complex of predators potentially attacking *A. tsugae*. However, many are known to feed on non-adelgid prey. Predators were most abundant when the two generations of *A. tsugae* eggs were present. The phenology of immature and adult predators suggests temporal partitioning of prey across all seasons. Fifteen predator

species were either reared from larvae to adult on a diet of *A. tsugae* in the laboratory or were observed feeding on *A. tsugae*. *L. argenticollis* and *L. atrifacies* were reared on *A. tsugae* in the laboratory and host records show them to feed exclusively on Adelgidae. Both species should be investigated as candidates for *A. tsugae* biological control in eastern North America.

Keywords

Adelges tsugae, *Tsuga heterophylla*, *Laricobius nigrinus*, *Leucopis argenticollis*, *Leucopis atrifacies*, predators

Introduction

In the eastern United States, the hemlock woolly adelgid, *Adelges tsugae* Annand, is an introduced pest of eastern hemlock, *Tsuga canadensis* (L.) Carrière, and Carolina hemlock, *Tsuga caroliniana* Engelmann. Originating from Japan, *A. tsugae* was first reported near Richmond, Virginia in 1951 (Stoetzel 2002; Havill et al. 2006). It is currently found from northeastern Georgia to southwestern Maine. It is thought the combination of bivoltine life cycle, wind dispersal, susceptible host trees, and few natural enemies contributes to the rapid spread of *A. tsugae* in the eastern U.S. (McClure 1989, 1990; Cheah and McClure 1996; Cheah et al. 2004). *A. tsugae* spreads at a rate of approximately 15.6 km per year in the southern part of its eastern U.S. range; however, expansion in the northern part is slowed to approximately 8.1 km per year where mean minimum temperatures are below -26° C (Shields and Cheah 2005; Evans and Gregoire 2006). Early symptoms of infestation, needle drop and reduced shoot growth, are followed in two to four years by limb dieback, increased exposure to blow down, and secondary attack by insects and diseases (Cheah et al. 2004). *T. canadensis* mortality can occur between four and ten years following initial infestation (McClure et al. 2001).

In its native range, *A. tsugae* is an innocuous pest of Japanese hemlocks [*Tsuga diversifolia* (Maxim.) Masters and *Tsuga sieboldii* Carrière] and Chinese hemlocks [*Tsuga chinensis* (Franchet) E. Pritzel, *Tsuga forrestii* Downie, and *Tsuga dumosa* (D. Don) Eichler] and only reaches high densities on ornamental or stressed trees (McClure et al. 2001; Del Tredici and Kitajima 2004). *A. tsugae* is also found in

western North America, from northern California to southeastern Alaska. Its hosts in this region are western hemlock, *Tsuga heterophylla* (Raf.) Sargent, and mountain hemlock, *Tsuga mertensiana* (Bong.) Carrière (Annand 1924; McClure 1992b). Also originating from Japan, the western *A. tsugae* are more genetically variable than those in eastern North America. This evidence, in addition to genetically tolerant host trees and the presence of a specialized predator, suggests an introduction to western North America that occurred long before the first *A. tsugae* specimen was collected from Washington in 1907 (Havill et al. 2006).

As with Asian hemlock species, *A. tsugae* infestations appear to cause negligible damage to the relatively tolerant *T. heterophylla* and *T. mertensiana*, rarely causing tree mortality in healthy stands (McClure 1992b). However, *A. tsugae* can reach high densities on orchard and ornamental *T. heterophylla*, occasionally causing injury and mortality (Furniss and Carolin 1977; McClure 1987, 1992b). These off-site trees grow in conditions which are known to increase susceptibility to *A. tsugae* attack; including compacted soil, xeric soil, deliberate stressing for seed production, or regular nitrogen fertilization (McClure 1987, 1992a, 1992b; Orwig et al. 2002; Zilahi-Balogh et al. 2003a).

Living within cottony flocculence at the base of hemlock leaves, *A. tsugae* is a minute (0.4-1.4 mm long) sucking insect that remains stationary for most its life. There are two generations per year, with oviposition occurring in late winter (progrediens eggs) and early summer (sistens eggs). A mobile crawler emerges from the egg and seeks out an unoccupied leaf base where it settles and molts to a first

instar nymph (McClure 1987). In early spring and summer the crawler stage can disperse to new trees via wind, nursery trade, birds, mammals, or humans (McClure 1990; Ward et al. 2004). The first instar nymph of the sistens generation will undergo a two to four month aestival diapause during late summer. There is no sexual reproduction of *A. tsugae* in North America, all individuals are reproduced parthenogenetically. In its native Asian range and in eastern North America, an alate sexuparae generation is produced in the spring. Sexuparae progeny (sexuales) are capable of sexual reproduction on spruce (*Picea* spp.) in Asia, but do not survive on any *Picea* spp. in eastern North America (McClure 1987, 1989). No alate sexuparae have been recorded in western North America (Zilahi-Balogh et al 2003a).

While impractical on a stand scale, immediate control for threatened ornamental hemlocks can be achieved by application of horticultural oils, insecticidal soaps, or pesticides (McClure 1992a; Webb et al. 2003; Ward et al. 2004). High mortality of hemlocks in the eastern U.S. is attributable to a combination of host-tree susceptibility and absence of natural enemies (Cheah and McClure 1996). Conversely, host tolerance traits and presence of endemic adelgid predators or pathogens may be contributing to the relative tolerance of western hemlock (Cheah and McClure 1996). Breeding for tolerance to *A. tsugae* in eastern hemlocks is being investigated and may provide management options in the future (Bentz et al. 2002). Several virulent fungal pathogens of *A. tsugae* have been discovered and are being evaluated as control agents (Costa et al. 2005). Unlike related families of Aphidoidea, *A. tsugae* has no known parasitoids (Cheah et al. 2004). It is believed that predators

play a role in regulating *A. tsugae* in western North America and Asia. Therefore, current efforts to prevent tree mortality in eastern North America are focused on developing a biological control program for *A. tsugae* (McClure 1992b; Ward et al. 2004; Cheah et al. 2004).

A large scale program for biological control of balsam woolly adelgid, *Adelges piceae* (Ratzeburg), in the U.S. and Canada was initiated in 1957. Twenty-five species of non-native predators were released, resulting in the establishment of eight species; none of which exerted any measurable control of *A. piceae* (Mitchell and Wright 1967; Harris and Dawson 1979; Schooley et al. 1984; Humble 1994). This failure has been attributed to poor seasonal synchrony with the host, low predator tolerance of winter conditions, and rapid host mortality preventing predator population increase (Montgomery and Lyon 1996; Mitchell and Buffam 2001; Zilahi-Balogh et al. 2002b).

A program for biological control of *A. tsugae* utilizing non-native predators was initiated in 1995 in the eastern U.S., resulting in importation of predators from Japan, China, and Canada. After thorough screening for host range and seasonal synchrony, three coleopteran predators of *A. tsugae* are currently being field evaluated for efficacy against *A. tsugae* in the eastern U.S. Two are coccinellid predators, *Sasajiscymnus tsugae* (Sasaji and McClure) from Japan and *Scymnus sinuanodulus* Yu et Yao from China, and one is a derodontid, *Laricobius nigrinus* Fender, from British Columbia. Foreign exploration for additional *A. tsugae* predators in China, Japan, and western North America is ongoing and efforts are being accelerated. Newly

discovered and promising foreign predators include new Asian species of Derodontidae and Coccinellidae (Cheah et al. 2004).

The only biological control agents to successfully reduce populations of adelgids are Chamaemyiidae (Diptera) and Anthocoridae (Hemiptera), employed in programs targeting *Pineus* spp (Aloo and Karanja 1986; Culliney et al. 1988; Zondag and Nuttall 1989). Zilahi-Balogh et al. (2002b) suggested future evaluation of natural enemies found in Asia should also include non-coleopteran orders. Cheah et al. (2004) consider both Asia and the Pacific Northwest (PNW) to be important areas for continued exploration for additional *A. tsugae* natural enemies.

Specific objectives of this study were to 1) identify native and introduced insect predators associated with *A. tsugae* infested western hemlocks in Oregon and Washington at regular intervals over two years, 2) describe phenology of predators in relation to *A. tsugae*, 3) assess correlation between abundance of predator species and prey density, and 4) record predator species reared from *A. tsugae* ovisacs or observed feeding directly on *A. tsugae*, with emphasis on identifying predators that have not previously been evaluated for *A. tsugae* feeding behavior. A secondary objective was to conduct seasonal surveys of predatory insects associated with *A. piceae* and *A. cooleyi* in the PNW for the purpose of documenting additional native and established predators of Adelgidae.

Materials and Methods

Field survey for predators of *A. tsugae*. Mature *T. heterophylla* representing both ornamental and seed orchard trees infested with *A. tsugae* were surveyed by beat sampling for potential insect predators every four to six weeks over 23 months beginning January 2005. By March 2005, 116 sample trees were established at 16 sites within 10 counties in western Oregon and Washington ranging from Corvallis, Oregon to Whidbey Island, Washington. Fourteen uninfested *T. heterophylla* were also sampled at five of these sites (Table 1). Twelve additional sites with *A. tsugae* infestations were visited but not included in sampling due to limited resources (Appendix A).

Predator sampling methods were modified from Montgomery and Lyon (1996) and Wallace and Hain (2000). Three branches per tree with similar *A. tsugae* density were selected at each visit and struck four times with PVC pipe above a plastic container with area of 0.16 m². Samples were pooled into one 0.5 m² area sample for each tree. The sampled areas were anywhere along the branch from tip to bole in the lower canopy (<2.5 m height), depending on where adelgids were located. Insects were collected with an aspirator or paintbrush. Adult insects were killed in sealed 9-dram plastic vials using Hot Shot No-Pest[®] Insecticide Strip (Spectrum Brands Inc., Atlanta, GA). Immature insects were killed in KAAD mixture (10 parts 95% ethanol, 1 part kerosene, 2 parts glacial acetic acid, and 1 part dioxane) and preserved in 70% ethanol (Borrer et al. 1989). Adult specimens were either identified by taxonomists or by comparison to previously identified museum specimens. Voucher specimens have

been deposited in the Oregon State Arthropod Collection, Department of Zoology, Oregon State University, Corvallis, Oregon. All winged Aphidoidea were collected in an effort to document the presence of alate *A. tsugae* sexuparae in western North America.

Developmental stages of *A. tsugae* present and a population score of *A. tsugae* woolly masses in the sample area were recorded at each visit. All 0.16 m² samples were assigned a hemlock woolly adelgid (HWA) population score at each visit based on the number of ovisacs visible in the sample area using the following scale: 0 = no ovisacs present, 1 = 1 to 25 ovisacs, 2 = 26-100 ovisacs, 3 = more than 100 ovisacs. The three scores were averaged for a single value per 0.5 m² sample. A similar trinomial scale was highly correlated with actual aphid population counts in an agricultural setting (Kohler and St. Clair 2005).

Field survey for predators of the balsam woolly adelgid and Cooley spruce gall adelgid. At nine dates from June 2005 to October 2006, predators were collected from balsam woolly adelgid, *Adelges piceae* (Ratzeburg), infestations on two grand fir, *Abies grandis* (Dougl. ex D. Don) Lindl., in northwest Oregon. Also at these dates, predators were collected from Cooley spruce gall adelgid, *Adelges cooleyi* (Gillette), infestations on two Douglas-fir, *Pseudotsuga menziesii* (Mirbel) Franco, and one Engelmann spruce, *Picea engelmannii* Parry ex Engelm., in western Oregon and Washington. *A. cooleyi* predators were collected using the same beat sampling methods used for *A. tsugae* sampling. *A. piceae* predators were collected by brushing adelgid wool on the bole with a 2-inch paintbrush over a beat sheet.

Laboratory rearing. Twig and bark samples with heavy *A. tsugae* and *A. piceae* infestations were removed for laboratory rearing of immature predators collected in the field. Twigs were placed in floral foam moistened with methylparaben (0.42 g/250 ml de-ionized water) to prevent fungal growth and kept in fine mesh screened quart sized jars or 9-dram plastic vials. Bark samples were placed in mesh screened 9-dram plastic vials. The rearing containers were held in a controlled environment chamber simulating light and temperature conditions of the field (Zilahi-Balogh et al. 2003b).

Analysis of alternate prey abundance. Scale insects (Coccoidea) feeding on *T. heterophylla* may be used as alternate sessile prey by some predator species. To assess the relative abundance of Coccoidea to *A. tsugae* on sample trees, both insects were counted on randomly selected terminal twig samples. Each twig sample consisted of several terminal growing points ranging from 2 to 10 cm in length, with a total cumulative twig length of 100 cm per sample. Eighty-one twigs were sampled from *A. tsugae* infested *T. heterophylla* at 12 survey sites and 12 twigs were taken from uninfested trees at 4 sites in November 2006. For *A. tsugae* infested twigs, Coccoidea abundance was subtracted from *A. tsugae* abundance to obtain difference values. A one-sample Student's t-test was used to determine if the difference between Coccoidea and *A. tsugae* abundances was significantly greater than zero. To satisfy assumptions of normality, the data was log transformed [$\log(x+5)$]. The student's t-test was performed using PROC TTEST in SAS/STAT software Version 9.1 (SAS Institute 1999).

Insect community structure analysis. Bivariate scatterplots among log transformed $[(\log(x+0.1))+1]$ insect taxa abundance and HWA population score values were examined to determine if linear relationships existed. Very few of these scatterplots had linear tendency and all exhibited clusters of points at the origin, or a “dust bunny” distribution, common in ecological community data due to a high proportion of zero values. An ordination was created using Non-metric Multidimensional Scaling (NMS) with PC-ORD software Version 5.57 beta, which did not require assumptions of normality and linearity (McCune and Grace 2002; McCune and Mefford 1999).

NMS was performed on a sample unit \times taxa abundance matrix. To reduce the affect of seasonality on taxa abundance, sample units (SUs) were pooled tree samples from a single site with abundance values summed over one year from December 2005 through November 2006. To correct for uneven sample size, the abundance of each taxon was divided by the number of 0.5 m² samples taken at each site over time. Five sites had both *A. tsugae* infested and uninfested trees; these sites were each divided into two separate SUs, for a total of 16 infested and 5 uninfested SUs (Table 1).

Rare taxa present in <10% of SUs were excluded from the analysis. 49 taxa were analyzed; including 10 immature predator families, 3 adult predator families, 26 adult predator species, and 10 non-predatory families. Some taxa, such as *Laricobius nigrinus*, were highly abundant relative to others by as much as three orders of magnitude in some SUs; therefore, a log transformation $[(\log(x+0.1))+1]$ was chosen to reduce this difference. To further equalize the influence of abundant and

uncommon families, SU abundances were relativized by the maximum value for each taxon. These adjustments reduced the beta diversity expressed as half-changes (β_D), skewness of taxa totals, and variability among taxa and SU totals (coefficients of variation, CV) in the taxa matrix.

A second matrix, sample unit \times environmental variable, contained latitude and HWA population score data averaged across each SU. Data were analyzed at the SU level; however, sample data were recorded separately for each tree and sample date to facilitate phenological observations.

NMS ordinales sample units in taxa space according to the best monotonic fit, or lowest stress, between ranked distances in the original data matrix and a random configuration of starting points in ordination space. Through iteration, NMS adjusts the positions of SUs in a stepwise fashion in the direction of steepest descent, or lowest stress. In order to avoid local stress minima, stress in the real data should be significantly lower than expected for random data, according to Monte Carlo tests (Kruskal 1964). NMS was performed using PC-ORD in autopilot mode with a Sørensen distance measure. Random starting points were used to begin 250 runs each of real and random data with a maximum of 500 iterations per run. Dimensionality of the ordination was determined by meeting criteria of lowest significant reduction in stress and minimum instability.

Nonparametric Multiplicative Regression (NPMR) was performed in HyperNiche version 1.12 to generate separate models for all 49 taxa using HWA population score as a predictor of taxa abundance (McCune and Mefford 2004). The

adjusted data from December 2005 through November 2006 used for NMS analysis were also used for NPMR. Models for rare taxa found in fewer than three SUs are not reported. Predicted taxon abundance was estimated with a multiplicative smoothing function using Gaussian weighted local means of abundance values against HWA population score within a forward scanning window. Leave-one-out crossvalidation was used to exclude the measured data value at the point of the predicted response value. Strength of model fit is expressed as cross-validated R^2 (xR^2), which can be negative in a weak model (McCune 2006). HyperNiche “free search” generated 16 models for each taxon, only models with the maximum xR^2 are reported.

Table 1. Attributes of *Tsuga heterophylla* at sixteen Pacific Northwest U.S. locations surveyed for predators of *Adelges tsugae*.

State, County, City	Site code	Latitude (N)	Longitude (W)	Elev. (m)	Mean tree height (m)	Mean DBH ^a (cm)	Trees sampled ^b
OR, Benton, Corvallis	OS	44° 34.064'	123° 16.563'	69	7	12.8	3
OR, Polk, Bethel Heights	EH	45° 02.928'	123° 07.494'	191	5.5	17.2	15 (4)
OR, Marion, St. Paul	SO	45° 08.693'	122° 59.022'	32	10.3	28.9	20 (3)
OR, Clackamas, Colton	HS	45° 13.680'	122° 23.220'	306	10.5	34.3	7 (2)
OR, Clackamas, Sandy	SA	45° 22.071'	122° 13.748'	400	13.3	39.3	9
OR, Multnomah, Portland	HA	45° 30.936'	122° 43.151'	226	22.3	71.7	9
OR, Multnomah, Portland	GP	45° 32.420'	122° 37.817'	61	17.3	63.6	4
WA, Thurston, Tumwater	DA	47° 00.672'	122° 53.754'	30	11.5	40.5	1
WA, Thurston, Olympia	TT	47° 02.454'	122° 54.054'	19	4.0	15.0	6
WA, Thurston, Olympia	JG	47° 02.448'	122° 53.460'	22	6.1	15.5	3
WA, Pierce, Tacoma	PD	47° 18.246'	122° 30.979'	10	17.3	53.7	5
WA, King, Vashon	AP	47° 27.048'	122° 30.087'	122	14.2	39.0	2
WA, King, Vashon	GR	47° 27.223'	122° 26.950'	60	13.3	61.0	3
WA, Clallam, Gardiner	RC	48° 04.077'	122° 57.607'	83	4.0	23.2	10 (3)

Table 1. (Continued).

State, County, City	Site code	Latitude (N)	Longitude (W)	Elev. (m)	Mean tree height (m)	Mean DBH ^a (cm)	Trees sampled ^b
WA, Clallam, Sequim	WS	48° 06.483'	123° 12.553'	46	5.8	19.8	9 (2)
WA, Island, Coupeville	WI	48° 12.036'	122° 37.740'	59	4.2	20.4	10
						Total	116 (14)

^a DBH = diameter at breast height (1.4 m).

^b Uninfested trees sampled in parentheses.

Results

Field survey for predators of *A. tsugae*. From January 2005 to November 2006, 2,230 beat samples were collected; from which 11,120 insect specimens were collected representing 104 insect families in 12 orders. 55 predatory insect species were identified from *A. tsugae* infested trees representing 43 genera in 14 families within four orders. The number of specimens, species, and genera collected in each predator family are listed in Table 2. A total of 6,389 predators were collected from *A. tsugae* infested *T. heterophylla* over 23 months. Three predator species comprise 59% of all adult and immature predators collected.

The most abundant predator species was *Laricobius nigrinus* Fender (Derodontidae) at 42.6% of the total. One individual out of 756 derodontid adults was identified as *Laricobius laticollis* Fall. Chamaemyiidae were the second most common predators at 16.3% of the total. Two species of chamaemyiid were collected, *Leucopis argenticollis* Zetterstedt and *Leucopis atrifacies* (Aldrich). Of the 99 adult Chamaemyiidae identified from all samples, 86 were *L. argenticollis* and 13 were *L. atrifacies*. Abundance of Hemerobiidae larvae, Derodontidae larvae, *L. nigrinus* adults, and Chamaemyiidae larvae per sample was considerably higher in samples collected from *A. tsugae* infested trees when compared to samples from uninfested trees at five locations (Table 3).

Table 2. Abundance of adult and immature predators collected from *Adelges tsugae* infested *Tsuga heterophylla* in the Pacific Northwest, January 2005 through November 2006.

Order: Family^a	Number of species and (genera) identified	Number of collection sites (n = 16)	Number of adults and (immatures)	Percentage of total abundance
Coleoptera: Derodontidae	2 (1)	16	756 (1,967)	42.6
Diptera: Chamaemyiidae	2 (1)	15	102 (937)	16.3
Neuroptera: Hemerobiidae	4 (1)	15	129 (402)	8.3
Coleoptera: Coccinellidae	13 (10)	16	366 (145)	8.0
Coleoptera: Cantharidae	4 (3)	9	408 (5)	6.5
Hemiptera: Reduviidae	2 (2)	16	140 (169)	4.8
Hemiptera: Miridae	5 (5)	15	159 (139)	4.7
Diptera: Syrphidae	4 (3)	16	7 (197)	3.2
Neuroptera: Chrysopidae	3 (2)	15	8 (139)	2.3
Neuroptera: Coniopterygidae	2 (2)	15	71 (70)	2.2
Coleoptera: Staphylinidae	6 (6)	6	41 (0)	0.6
Hemiptera: Anthocoridae	4 (4)	9	16 (2)	0.3
Hemiptera: Nabidae	3 (2)	7	10 (3)	0.2

Table 2. (Continued).

Order: Family	Number of species and (genera) identified	Number of collection sites (n = 16)	Number of adults and (immatures)	Percentage of total abundance
Neuroptera: Raphidiidae	1 (1)	1	1 (0)	0.02
Totals	55 (43)		2,214 (4,175)	

^a Listed in order of descending abundance.

Table 3. Comparison of predator abundance among *Adelges tsugae* infested and uninfested *Tsuga heterophylla* at five locations in the Pacific Northwest. Mean per sample abundance data are pooled across location and time from December 2005 through November 2006.

Order	Taxa ^a	Mean abundance per 100 samples (\pm SE)	
		<i>A. tsugae</i> infested samples (n = 525)	uninfested samples (n = 129)
Hemiptera	Miridae nymphs	10.9 (\pm 3.0)	11.6 (\pm 5.5)
	<i>Ceratocapsus apicatus</i> Van Duzee adults	6.9 (\pm 2.0)	14.7 (\pm 7.4)
	<i>Deraeocoris brevis</i> (Uhler) adults	3.0 (\pm 1.5)	0.8 (\pm 0.8)
	Nabidae adults	0.2 (\pm 0.2)	0
	Anthocoridae adults	1.3 (\pm 0.6)	1.6 (\pm 1.1)
	Reduviidae nymphs	5.0 (\pm 1.6)	0.8 (\pm 0.8)
	<i>Empicoris rubromaculatus</i> (Blackburn) adults	5.5 (\pm 1.9)	0
Neuroptera	Coniopterygidae larvae	1.3 (\pm 0.6)	0
	<i>Conwentzia californica</i> Meinander adults	1.3 (\pm 0.5)	1.6 (\pm 1.1)
	Hemerobiidae larvae	20.2 (\pm 3.0)	0.8 (\pm 0.8)
	<i>Hemerobius</i> spp. adults	6.7 (\pm 1.2)	0
	Chrysopidae larvae	5.7 (\pm 1.2)	1.6 (\pm 1.1)
Coleoptera	Staphylinidae adults	3.0 (\pm 0.9)	1.6 (\pm 1.1)

Table 3. (Continued).

Order	Taxa ^a	Mean abundance per 100 samples (\pm SE)	
		<i>A. tsugae</i> infested samples (n = 525)	uninfested samples (n = 129)
Coleoptera	Cantharidae		
	<i>Dichelotarsus piniphilus</i> (Eschscholtz) adults	39.6 (\pm 26.0)	2.3 (\pm 1.7)
	Derodontidae larvae	79.4 (\pm 23.0)	0.8 (\pm 0.8)
	<i>Laricobius nigrinus</i> Fender adults	46.9 (\pm 8.1)	0
	Coccinellidae larvae	3.2 (\pm 1.4)	0.8 (\pm 0.8)
	<i>Coccinella septempunctata</i> L. adults	1.9 (\pm 0.7)	4.7 (\pm 3.3)
	<i>Cycloneda polita</i> Casey adults	1.9 (\pm 0.6)	1.6 (\pm 1.1)
	<i>Mulsantina picta</i> (Randall) adults	1.3 (\pm 0.5)	0.8 (\pm 0.8)
	<i>Rhyzobius lophanthae</i> (Blaisdell) adults	0.2 (\pm 0.2)	2.3 (\pm 2.3)
	<i>Stethorus punctillum</i> Weise adults	1.9 (\pm 0.8)	3.1 (\pm 1.5)
	<i>Zilus</i> sp. adults	4.4 (\pm 1.4)	6.2 (\pm 4.5)
Diptera	Syrphidae larvae	9.0 (\pm 1.9)	0
	Chamaemyiidae larvae	15.0 (\pm 5.1)	0
	<i>Leucopis argenticollis</i> Zetterstedt adults	2.9 (\pm 0.8)	0

^a Only the most abundant species are shown. For a complete species list, see Appendix B.

The third most abundant predator family was Hemerobiidae at 8.3% of the total, represented by four species of *Hemerobius*. Both adult and larval hemerobiids were difficult to visually identify to species.

Thirteen species of coccinellids represented 8% of all predators. The most common species of adult coccinellids were *Stethorus punctillum* Weise, *Mulsantina picta* (Randall), *Coccinella septempunctata* L., *Rhyzobius lophanthae* (Blaisdell), *Zilus* sp. Mulsant, and *Cycloneda polita* Casey, in order of abundance (Appendix B). Abundance of these coccinellid species per sample was not noticeably higher in samples from *A. tsugae* infested trees when compared to samples from uninfested trees (Table 3). *M. picta* adults were present at 14 out of the 16 *A. tsugae* infested sites, more than any other coccinellid predator (Appendix B). Three coccinellid species, *Exochomus quadripustulatus* (L.), *Harmonia axyridis* (Pallas), and *M. picta* were identified as larvae; 83% of which were *M. picta* (n = 76). A non-predatory coccinellid, *Psyllobora vigintimaculata* (Say), was more abundant on *A. tsugae* infested trees than any predatory coccinellid species; it was not included in any analyses of coccinellid predators (data not shown).

Four species of Cantharidae represented 6.5% of all predators, 98% of which were *Dichelotarsus piniphilus* (Eschscholtz) adults. However, 133 adult *D. piniphilus* were collected in one sample from a single tree in April 2006, which was 33% of all *D. piniphilus* collected from infested trees in two years. In the spring, *D. piniphilus* adults were observed aggregating in high numbers on some *A. tsugae* infested trees

and feeding on *A. tsugae* progrediens eggs. *D. piniphilus* is likely also consuming *L. nigrinus* and *Leucopis* spp. larvae that are present in *A. tsugae* ovisacs at that time.

Observations of *A. tsugae* life cycle in Oregon and Washington during this study were similar to those recorded by Zilahi-Balogh (2003a) in British Columbia (Figs. 1 - 3). At several sites, high *A. tsugae* densities were similar to those that would induce density dependant alate sexuparae production in the eastern U.S. In spite of this, no alate *A. tsugae* were found during two years of sampling.

Predators were present throughout the year on *A. tsugae* infested *T. heterophylla*; however, annual peak abundances tended to occur during the spring and/or early summer when *A. tsugae* eggs were present (Figs. 1 - 6). The phenology of predators beginning fall 2005 shows the peak abundance of Hemipteran predators and Chrysopidae larvae occurred during the summer months across all sites, when *A. tsugae* sistens were present (Figs. 1 - 3). The numbers of both adult and immature Hemiptera were similar during times of peak abundance at most sites (Figs. 1 - 3). With the exception of Coccinellidae near Salem, Oregon (Fig. 4A), the numbers of holometabolous predator larvae far exceeded numbers of adults during the spring and summer (Figs. 1 - 6). Hemerobiidae larvae were most abundant during the spring across all sites, likely feeding on *A. tsugae* progrediens eggs. In Washington, hemerobiid larvae were also most abundant during the summer (Fig. 3B). Hemerobiid adults were collected in low numbers throughout the year at most sites (Figs. 1 - 3).

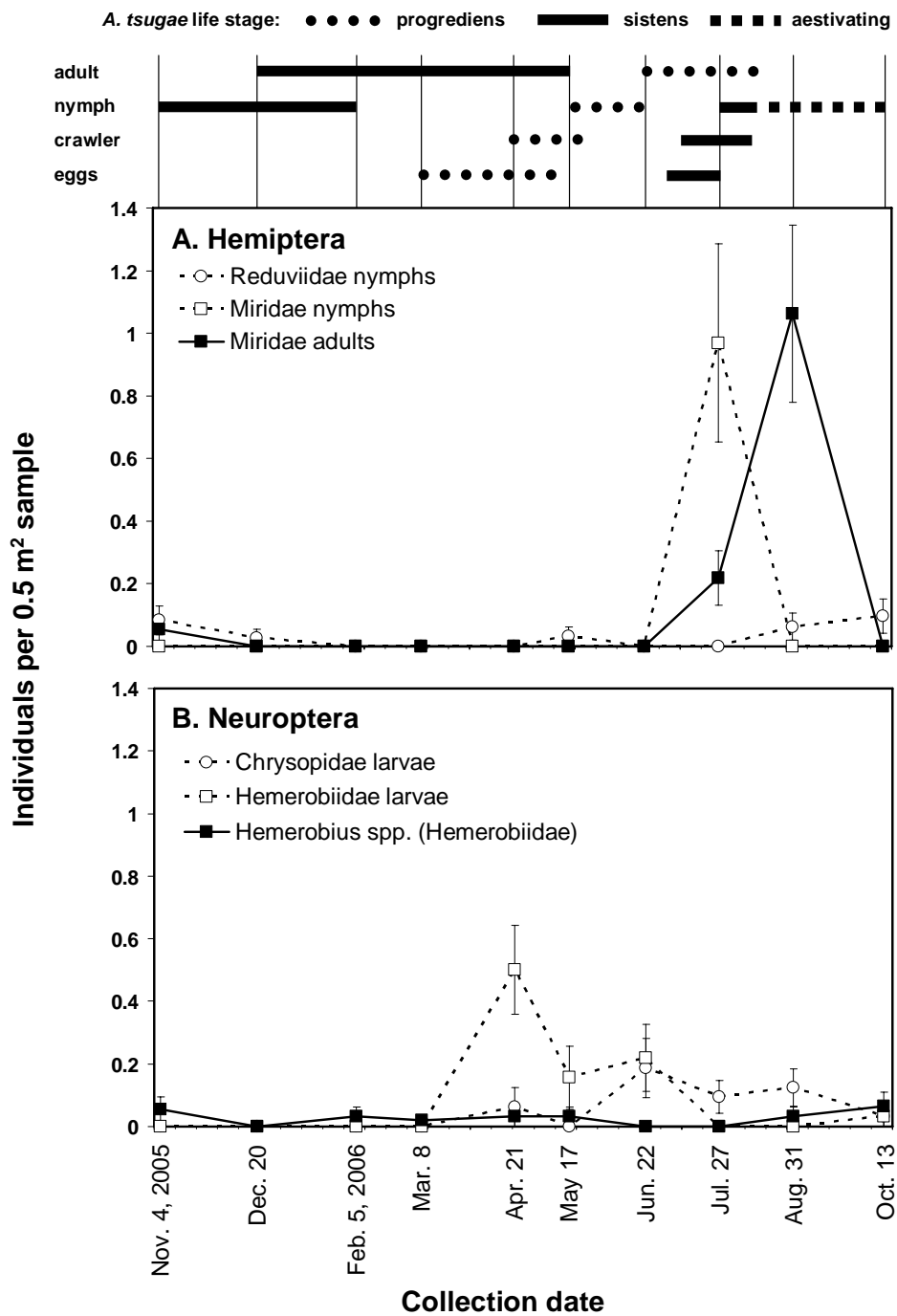


Figure 1. Abundance of predatory Hemiptera (A) and Neuroptera (B) sampled from *A. tsugae* infested western hemlock in the Salem area of northwest Oregon over one year beginning fall 2005. *A. tsugae* life cycle based on observations at Salem locations. Adults, solid lines; immatures, dashed lines. Error bars are \pm standard error.

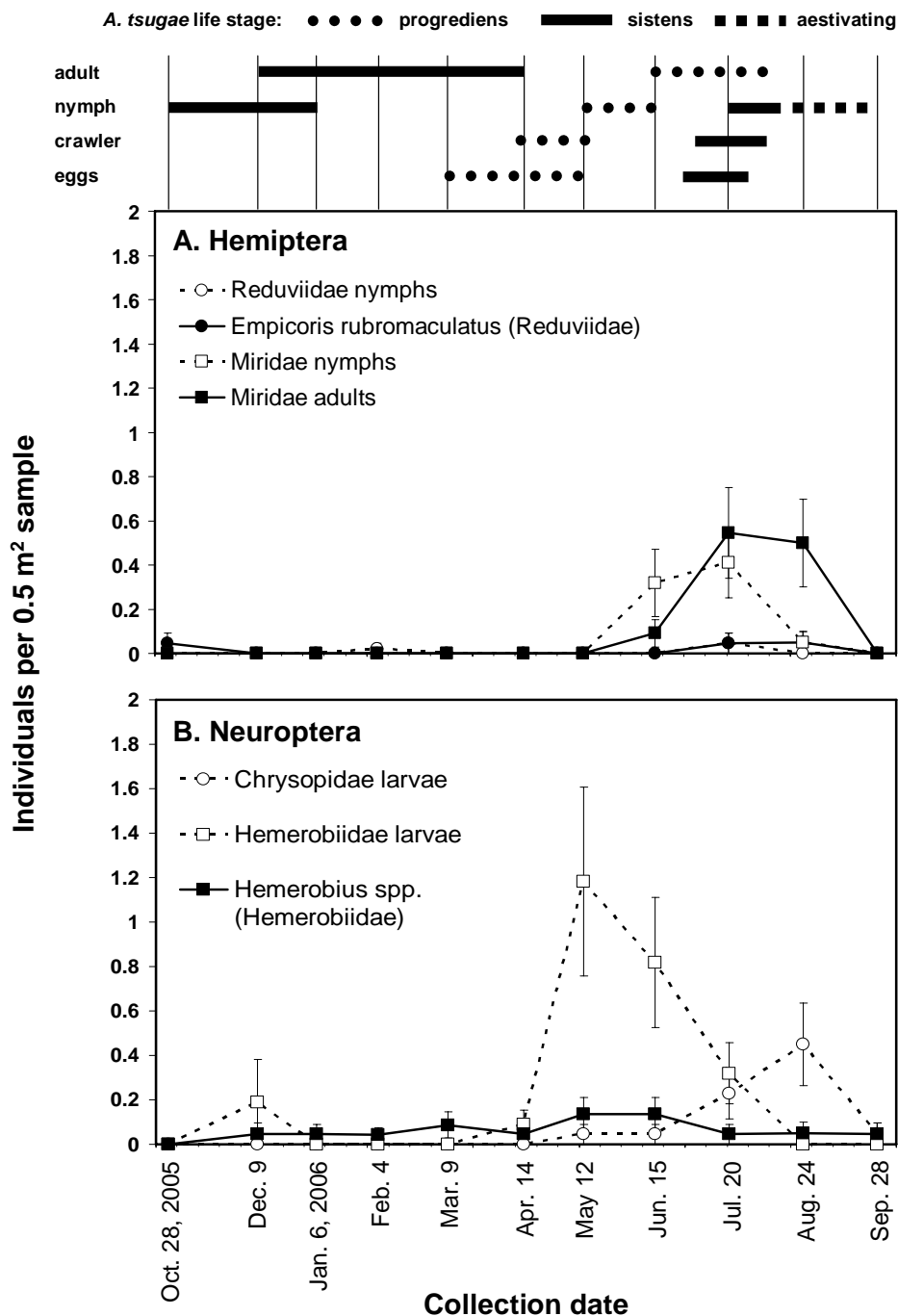


Figure 2. Abundance of predatory Hemiptera (A) and Neuroptera (B) sampled from *A. tsugae* infested western hemlock in the Portland area of northwest Oregon over one year beginning fall 2005. *A. tsugae* life cycle based on observations at Portland locations. Adults, solid lines; immatures, dashed lines. Error bars are \pm standard error.

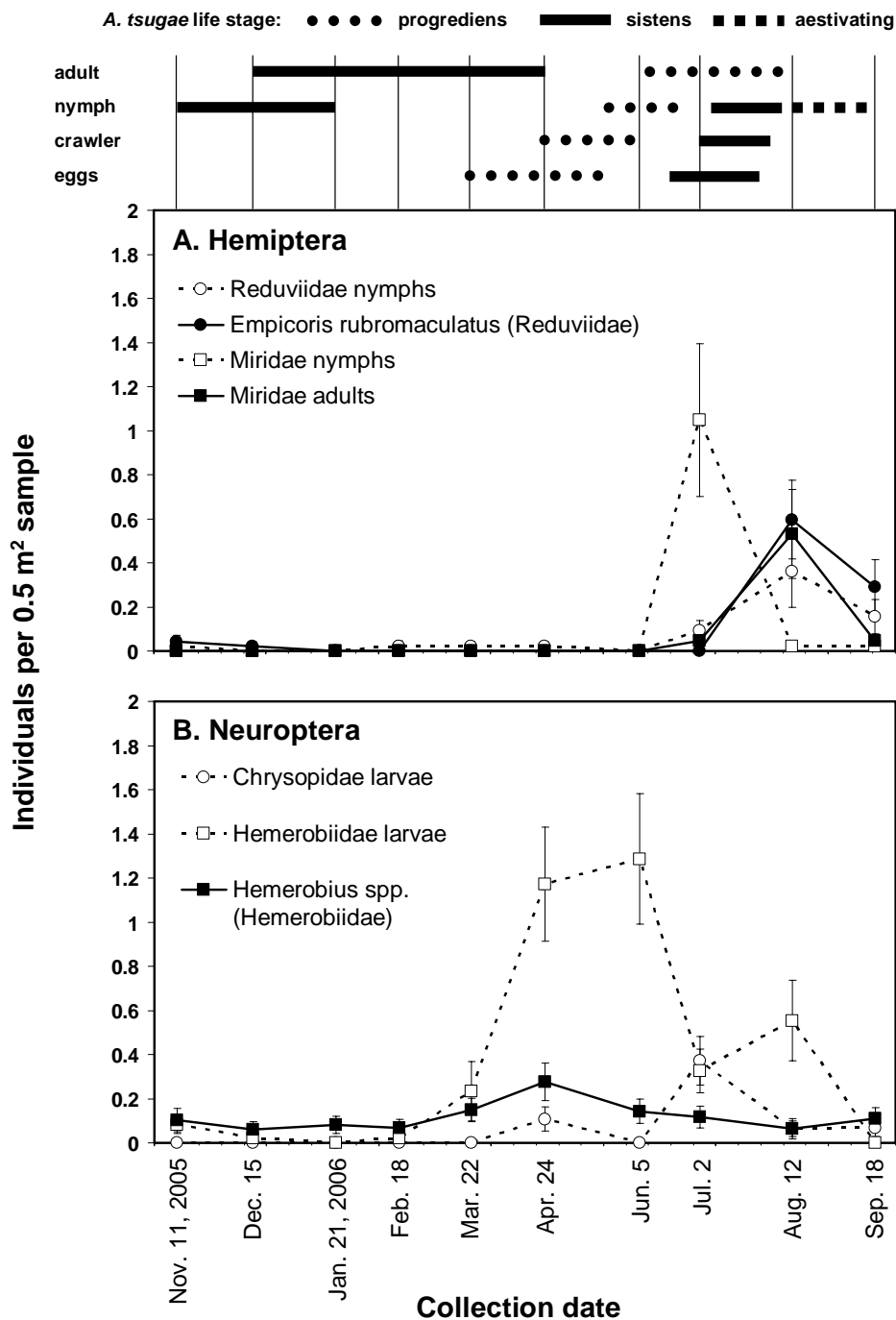


Figure 3. Abundance of predatory Hemiptera (A) and Neuroptera (B) sampled from *A. tsugae* infested western hemlock in western Washington over one year beginning fall 2005. *A. tsugae* life cycle based on observations at all Washington locations. Adults, solid lines; immatures, dashed lines. Error bars are \pm standard error.

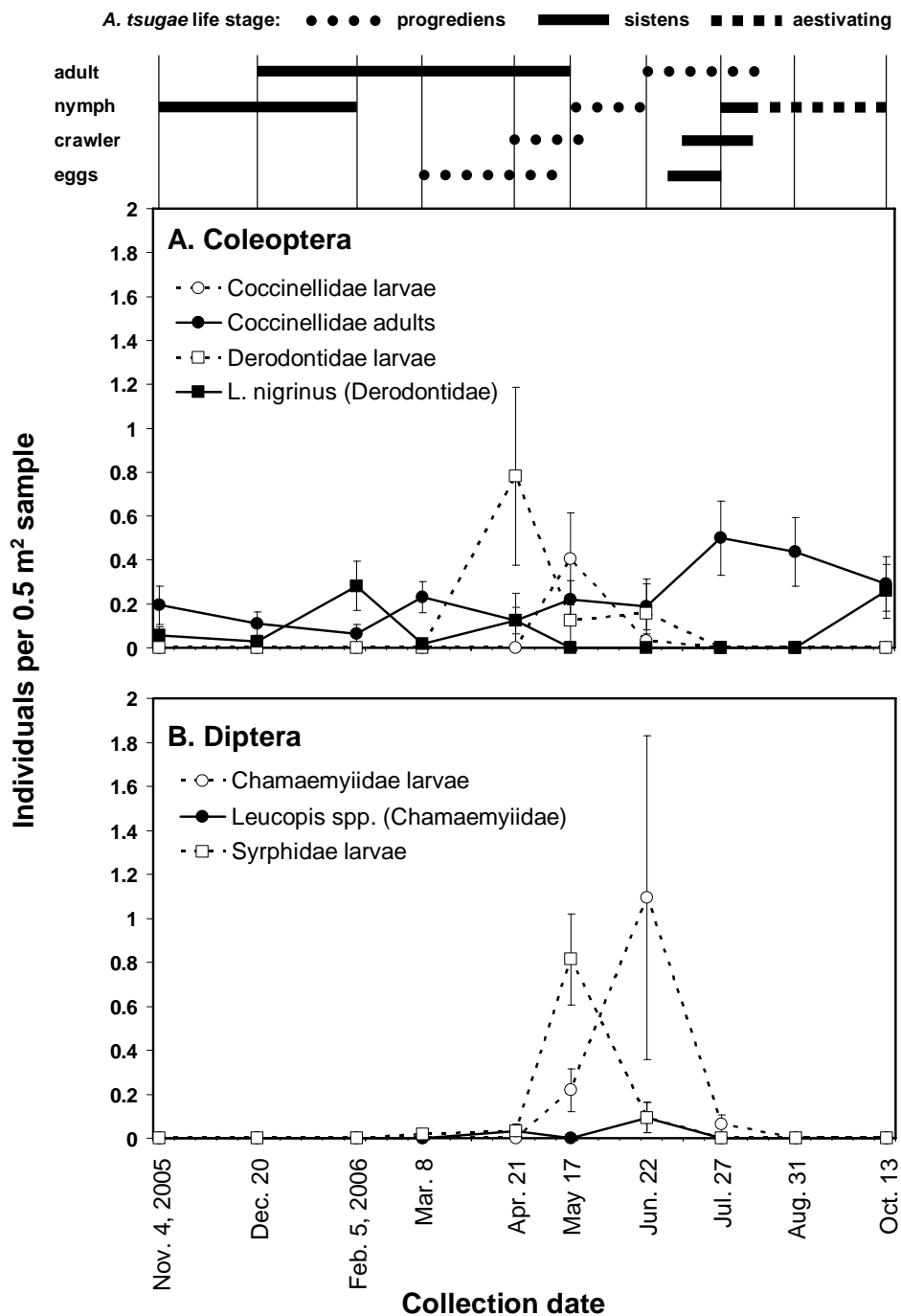


Figure 4. Abundance of predatory Coleoptera (A) and Diptera (B) sampled from *A. tsugae* infested western hemlock in the Salem area of northwest Oregon over one year beginning fall 2005. *A. tsugae* life cycle based on observations at Salem locations. Adults, solid lines; immatures, dashed lines. Error bars are \pm standard error.

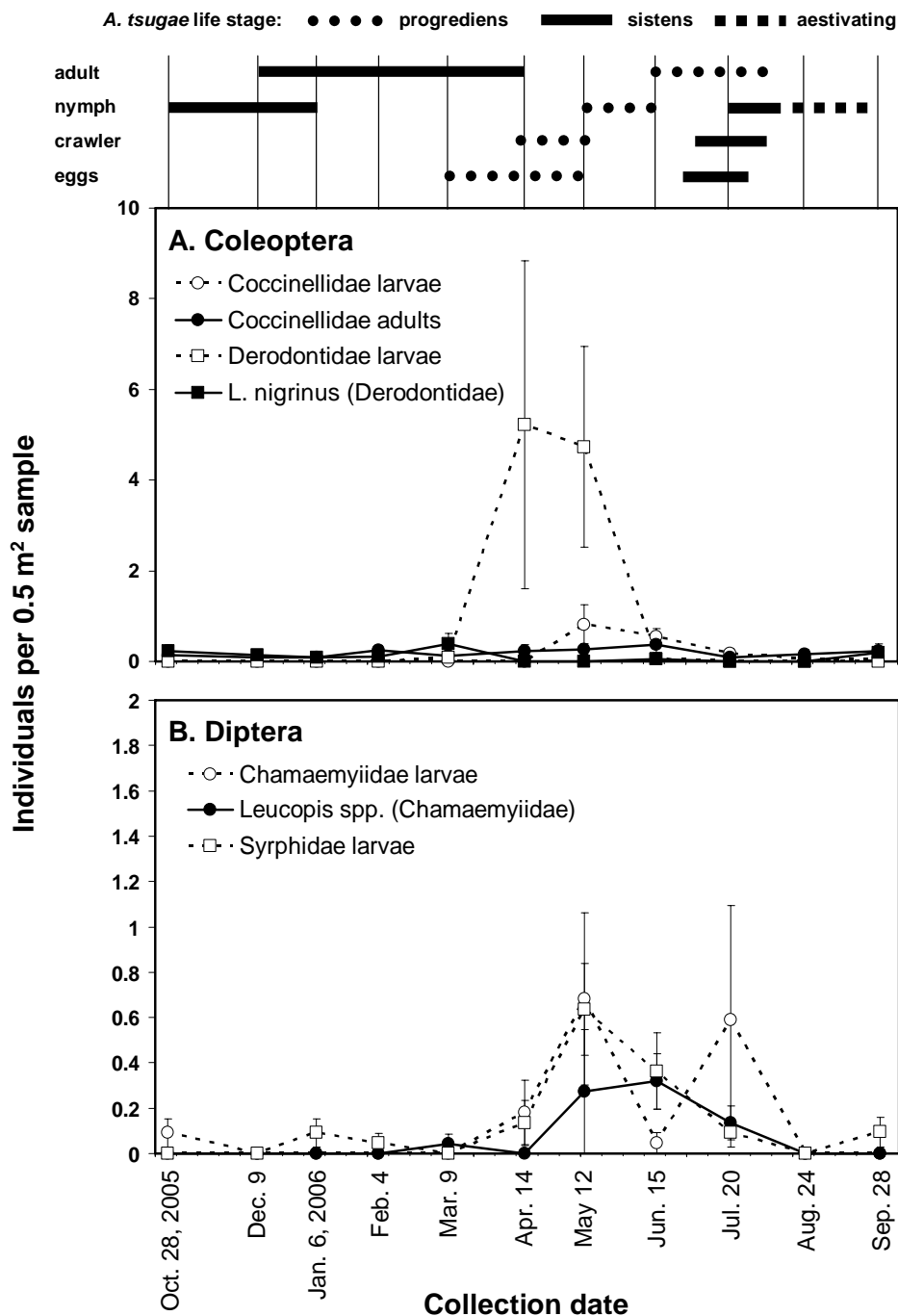


Figure 5. Abundance of predatory Coleoptera (A) and Diptera (B) sampled from *A. tsugae* infested western hemlock in the Portland area of northwest Oregon over one year beginning fall 2005. *A. tsugae* life cycle based on observations at Portland locations. Adults, solid lines; immatures, dashed lines. Error bars are \pm standard error.

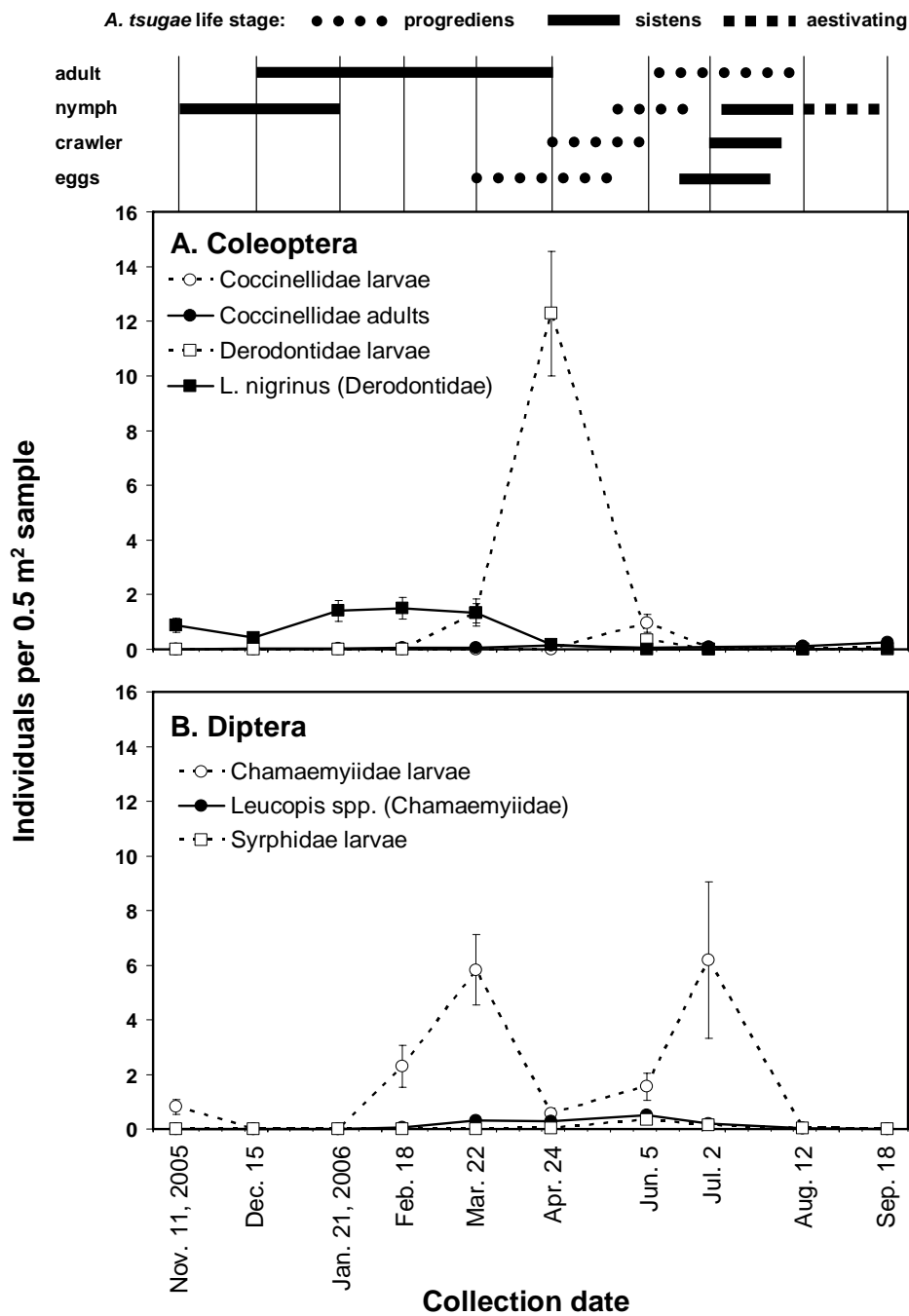


Figure 6. Abundance of predatory Coleoptera (A) and Diptera (B) sampled from *A. tsugae* infested western hemlock in western Washington over one year beginning fall 2005. *A. tsugae* life cycle based on observations at all Washington locations. Adults, solid lines; immatures, dashed lines. Error bars are \pm standard error.

Derodontid larvae were the most abundant Coleopteran predators during the spring at all sites (Figs. 4A, 5A, and 6A). They were the most abundant of all predators during the spring at Portland, Oregon and Washington sites (Figs. 5A and 6A). All the derodontid larvae are probably *L. nigrinus* and appear to feed exclusively on *A. tsugae* progrediens eggs and nymphs. *L. nigrinus* adults were collected throughout the year except during the summer when *L. nigrinus* aestivates as pupae in the soil. Coccinellid larvae of various species were also collected during the spring and early summer, but were far less abundant than derodontid larvae at Portland and Washington sites. Coccinellid adults were collected in low numbers throughout the year (Figs. 4A, 5A, and 6A).

Chamaemyiidae larvae were the most abundant of the holometabolous predators collected during the early summer at all sites, suggesting that chamaemyiids may be important predators of *A. tsugae* sistens eggs and nymphs (Figs. 4B, 5B, and 6B). At Portland and Washington sites, chamaemyiid larval abundance showed two distinct peaks of equivalent numbers during the spring and early summer, indicating that they feed on both progrediens and sistens eggs (Figs. 5B and 6B). At these sites, a smaller number of chamaemyiid larvae were collected in November. Chamaemyiid and syrphid larvae were collected during the spring in similar quantities at Oregon sites, suggesting the possibility of competition for progrediens eggs (Fig. 4B and 5B). Competition between chamaemyiid and derodontid larvae for progrediens eggs is also possible during the spring (Figs. 4 - 6).

Analysis of alternate prey abundance. At least one individual of two scale insect species, *Chionaspis pinifoliae* (Fitch) (Diaspididae) and an unidentified Coccidae, were present on 77% (n = 81) of *A. tsugae* infested *T. heterophylla* twig samples. Across 12 sites, the mean (\pm SE) density of *A. tsugae* was ten-fold that of scale insects; 111.3 ± 7.8 and 11.9 ± 2.0 (n = 81), respectively. The differences between abundance of *A. tsugae* and scale insects were significantly greater than zero (t = 24.1; df = 80; $P < 0.0001$). Scale insects were also present on twigs that were not infested with *A. tsugae* at a mean (\pm SE) density of 6.8 ± 2.4 individuals per twig sample (n = 12).

Field survey for predators of *A. piceae* and *A. cooleyi*. Nine predator families representing four orders were collected from *A. cooleyi*. Eleven species were identified as adults, all of which were also found associated with *A. tsugae* (Appendix C). One alate *A. cooleyi* was collected. Only two predator families, Reduviidae and Chamaemyiidae, were collected from *A. piceae* (Appendix C). Four of the chamaemyiid larvae were reared to adults in the lab and identified as *Neoleucopis* [= *Leucopis*] *tapiae* (Blanchard), a native species.

Laboratory rearing. The following predators were reared from field collected larvae to adults on a diet of *A. tsugae* in the laboratory: *Conwentzia californica* Meinander (Coniopterygidae), *Semidalis angusta* (Banks) (Coniopterygidae), *Hemerobius bistrigatus* Currie (Hemerobiidae), *Hemerobius pacificus* Banks (Hemerobiidae), *Chrysoperla downesi* (Smith) (Chrysopidae), *E. quadripustulatus* (Coccinellidae), *Harmonia axyridis* (Pallas) (Coccinellidae), *M. picta* (Coccinellidae),

L. argenticollis (Chamaemyiidae), *L. atrifacies* (Chamaemyiidae), and *Syrphus opinator* (Osten Sacken) (Syrphidae).

Chamaemyiid larvae attacked eggs and nymphs of both progrediens and sistens generation *A. tsugae* in the lab. Larval development lasted approximately one week. Pupation occurred on the stem near adelgid ovisacs where puparia were firmly attached. Larvae that pupated in November and were held in a controlled environment chamber approximating field temperature and light regimes did not emerge as adults until the following March; these were exclusively *L. argenticollis*. Larvae of both *L. argenticollis* and *L. atrifacies* that pupated in the spring emerged as adults one to two months later. Adult *L. argenticollis* were field collected from February through July and emerged in the lab from March through July. Adult *L. atrifacies* were only present in the field and emerging in the lab from May through July. This evidence suggests that *L. argenticollis* is bivoltine with larvae present in both spring and fall. *L. argenticollis* larvae may be feeding on early instar *A. tsugae* sistens nymphs in the fall.

Field collected larvae of *L. nigrinus*, *Chrysopodes placita* (Banks) (Chrysopidae), *Empicoris rubromaculatus* (Blackburn) (Reduviidae) nymphs, and adults of *D. piniphilus* were observed feeding on *A. tsugae* eggs in the field and laboratory. Miridae, Nabidae, Anthocoridae, Raphidiidae, and Staphylinidae were not observed feeding on *A. tsugae*.

Nineteen families of parasitic Hymenoptera were collected from *T. heterophylla* in the field. There are no recorded parasites of adelgids, therefore all Hymenoptera were presumably attacking insects other than *A. tsugae*. *Megastigmus*

spp. (Torymidae), a seed chalcid that attacks *Tsuga* spp., were also collected (Appendix D). Five families of Hymenoptera were reared from pupae of *A. tsugae* predators. A *Pachyneuron* n. sp. (Pteromalidae), an unidentified *Pachyneuron* sp., and an unidentified *Melanips* sp. (Figitidae) were reared from *Leucopis* spp. pupae. The parasitism rate of *Leucopis* spp. pupae was moderate at 23% (n = 91). Syrphid pupae suffered a high parasitism rate of 89% (n = 18). *Syrphoctonus pallipes* (Gravenhorst) (Ichneumonidae) was the most common syrphid pupal parasitoid in addition to *Woldstedtius flavolineatus* (Gravenhorst) (Ichneumonidae), *Syrphophagus* sp. (Encyrtidae), and *Pachyneuron albutius* Walker (Pteromalidae). *Syrphophagus* sp. and *P. albutius* are both gregarious parasitoids; of the two syrphid pupae parasitized, each yielded 12 and 6 individuals, respectively. One specimen of *Helorus* sp. (Heloridae) emerged from a *Chrysoperla* spp. pupae.

Insect community structure analysis. A three-dimensional NMS solution was selected based on lowest stress of 10.82 with the highest rate of stress reduction evident in the NMS scree plot. Monte Carlo tests were significant for three dimensions and the solution was stable ($P = 0.004$, instability $< 1 \times 10^{-5}$). The cumulative proportion of total variance represented (r^2) by the three axes was 0.87. Beta diversity as expressed in half-changes (β_D) was 1.7 for the 49 most common insect taxa across all sample units.

The insect taxa composition of uninfested SUs is clearly different than the majority of *A. tsugae* infested SUs (Fig. 7). The ordination of axis 3 on 2 is rotated to load all the variation of HWA population score on axis 2. In this orientation, *A. tsugae*

density appears to be a strong gradient within the insect community ($r^2 = 0.77$). This orientation was also used to generate correlation statistics of insect taxa with axis 2; thereby, quantifying any possible relationship with HWA population score. The overlay of weighted taxon averages (centroids) in Figure 7 shows two groupings of taxa correlated with axis 2 ($r^2 > 0.2$). The nine taxa centroids to the right of the ordination center were positively correlated with axis 2, indicating an association with *A. tsugae* infested trees. Both larval and adult Derodontidae and Chamaemyiidae show a strong positive relationship to HWA population score. The two non-predatory taxa centroids to the left of center were negatively correlated with axis 2. The majority of the 39 predatory taxa included in the ordination had no strong relationship to axis 2, which indicates they may be feeding on something other than *A. tsugae*.

The ordination of axis 3 on 2 was subsequently rotated to load all the variation of latitude onto axis 2 ($r^2 = 0.23$). The variation of HWA population score on axis 2 in this orientation ($r^2 = 0.43$) had a stronger influence on insect community structure than latitude. In spite of ranging from Corvallis, Oregon to the northern Puget Sound in Washington, the composition of the *A. tsugae* predator community appears generally homogeneous. The most abundant predator families recovered were found at a majority of sites (Table 2).

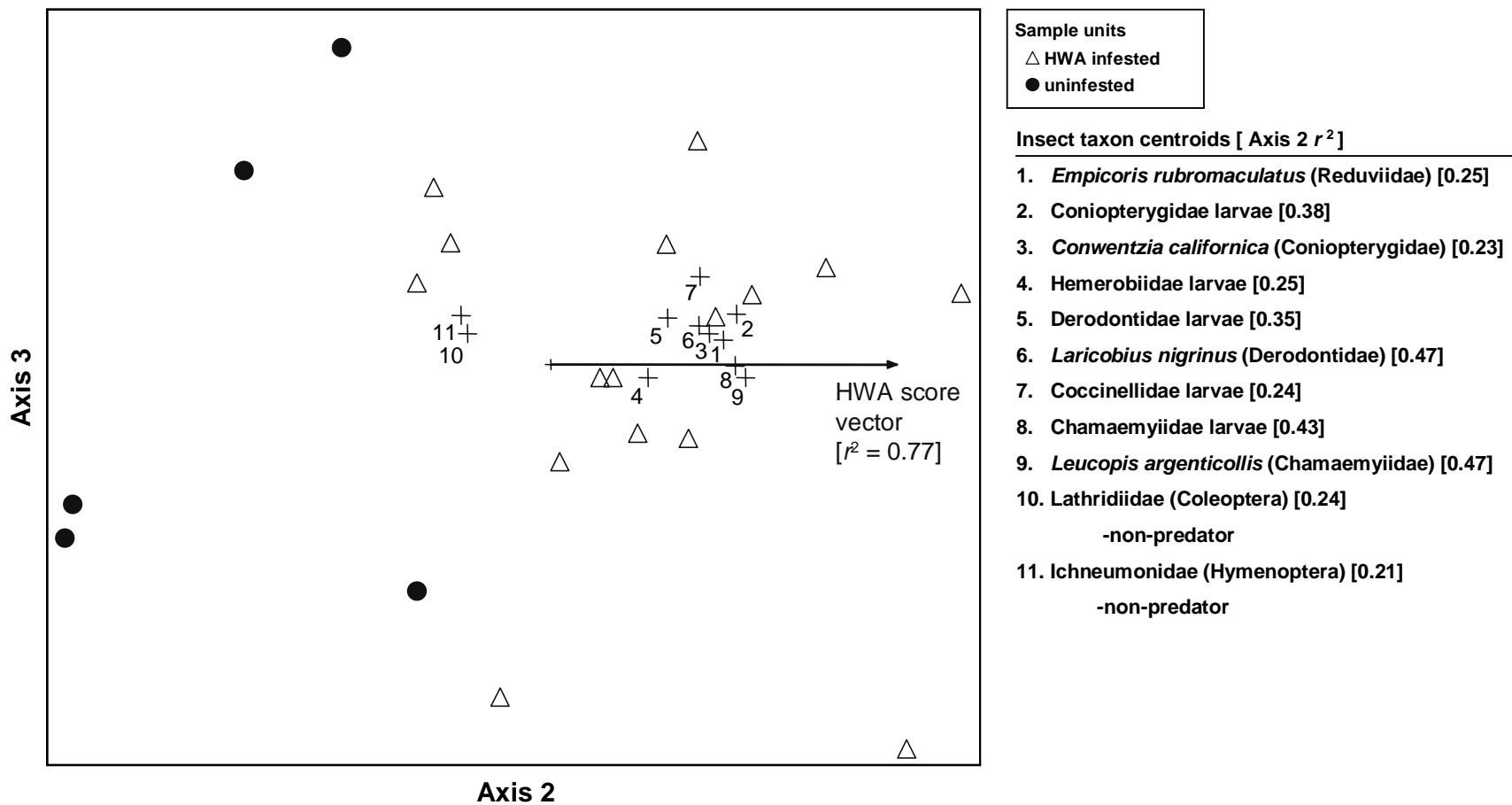


Figure 7. Three dimensional nonmetric multidimensional scaling (NMS) ordination joint plot of sample units in species space with ordination rotated to load variance of hemlock woolly adelgid (HWA) population score on axis 2 (r^2 -value = 0.77). A cross indicates weighted-mean centroid of insect taxa with r^2 -value > 0.2 on Axis 2. Sample units are per sample taxa abundance values pooled by location across one year, December 2005 through November 2006. All taxa are adults except where larvae is indicated.

To determine the effect of dominant predators on insect community structure, an NMS ordination was created following removal of adult and immature Derodontidae and Chamaemyiidae from the data set. A three-dimensional NMS solution was selected based on lowest stress of 11.08. Monte Carlo tests were significant for three dimensions and the solution was stable ($P = 0.0196$, instability $< 1 \times 10^{-5}$). The cumulative proportion of total variance represented (r^2) by the three axes was 0.77. Beta diversity as expressed in half-changes (β_D) was 1.5 for the 44 remaining insect taxa across all sample units.

There was little change in overall community structure following removal of the dominant predators from the ordination. Insect taxa composition of uninfested SUs remained different than the majority of *A. tsugae* infested SUs. The *A. tsugae* density gradient remained a strong influence on insect community composition ($r^2 = 0.80$). Correlation coefficients with the *A. tsugae* density gradient increased for some predators, such as *Deraeocoris brevis* (Uhler) (Miridae) adults ($r^2 = 0.22$), Hemerobiidae larvae ($r^2 = 0.37$), *Hemerobius* spp. adults ($r^2 = 0.22$), Coccinellidae larvae ($r^2 = 0.39$), *M. picta* adults ($r^2 = 0.27$), and Syrphidae larvae ($r^2 = 0.21$). Correlation coefficients of other predators decreased, such as *E. rubromaculatus* adults ($r^2 = 0.19$), Coniopterygidae larvae ($r^2 = 0.33$), and *C. californica* adults ($r^2 = 0.13$).

Six of the best NPMR models generated for 39 predatory taxa had cross-validated R^2 greater than 0.3 (Fig. 8). All six of these predator taxa show a predicted positive numerical response to increased *A. tsugae* density, indicating a possible

preference for trees with high *A. tsugae* infestation levels. In some cases, predicted per sample abundance values in Figure 8 were lower than actual peak abundances shown in Figures 1 through 6 because values used to generate NPMR models were averaged over a year. This difference was more pronounced for taxa with high peak abundance over narrow time periods, such as derodontid and chamaemyiid larvae. Models of larval and adult Derodontidae and Chamaemyiidae had strong positive correlations with HWA population score. Their abundance was predicted to increase in proportion to *A. tsugae* density. These predators also showed a positive relationship with HWA population score in the NMS ordination (Fig. 7).

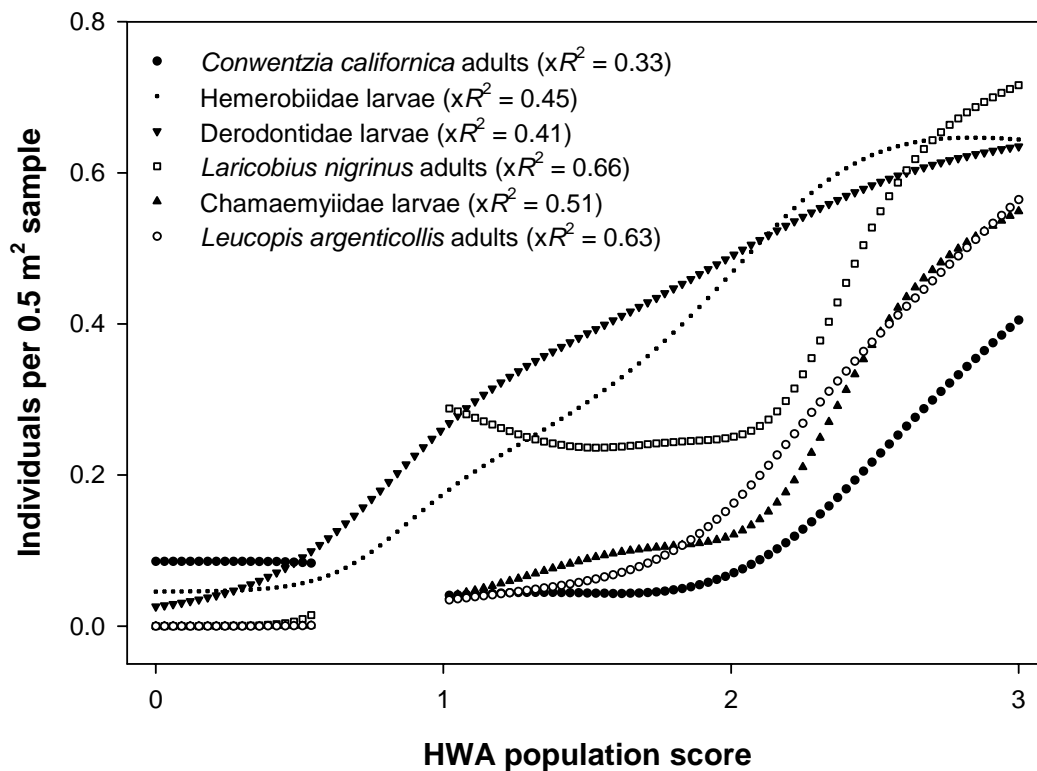


Figure 8. Response curves for six two-dimensional models of abundance predicted by hemlock woolly adelgid (HWA) population score from per sample abundance data pooled by location across one year, December 2005 through November 2006. Models generated by Gaussian local-mean nonparametric multiplicative regression (LM-NPMR). Breaks in the curves are due to insufficient predictor data. xR^2 , cross-validated R^2 ; HWA population score by sample, 0 = no ovisacs, 1 = 1-25, 2 = 26-100, 3 = >100.

Discussion

L. nigrinus was the most abundant *A. tsugae* predator on *T. heterophylla* in the Pacific Northwest during 2005 and 2006. The next most abundant predators were a mixture of *L. argenticollis* and *L. atrifacies*. These three species were most abundant as larvae feeding in *A. tsugae* ovisacs. Their numbers appear to increase in proportion to *A. tsugae* density, indicating a possible preference for highly infested trees. *L. nigrinus* and at least one *Leucopis* spp. feed on *A. tsugae* progrediens eggs in the spring. At least one *Leucopis* spp. also feeds on sistens eggs in early summer when *L. nigrinus* is not present.

An additional 52 predatory species representing thirteen families were collected from *A. tsugae* infested trees. The majority of these predators are recorded in the literature as generalists or specialist predators of non-adelgid prey, such as scale insects or spider mites. In total, these 52 species account for 41% of individuals collected during 2005 and 2006. Twelve of the 52 species were either reared on a diet of *A. tsugae* in the laboratory or observed feeding on *A. tsugae*. A separate community analysis of these less common predators showed insect composition and abundance to be strongly influenced by *A. tsugae* density. As a predator complex, they are likely contributing to some *A. tsugae* mortality; however, some species may also feed on other predators. No generalist predators should be considered good candidates for biological control (Kimberling 2004).

L. nigrinus is a well known specialist predator on *A. tsugae* that is well synchronized to the *A. tsugae* life cycle (Zilahi-Balogh 2003a). Female *L. nigrinus*

oviposit singly into *A. tsugae* ovisacs, where wool covered larvae feed, each consuming up to 250 eggs. *L. nigrinus* pupae aestivate at the same time and for the same duration as *A. tsugae*. *L. nigrinus* is active from October to May when the *A. tsugae* sistens generation is active and *L. nigrinus* larvae emerge during oviposition of progrediens eggs from February to May (Zilahi-Balogh et al. 2003a, 2003b).

L. nigrinus will feed on other adelgid species in the lab, but can only complete its development on a diet of *A. tsugae* (Zilahi-Balogh 2002a). *L. nigrinus* has been collected rarely from *A. piceae* in the PNW (Mitchell 1962). The specificity of *L. nigrinus* to its prey supports new evidence that *A. tsugae* was not recently introduced to western North America (Havill et al. 2006). *L. nigrinus* is currently being evaluated as a biological control agent of *A. tsugae* in the eastern U.S. As of 2005, 7,350 adults have been field released in eight states from Massachusetts to Georgia (Cheah et al. 2004; Mausel et al. 2005). *L. laticollis*, the other native derodontid species recovered as a single specimen in this survey, has no published adelgid host records but has been collected previously from *A. cooleyi* on Douglas-fir (Zilahi-Balogh et al. 2003a; R.G. Mitchell, personal communication, March 22, 2007).

L. argenticollis and *L. atrifacies* appear to be well synchronized to *A. tsugae* in the PNW so that larvae are present during oviposition of the two *A. tsugae* generations. Both species are specialist predators of Adelgidae. *L. argenticollis* is found in North America, Europe, and Asia. It has been recorded on *A. piceae* in eastern North America and on four *Pineus* species throughout its range (McAlpine and Tanasijtshuk 1972). The range of *L. atrifacies* is restricted to the western U.S.

(Tanasijtshuk 2002). Chamaemyiid specimens collected by R.G. Mitchell from *A. piceae* in Washington State during 1959 and 1960 were later identified by Tanasijtshuk (2002) as *L. atrifacies*. Both *L. atrifacies* and *L. argenticollis* were collected in large numbers from unidentified *Pineus* spp. on various pines in the San Francisco Bay area of California (Greathead 1995). Very little is known about the biology and life cycles of these species. Unidentified larval *Leucopis* spp. have been recovered from *A. tsugae* infestations in eastern North America, China, and Japan (Wallace and Hain 2000; M.E. Montgomery, personal communication, November 15, 2006).

Coccinellidae was the most speciose predator family in the PNW, as they are in China (Yu et al. 2000). Of the four most abundant coccinellid species, only *M. picta* was observed feeding on *A. tsugae*. The most common coccinellid larvae identified in this survey were *M. picta*. However, *M. picta* also feeds on *Myzocallis coryli* (Goetze) (Aphididae) and has been recorded in pear and apple orchards, suggesting it may be a generalist predator (Messing and AliNiazee 1985; Miliczky and Horton 2005). Other coccinellids abundant in this survey include a well known generalist, *C. septempunctata*, a spider mite specialist, *S. punctillum*, and a scale insect predator, *R. lophanthae*; all are introduced species (Elliot et al. 1996; Stathas 2000; Raworth, and Robertson. 2002). Coccinellids collected in this survey that have been recorded feeding on *Adelges* spp. include *C. polita*, *C. septempunctata*, *E. quadripustulatus*, *H. axyridis*, and *M. picta* (Mitchell 1962; Eichhorn 1969; Rao and Ghani 1972; Wallace and Hain 2000).

E. rubromaculatus (Reduviidae) and *C. californica* (Coniopterygidae) were not among the most abundant predators collected from *A. tsugae*; however, they both had a positive relationship with HWA population score (Fig. 7). *C. californica* was also predicted to increase with *A. tsugae* density (Fig. 8). Both of these species also feed on non-adelgid prey. *E. rubromaculatus* has been recorded on hazelnut trees (*Corylus* spp.) and feeds on citrus blackfly, *Aleurocanthus woglumi* Ashby (Aleyrodidae) (Medina-Gaud et al. 1991; Lattin and Wetherill 2001). *C. californica* is known to feed on a scale insect, *Aonidiella citrina* (Coquillett) (Diaspididae) (Miller et al. 2004).

Adult chrysopids, syrphids, and chamaemyiids are strong flyers. Occasionally, individual adults of these families escaped collection because beat samples were not fully contained in a net. When compared to larvae or adults that are not strong flyers, such as derodontids, the abundance of adult chrysopids, syrphids, and chamaemyiids in the samples may not as accurately represent the actual population in the sample area. For example, the number of derodontid adults collected for each derodontid larva collected was 3.5 times greater than the same ratio for chamaemyiids (Table 2).

Predaceous Cecidomyiidae comprised 20 to 30 percent of all *A. tsugae* predators collected at two sites in North Carolina and Virginia by Wallace and Hain (2000). Interestingly, no cecidomyiid larvae were collected from *A. tsugae* in the PNW and none of the adults were identified to known aphidophagous genera.

Three surveys of endemic predators associated *A. tsugae* infestations on *T. canadensis* in Connecticut, North Carolina, and Virginia recovered at least ten species representing seven families that commonly feed on adelgids, including Hemerobiidae,

Chrysopidae, Derodontidae, Coccinellidae, Cecidomyiidae, Syrphidae, and Chamaemyiidae (McClure 1987; Montgomery and Lyon 1996; Wallace and Hain 2000). All studies concluded that numbers of predators were too low to have a significant impact on *A. tsugae*. Due to the recent introduction of *A. tsugae* to eastern North America, predators that feed on other adelgids, such as *P. strobi*, may not have had sufficient time to develop host switching behavior (Montgomery and Lyon 1996).

In contrast, predators associated with *A. tsugae* infestations on *T. heterophylla* in the PNW were more diverse and abundant. *A. tsugae* may have been present far longer in western North America, allowing at least one specialist predator to develop a close association (Havill et al. 2006). In addition, there is a wide diversity of conifers and other host plants in proximity to the PNW survey sites. Most PNW seed orchards include *Abies* spp., *Pinus* spp., and *P. menziesii*; all of which can host adelgids and scale insects. All PNW seed orchards are located near land used for agriculture or grazing. Most other survey sites were parks, arboreta, or ornamental plantings where a variety of tree species grow together. Not surprisingly, many of the generalist predators collected in this survey are associated with a wide variety of prey species and host plants (Miliczky and Horton 2005).

The lack of alate sexuparae in the PNW during 2005 and 2006 confirms similar observations by Zilahi-Balogh (2003a) in British Columbia and by Annand (1924) in Oregon. This apparent difference in biology between the eastern and western North American *A. tsugae* populations and the recent evidence of genetic variation among the geographic and host tree groupings of *A. tsugae* by Havill et al. (2006) warrant

future studies of possible biological and morphological differences among the various *A. tsugae* lineages.

In the PNW, predators of *A. cooleyi* were far more diverse than those found on *A. piceae*. Furthermore, *A. cooleyi* shares many of the same enemies with *A. tsugae*. This could be related to the fact that *A. cooleyi* is native to western North America and *A. piceae* is a recently introduced species. However, Mitchell (1962) found a wide variety of predators attacking *A. piceae* in the PNW. Therefore the difference in this study could be due to small sample size and/or limitations of the collection method.

Neoleucopis tapiae collected from *A. piceae* in this survey is not one of the four European chamaemyiid species that established following release for *A. piceae* biological control in North America. Following release in New Zealand and Hawaii, *N. tapiae* has been responsible for control of *Pineus boernerii* [= *P. laevis* (Maskell)] Annand and *Pineus pini* (Macquart) (Adelgidae), respectively (Culliney et al. 1988; Zondag and Nutall 1989; Greathead 1995).

Biological control on *A. tsugae* in eastern North America may be more effective when multiple predator species are released (Montgomery and Lyon 1996; Zilahi-Balogh et al. 2002b; Lamb et al. 2005; Flowers et al. 2006). The meta-analysis of biological control projects targeting insect pests performed by Denoth et al. (2002) revealed that the introduction of multiple agents does not significantly increase success over a single species introduction. However, in 40% of successful programs targeting an insect pest, multiple agents were responsible for success. Denoth et al. (2002) acknowledge that some targets may require multiple agents for control,

especially if the target pest occurs over a wide range of environments where a single agent is not always present. In the case of bivoltine *A. tsugae*, vulnerable life-stages are present throughout the year, with oviposition occurring in early spring and summer. Flowers et al. (2006) demonstrated that two *A. tsugae* predators with different phenologies could increase the overall impact on *A. tsugae* populations without significant negative competitive interactions in spite of some seasonal overlap. Flowers et al. (2006) also suggest that minimizing seasonal overlap among predators can reduce competition for *A. tsugae*. Therefore, the introduction of multiple predator species could enhance successful control of *A. tsugae*, provided the peak feeding activity of those predators occur at different times. To reduce the risk of non-target effects, only carefully evaluated specialist predators should be released (Kimberling 2004).

Anthocoridae are the only Hemipteran predators to have been considered candidates for biological control of adelgids (Mills 1990; Zilahi-Balogh et al. 2002b). The abundance of the four species recovered from *A. tsugae* in the PNW is too low for consideration as self-sustaining biological control candidates (Table 2). Several adelgid specific Asian Coccinellidae are being evaluated for efficacy as biological control agents against *A. tsugae* (Cheah et al. 2004). No such specialist coccinellids were identified from *A. tsugae* in the PNW. The most abundant coccinellids were all known to feed on taxa other than adelgids and the larval abundance of any one species is much lower than that of larval derodontids, which co-occur in the spring.

Two Chamaemyiidae species, *Neoleucopis* [= *Leucopis*] *obscura* (Haliday) and *N. tapiae*, are among the rare biological control agents that have been responsible for measurable control of Adegidae, specifically *Pineus* species (Culliney et al. 1988; Zondag and Nuttall 1989). *Leucopis* spp. larvae recovered in this survey were numerous and present in both progreiens and sistens *A. tsugae* ovisacs. *L. argenticollis* and *L. atrifacies* larvae completed development on a diet of *A. tsugae* in the laboratory. *L. argenticollis* adults and *Leucopis* spp. larvae were strongly correlated with *A. tsugae* infestations. Species of *Leucopis* may be adaptable to a range of climates due to their wide geographic distribution (Mills 1990). For these reasons, *L. argenticollis* and *L. atrifacies* have potential as candidates for biological control of *A. tsugae*. Research on their biology, host range, and seasonal synchrony with *A. tsugae* is warranted.

References Cited

- Aloo, T.C., and M. Karanja. 1986.** The biological control of pine woolly aphid in Kenya using *Tetrableps raoi* (Hemiptera: Anthocoridae). Edgerton, Univ. College Res. Paper Ser. Njoro, Kenya, No. 10. 16pp.
- Annand, P.N. 1924.** A new species of *Adelges* (Hemiptera, Phylloxeridae). Pan-Pacific Entomol. **1**: 79-82.
- Bentz, S.E., L.G.H. Riedel, M.R. Pooler, and A.M. Townsend. 2002.** Hybridization and self-compatibility in controlled pollinations of eastern North American and Asian hemlock (*Tsuga*) species. J. Arbor. **28**: 200-205.
- Borror, D.J., C.A. Tripplehorn, and N.F. Johnson. 1989.** An Introduction to the Study of Insects, 6th ed. Saunders College Publishing, Philadelphia. 875 pp.
- Cheah, C., M.E. Montgomery, S. Salom, B.L. Parker, S. Costa, and M. Skinner. 2004.** Biological control of hemlock woolly adelgid. USDA Forest Service, Morgantown, WV, FHTET-2004-04. 22 pp.
- Cheah, C.A.S.-J., and M.S. McClure. 1996.** Exotic natural enemies of *Adelges tsugae* and their prospect for biological control, pp. 103-112. In S.M. Salom, T.C. Tigner, and R.C. Reardon [eds.], Proceedings: First Hemlock Woolly Adelgid Review, Oct. 12, 1995, Charlottesville, VA. USDA Forest Service, Morgantown, WV, FHTET-96-10.
- Costa, S.D., B.L. Parker, V. Gouli, M. Brownbridge, M. Skinner, and S. Gouli. 2005.** Insect-killing fungi as a component of hemlock woolly adelgid integrated pest management. pp. 155-160. In B. Onken, and R. Reardon [eds.], Third Symposium on Hemlock Woolly Adelgid in the Eastern United States, Feb. 1-3, 2005, Asheville, NC. USDA Forest Service, Morgantown, WV, FHTET-2005-01.
- Culliney, T.W., J.W. Beardsley, Jr., and J.J. Drea. 1988.** Population regulation of the Eurasian pine adelgid (Homoptera: Adelgidae) in Hawaii. J. Econ. Entomol. **81**: 142-147.
- Del Tredici, P., and A. Kitajima. 2004.** Introduction and cultivation of Chinese hemlock (*Tsuga chinensis*) and its resistance to hemlock woolly adelgid (*Adelges tsugae*). J. Arbor. **30**: 282-287.
- Denoth, M., L. Frid, and J.H. Myers. 2002.** Multiple agents in biological control: improving the odds? Biological Control **24**: 20-30.

- Eichhorn, O. 1969.** Investigations on woolly aphids of the genus *Adelges* An. (Homoptera: Adelgidae) and their predators in Turkey. Commonwealth Institute of Biological Control, Tech. Bull. No. 12: 83-103.
- Elliott, N., R. Kieckhefer, and W. Kauffman. 1996.** Effects of an invading coccinellid on native coccinellids in an agricultural landscape. *Oecologia* **105**: 537–544.
- Evans, A.M., and T.G. Gregoire. 2006.** A geographically variable model of hemlock woolly adelgid spread. *Biol. Invasions*: DOI 10.1007/s10530-006-9039-z.
- Flowers, R.W., S.M. Salom, and L.T. Kok. 2006.** Competitive interactions among two specialist predators and a generalist predator of hemlock woolly adelgid, *Adelges tsugae* (Hemiptera : Adelgidae) in south-western Virginia. *Agr. For. Entomol.* **8**: 253-262.
- Furniss, R.L., and V.M. Carolin. 1977.** Western Forest Insects. USDA Forest Service Misc. Pub. 1339. 654 pp.
- Greathead, D.J. 1995.** The *Leucopis* spp. (Diptera: Chamaemyiidae) introduced for biological control of *Pineus* sp. (Homoptera: Adelgidae) in Hawaii: implications for biological control of *Pineus ?boernerii* in Africa. *The Entomologist* **114**: 83-90.
- Harris, J.W.E., and A.F. Dawson. 1979.** Predator release program for balsam woolly aphid, *Adelges piceae* (Homoptera: Adelgidae), in British Columbia, 1960-1969. *J. Entomol. Soc. Brit. Columbia* **76**: 21-26.
- Havill, N.P., M.E. Montgomery, G. Yu, S. Shiyake, and A. Caccone. 2006.** Mitochondrial DNA from hemlock woolly adelgid (Hemiptera: Adelgidae) suggests cryptic speciation and pinpoints the source of the introduction to eastern North America. *Ann. Entomol. Soc. Amer.* **99**: 195-203.
- Humble, L.M. 1994.** Recovery of additional exotic predators of balsam woolly adelgid, *Adelges piceae* (Ratzeburg) (Homoptera: Adelgidae), in British Columbia. *Can. Entomol.* **126**: 1101-1103.
- Kimberling, D.N. 2004.** Lessons from history: predicting successes and risks of intentional introductions for arthropod biological control. *Biological Invasions* **6**: 301-318.
- Kohler, G.R., and D.A. St. Clair. 2005.** Variation for resistance to aphids (Homoptera: Aphididae) among tomato inbred backcross lines derived from wild *Lycopersicon* species. *J. Econ. Entomol.* **98**: 988-995.

- Kruskal, J.B. 1964.** Nonmetric multidimensional scaling: a numerical method. *Psychometrika* **29**: 115-129.
- Lamb, A.B., S.M. Salom, and L.T. Kok. 2005.** Survival and reproduction of *Laricobius nigrinus* Fender (Coleoptera: Derodontidae), a predator of hemlock woolly adelgid, *Adelges tsugae* Annand (Homoptera: Adelgidae) in field cages. *Biological Control* **32**: 200-207.
- Lattin, J.D., and K. Wetherill. 2001.** Five species of *Empicoris* Wolff from *Corylus cornuta* and *Corylus avellana* in Oregon (Hemiptera: Reduviidae). *Pan.-Pac. Entomol.* **77**: 275-276.
- Mausel, D.L., S.M. Salom, and L.T. Kok. 2005.** Experimental releases of *Laricobius nigrinus* for biological control of hemlock woolly adelgid in the eastern U.S., p. 134. In B. Onken, and R. Reardon [eds.], Third Symposium on Hemlock Woolly Adelgid in the Eastern United States, Feb. 1-3, 2005, Asheville, NC. USDA Forest Service, Morgantown, WV, FHTET-2005-01.
- McAlpine, J.F., and V.N. Tanasijtshunk. 1972.** Identity of *Leucopis argenticollis* and description of a new species (Diptera: Chamaemyiidae). *Can. Entomol.* **104**: 1865-1875.
- McClure, M.S. 1987.** Biology and control of hemlock woolly adelgid. *Bull. Conn. Agric. Exp. Stn.* 851, New Haven, CT. 9 pp.
- McClure, M.S. 1989.** Evidence of a polymorphic life cycle in the hemlock woolly adelgid, *Adelges tsugae* (Homoptera: Adelgidae). *Ann. Entomol. Soc. Amer.* **82**: 50-54.
- McClure, M.S. 1990.** Role of wind, birds, deer, and humans in the dispersal of hemlock woolly adelgid (Homoptera: Adelgidae). *Environ. Entomol.* **19**: 36-43.
- McClure, M.S. 1992a.** Effects of implanted and injected pesticides and fertilizers on the survival of *Adelges tsugae* (Homoptera: Adelgidae) and on the growth of *Tsuga canadensis*. *J. Econ. Entomol.* **85**: 468-472.
- McClure, M.S. 1992b.** Hemlock woolly adelgid. *Amer. Nurseryman* **175**: 82-89.
- McClure, M.S., S.M. Salom, and K.S. Shields. 2001.** Hemlock Woolly Adelgid. USDA Forest Service Forest Health Technology Enterprise Team, Technology Transfer, FHTET-2001-03. 14pp.
- McCune, B. 2006.** Nonparametric Multiplicative Regression for Habitat Modeling. <<http://www.pcord.com/NPMRintro.pdf>>.

- McCune, B., and J.B. Grace. 2002.** Analysis of ecological communities. MjM Software Design, Glendon Beach, OR.
- McCune, B., and M.J. Mefford. 1999.** PC-ORD. Multivariate analysis of ecological data. Version 5.57 beta. MjM Software, Glendon Beach, OR.
- McCune, B., and M.J. Mefford. 2004.** HyperNiche. Nonparametric multiplicative habitat modeling. Version 1.12. MjM Software, Glendon Beach, OR.
- Medina-Gaud, S., A.E. Segarra-Carmona, and R.A. Franqui. 1991.** The citrus blackfly, *Aleurocanthus woglumi* Ashby (Homoptera: Aleyrodidae), in Puerto Rico. J. Agric. Univ. Puerto Rico **75**: 301-305.
- Messing R.H., and M.T. Aliniaze. 1985.** Natural enemies of *Myzocallis coryli* (Hom.: Aphididae) in Oregon hazelnut orchards. J. Entomol. Soc. Brit. Columbia **82**: 14-18.
- Miliczky, E.R., and D.R. Horton. 2005.** Densities of beneficial arthropods within pear and apple orchards affected by distance from adjacent native habitat and association of natural enemies with extra-orchard host plants. Biological control **33**: 249-259.
- Mills, N.J. 1990.** Biological control of forest pests in Africa. Bulletin of Entomological Research **80**: 31-36.
- Miller, G.L., J.D. Oswald, and D.R. Miller. 2004.** Lacewings and scale insects: A review of predator/prey associations between the Neuropterida and Coccoidea (Insecta: Neuroptera, Raphidioptera, Hemiptera). Ann. Entomol. Soc. Am. **97**: 1103-1125.
- Mitchell, R.G. 1962.** Balsam woolly adelgid predators native to Oregon and Washington. Oregon St. Univ. Agric. Exp. Stn. Tech. Bull. 62, Corvallis, OR. 63 pp.
- Mitchell, R.G., and P.E. Buffam. 2001.** Patterns of long term balsam woolly adelgid infestations and effects in Oregon and Washington. West. J. App. For. **16**: 121-126.
- Mitchell, R.G., and K.H. Wright. 1967.** Foreign predator introductions for control of the balsam woolly aphid in the Pacific Northwest. J. Econ. Entomol. **60**: 140-147.
- Montgomery, M.E., and S.M. Lyon. 1996.** Natural enemies of adelgids in North America: their prospect for biological control of *Adelges tsugae* (Homoptera:

Adelgidae), pp. 89-102. *In* S.M. Salom, T.C. Tigner, and R.C. Reardon [eds.], Proceedings: First Hemlock Woolly Adelgid Review, Oct. 12, 1995, Charlottesville, VA. USDA Forest Service, Morgantown, WV, FHTET-96-10.

Orwig, D.A., D.R. Foster, and D.L. Mausel. 2002. Landscape patterns of hemlock decline in New England due to the introduced hemlock woolly adelgid. *Biogeography* **29**: 1475-1487.

Rao, V.P., and M.A. Ghani. 1972. Studies on predators of *Adelges* spp. in the Himalayas. Misc. Pub. No. 3, Commonwealth Agricultural Bureau. Farnham Royal, UK. 116 pp.

Raworth, D.A., and M.C. Robertson. 2002. Occurrence of the spider mite predator *Stethorus punctillum* (Coleoptera: Coccinellidae) in the Pacific Northwest. *J. Entomol. Soc. Brit. Columbia* **99**: 81-82.

SAS Institute. 1999. SAS/STAT user's guide, version 8. SAS Institute, Cary, NC.

Schooley, H.O., J.W.E. Harris, and B. Pendrel. 1984. *Adelges piceae* (Ratz.), balsam woolly adelgid (Homoptera: Adelgidae), pp. 229-234. *In* J.S. Kelleher and M.A. Hulme [eds.], Biological control programmes against insects and weeds in Canada 1969-1980. Commonwealth Agricultural Bureau, Farnham Royal, Slough, UK.

Stathas, G.J. 2000. *Rhyzobius lophanthae* prey consumption and fecundity. *Phytoparasitica* **28**: 203-211.

Stoetzel, M.B. 2002. History of the introduction of *Adelges tsugae* based on voucher specimens in the Smithsonian Institute National Collection of Insects, p. 12. *In* B. Onken, R. Reardon, and J. Lashomb [eds.], Proceedings: Hemlock Woolly Adelgid in Eastern North America Symposium, Feb. 5-7, 2002, East Brunswick, NJ. USDA Forest Service and State Univ. of N.J. Rutgers, East Brunswick, NJ.

Tanasijtshuk, V.N. 2002. Studies on Nearctic species of *Leucopis* (Diptera: Chamaemyiidae). I. The redescription of Nearctic *Leucopis* published before 1965. *Zoosyst. Rossica* **11**: 193-207.

Wallace, M.S., and F.P. Hain. 2000. Field surveys and evaluation of native and established predators of the hemlock woolly adelgid (Homoptera: Adelgidae) in the southeastern United States. *Environ. Entomol.* **29**: 638-644.

Ward, J.S., M.E. Montgomery, C.A.S.-J. Cheah, B.P. Onken, and R.S. Cowles. 2004. Eastern Hemlock Forests: Guidelines to Minimize the Impacts of Hemlock

Woolly Adelgid. USDA Forest Service Northeastern Area State & Private Forestry, NA-TP-03-04. 27 pp.

- Webb, R.E., J.R. Frank, and M.J. Raupp. 2003.** Eastern hemlock recovery from hemlock woolly adelgid damage following imidacloprid therapy. *J. Arbor.* **29**: 298-301.
- Yu, G., M.E. Montgomery, and D. Yao. 2000.** Lady beetles (Coleoptera: Coccinellidae) from Chinese hemlocks infested with the hemlock woolly adelgid, *Adelges tsugae* Annand (Homoptera: Adelgidae). *Coleopt. Bull.* **54**: 154-199.
- Zilahi-Balogh, G.M.G., L.M. Humble, A.B. Lamb, S.M. Salom, and L.T. Kok. 2003a.** Seasonal abundance and synchrony between *Laricobius nigrinus* (Coleoptera: Derodontidae) and its prey, the hemlock woolly adelgid (Homoptera: Adelgidae). *Can. Entomol.* **135**: 103-115.
- Zilahi-Balogh, G.M.G., L.T. Kok, and S.M. Salom. 2002a.** Host specificity of *Laricobius nigrinus* Fender (Coleoptera: Derodontidae), a potential biological control agent of the hemlock woolly adelgid, *Adelges tsugae* Annand (Homoptera: Adelgidae). *Biol. Contr.* **24**: 192-198.
- Zilahi-Balogh, G.M.G., L.T. Kok, and S.M. Salom. 2002b.** A review of world-wide biological control efforts for the family Adelgidae, pp. 129-140. *In* B. Onken, R. Reardon, and J. Lashomb [eds.], *Proceedings: Hemlock Woolly Adelgid in Eastern North America Symposium*, Feb. 5-7, 2002, East Brunswick, NJ. USDA Forest Service and State Univ. of N.J. Rutgers, East Brunswick, NJ.
- Zilahi-Balogh, G.M.G., S.M. Salom, and L.T. Kok. 2003b.** Development and reproductive biology of *Laricobius nigrinus*, a potential biological control agent of *Adelges tsugae*. *BioControl* **48**: 293-306.
- Zondag, R., and M.J. Nuttall. 1989.** *Pineus laevis* (Maskell), pine twig chermes or pine woolly aphid (Homoptera: Adelgidae), pp. 295-297. *In* P.J. Cameron, R.L. Hill, J. Bain, and W.P. Thomas [eds.], *A Review of Biological Control of Invertebrate Pests and Weeds in New Zealand 1874 to 1987*. Commonwealth Institute of Biological Control, Technical communication No. 10.

Chapter 3: Conclusion

The hemlock woolly adelgid, *Adelges tsugae*, is an introduced pest that has caused widespread mortality to eastern hemlocks, *Tsuga canadensis* and *Tsuga caroliniana*, along the Appalachian range in the eastern United States. Its distribution continues to expand at a rate of approximately 8.1 to 15.6 km per year in the northern and southern parts of its eastern range, respectively (Evans and Gregoire 2006). If minimum winter temperatures increase, *A. tsugae* may eventually threaten *T. canadensis* stands in Canada and the Great Lakes states. Being the only conifer in some ecosystems, *T. canadensis* provides cover habitat in both summer and winter and is considered a keystone species for many other organisms, including birds, fish, and aquatic invertebrates (Ward et al. 2004). To date, the only effective large scale *A. tsugae* mortality agent has been winter temperatures below -26° C (Shields and Cheah 2005; Evans and Gregoire 2006). Efforts to develop methods of effective *A. tsugae* control should remain integrated in approach; including not only biological control, but also host tree breeding, entomopathogens, cultural control, antibiotics, and insecticides. Ultimately, effective control may rely on any number of these technologies.

Fifteen years of exploration for *A. tsugae* natural enemies and careful biological research have yielded several good candidates for biological control of *A. tsugae* in eastern North America. As of this writing, only two introduced predator species have established, bred and overwintered following release in the eastern U.S.: *Sasajiscymnus tsugae* and *Laricobius nigrinus* (Cheah et al. 2004; Cheah et al. 2005; Lamb et al. 2006). Of these, *S. tsugae* is the only exotic predator to have significant

control of *A. tsugae* populations following free release, albeit on a small scale (Cheah et al. 2005). It may take many years for predator populations to build densities high enough to have large scale measurable impact on *A. tsugae*.

Modern biological control research programs must avoid releasing numerous exotic natural enemies onto a target host in order to determine which is most effective. This “shotgun” approach was commonly used in past programs. For example, more than 25 species were introduced in a failed effort to control *Adelges piceae* in North America (Schooley et al. 1984; Mitchell and Buffam 2001). Releasing only carefully evaluated specialist predators increases the probability of successful control while minimizing risk to non-target organisms and the environment (van Lenteren 2003; Kimberling 2004). All predator candidates should be subjected to prey suitability and predator competition evaluations prior to release. Unfortunately, this more focused approach to biological control research is time consuming. The time between first recovery of an *A. tsugae* predator and its free field release has ranged from three to six years (Cheah et al. 2004). To increase the probability of biological control success, it is important to continue exploration and basic research on any promising new natural enemies as they are discovered in the range of *A. tsugae*.

Over two years, this survey recovered a diverse community of 55 predator species from *A. tsugae* infested *Tsuga heterophylla* in the Pacific Northwest (PNW). Only three of these species are adelgid specialists. As a complex, the remaining predators may be contributing to *A. tsugae* mortality, but none would be considered suitable biological control candidates. At least two of the adelgid specialists

recovered, *L. nigrinus* and *Leucopis argenticollis*, were strongly correlated to *A. tsugae* density. *L. nigrinus* has already been established as an *A. tsugae* biological control agent (Lamb et al. 2006). *L. argenticollis* and its congener, *Leucopis atrifacies*, should be considered for research into their suitability as biological control agents of *A. tsugae*.

At least one life stage of *A. tsugae* is available as prey year-round on hemlock branches. The most effective *A. tsugae* biological control predator complex would include several predators that are actively feeding on *A. tsugae* during different seasons. This should increase the overall impact of predation and reduce competition among the predators (Lamb et al. 2005; Flowers et al. 2006). This concept should be an important criterion for selection of new *A. tsugae* predators found in current explorations in western North America and Asia. In the PNW, larvae of at least one Chamaemyiidae species feed on *A. tsugae* sistens during the early summer when *L. nigrinus* are not present.

Although eastern hemlocks continue to be killed at a rapid rate across the eastern U.S., there are hopeful signs for its future recovery. *A. tsugae* has a low cold tolerance threshold; however, its mortality has been shown to increase with more northern latitude and decreasing winter temperatures. *A. tsugae* mortality reached as high as 93% in some New England states (Skinner et al. 2003; Shields and Cheah 2005). In Connecticut and New Jersey, free released *S. tsugae* are thought to be responsible for significant increases in *A. tsugae* mortality. Some of these stands have recovered from *A. tsugae* infestation (Cheah et al. 2005). Once more effective

biological and integrated control options are available to manage *A. tsugae*, surviving eastern hemlock stands can be a source of recovery for more heavily impacted areas (Ward 2002).

Bibliography

- Aloo, T.C., and M. Karanja. 1986.** The biological control of pine woolly aphid in Kenya using *Tetrableps raoi* (Hemiptera: Anthocoridae). Edgerton, Univ. College Res. Paper Ser. Njoro, Kenya, No. 10. 16pp.
- Amman, G.D., and C.F. Speers. 1971.** Introduction and evaluation of predators from India and Pakistan for control of the balsam woolly aphid (Homoptera: Adelgidae) in North Carolina. *Can. Entomol.* **103**: 528-533.
- Annand, P.N. 1924.** A new species of *Adelges* (Hemiptera, Phylloxeridae). *Pan-Pacific Entomol.* **1**: 79-82.
- Annand, P.N. 1928.** A contribution toward a monograph of the Adelginae (Phylloxeridae) of North America, Vol. 6. Stanford Univ. Pub. Univ. Ser. Biol. Sci., No. 1, Stanford Univ. Press, Palo Alto, CA. 146 pp.
- Asaro, C., C.W. Berisford, M.E. Montgomery, J. Rhea, and J. Hanula. 2005.** Biological control of the hemlock woolly adelgid in the southern Appalachians, pp. 248-251. *In* B. Onken and R. Reardon [eds.], *Third Symposium on Hemlock Woolly Adelgid in the Eastern United States*, Feb. 1-3, 2005, Asheville, NC. USDA Forest Service, Morgantown, WV, FHTET-2005-01.
- Balch, R.E., R.C. Clark, and N.R. Brown. 1958.** *Adelges piceae* (Ratz.) in Canada with reference to biological control. *Proc. 10th Inter. Cong. Entomol.* **4**: 807-817.
- Bentz, S.E., L.G.H. Riedel, M.R. Pooler, and A.M. Townsend. 2002.** Hybridization and self-compatibility in controlled pollinations of eastern North American and Asian hemlock (*Tsuga*) species. *J. Arbor.* **28**: 200-205.
- Blumenthal, E.M., and S.M. Werner. 2005.** An overview of hemlock woolly adelgid IPM in Pennsylvania: 1999-2004, pp. 220-231. *In* B. Onken and R. Reardon [eds.], *Third Symposium on Hemlock Woolly Adelgid in the Eastern United States*, Feb. 1-3, 2005, Asheville, NC. USDA Forest Service, Morgantown, WV, FHTET-2005-01.
- Borrer, D.J., C.A. Tripplehorn, and N.F. Johnson. 1989.** *An Introduction to the Study of Insects*, 6th ed. Saunders College Publishing, Philadelphia. 875 pp.
- Brown, M.W. 2003.** Intraguild responses of aphid predators on apple to the invasion of an exotic species, *Harmonia axyridis*. *BioControl* **48**: 141-153.

- Brown, N.R., and R.C. Clark. 1956.** Studies of predators of the balsam woolly aphid *Adelges piceae* (Ratz.) (Homoptera: Adelgidae) II. An annotated list of the predators associated with the balsam woolly aphid in eastern Canada. *Can. Entomol.* **88**: 678-683.
- Butin, E., J. Elkinton, N. Havill, and M. Montgomery. 2003.** Comparison of numerical response and predation effects of two coccinellid species on hemlock woolly adelgid (Homoptera: Adelgidae). *J. Econ. Entomol.* **96**: 763-767.
- Butin, E.E., N.P. Havill, J.S. Elkinton, and M.E. Montgomery. 2004.** Feeding preference of three lady beetle predators of the hemlock woolly adelgid (Homoptera: Adelgidae). *J. Econ. Entomol.* **97**: 1635-1641.
- Byrkit, M.K. 2004.** Predators of hemlock woolly adelgid in northwestern Oregon. M.S. thesis. Oregon State Univ., Corvallis, OR. 49 pp.
- Cheah, C., M.E. Montgomery, S. Salom, B.L. Parker, S. Costa, and M. Skinner. 2004.** Biological control of hemlock woolly adelgid. USDA Forest Service, Morgantown, WV, FHTET-2004-04. 22 pp.
- Cheah, C.A.S.-J., and C. Donahue. 2002.** Potential biological control of balsam woolly adelgid, p. 2 *In Proc. 62nd Ann. Meeting Acadian Entomol. Soc.*, July 21-23, 2002, Univ. of Maine, Machias, ME.
- Cheah, C.A.S.-J., M.A. Mayer, D. Palmer, T. Scudder, and R. Chianese. 2005.** Assessments of biological control of hemlock woolly adelgid with *Sasajiscymnus tsugae* in Connecticut and New Jersey, pp. 116-130. *In* B. Onken and R. Reardon [eds.], Third Symposium on Hemlock Woolly Adelgid in the Eastern United States, Feb. 1-3, 2005, Asheville, NC. USDA Forest Service, Morgantown, WV, FHTET-2005-01.
- Cheah, C.A.S.-J., and M.S. McClure. 1996.** Exotic natural enemies of *Adelges tsugae* and their prospect for biological control, pp. 103-112. *In* S.M. Salom, T.C. Tigner, and R.C. Reardon [eds.], Proceedings: First Hemlock Woolly Adelgid Review, Oct. 12, 1995, Charlottesville, VA. USDA Forest Service, Morgantown, WV, FHTET-96-10.
- Clark, R.C., and N.R. Brown. 1960.** Studies of predators of the balsam woolly aphid, *Adelges piceae* (Ratz.) (Homoptera: Adelgidae) VII. *Laricobius rubidus* Lec. (Coleoptera: Derodontidae), a predator of *Pineus strobi* (Htg.) (Homoptera: Adelgidae). *Can. Entomol.* **92**: 237-240.

- Clausen, C.P. 1978.** Chermidae, pp. 49-55. *In* Clausen, C.P. [ed.], *Introduced Parasites and Predators of Arthropod Pests and Weeds: A World Review*. USDA Agr. Handbook. No. 480.
- Conway, H.E., and J.D. Culin. 2005.** Update on rearing *Sasajiscymnus tsugae* at the Clemson insectary and field monitoring of the first release site, pp. 269-275. *In* B. Onken and R. Reardon [eds.], *Third Symposium on Hemlock Woolly Adelgid in the Eastern United States*, Feb. 1-3, 2005, Asheville, NC. USDA Forest Service, Morgantown, WV, FHTET-2005-01.
- Costa, S.D., B.L. Parker, V. Gouli, M. Brownbridge, M. Skinner, and S. Gouli. 2005.** Insect-killing fungi as a component of hemlock woolly adelgid integrated pest management, pp. 155-160. *In* B. Onken and R. Reardon [eds.], *Third Symposium on Hemlock Woolly Adelgid in the Eastern United States*, Feb. 1-3, 2005, Asheville, NC. USDA Forest Service, Morgantown, WV, FHTET-2005-01.
- Culliney, T.W., J.W. Beardsley, Jr., and J.J. Drea. 1988.** Population regulation of the Eurasian pine adelgid (Homoptera: Adelgidae) in Hawaii. *J. Econ. Entomol.* **81**: 142-147.
- Del Tredici, P., and A. Kitajima. 2004.** Introduction and cultivation of Chinese hemlock (*Tsuga chinensis*) and its resistance to hemlock woolly adelgid (*Adelges tsugae*). *J. Arbor.* **30**: 282-287.
- Denoth, M., L. Frid, and J.H. Myers. 2002.** Multiple agents in biological control: improving the odds? *Biological Control* **24**: 20-30.
- Eichhorn, O. 1969.** Investigations on woolly aphids of the genus *Adelges* An. (Homoptera: Adelgidae) and their predators in Turkey. Commonwealth Institute of Biological Control, Tech. Bull. No. 12: 83-103.
- Elliott, N., R. Kieckhefer, and W. Kauffman. 1996.** Effects of an invading coccinellid on native coccinellids in an agricultural landscape. *Oecologia* **105**: 537-544.
- Evans, A.M., and T.G. Gregoire. 2006.** A geographically variable model of hemlock woolly adelgid spread. *Biol. Invasions*: DOI 10.1007/s10530-006-9039-z.
- Evans, R.A. 2002.** An ecosystem unraveling?, pp. 23-33. *In* B. Onken, R. Reardon, and J. Lashomb [eds.], *Proceedings: Hemlock Woolly Adelgid in Eastern North America Symposium*, Feb. 5-7, 2002, East Brunswick, NJ. USDA Forest Service and State Univ. of N.J. Rutgers, East Brunswick, NJ.

- Flowers, R.W., S.M. Salom, and L.T. Kok. 2005.** Competitive interactions among two specialist predators and a generalist predator of hemlock woolly adelgid, *Adelges tsugae* (Homoptera: Adelgidae), in the laboratory. *Environ. Entomol.* **34**: 664-675.
- Flowers, R.W., S.M. Salom, and L.T. Kok. 2006.** Competitive interactions among two specialist predators and a generalist predator of hemlock woolly adelgid, *Adelges tsugae* (Homoptera : Adelgidae) in south-western Virginia. *Agr. For. Entomol.* **8**: 253-262.
- Fondren, K.M., D.G. McCullough, and A.J. Walter. 2004.** Insect predators and augmentative biological control of balsam twig aphid (*Mindarus abietinus* Koch) (Homoptera: Aphididae) on Christmas tree plantations. *Environ. Entomol.* **33**: 1652-1661.
- Furniss, R.L., and V.M. Carolin. 1977.** Western Forest Insects. USDA Forest Service Misc. Pub. 1339. 654 pp.
- Gaimari, S.D., and W.J. Turner. 1996.** Larval feeding and development of *Leucopis ninae* Tanasijtshuk and two populations of *Leucopis gaimarii* Tanasijtshuk (Diptera: Chamaemyiidae) on Russian wheat aphid, *Diuraphis noxia* (Mordvilko) (Homoptera: Aphididae), in Washington. *Proc. Entomol. Soc. Wash.* **98**: 667-676.
- Gatton, H. 2004.** A new species of *Laricobius* predator of hemlock woolly adelgid from China, p. 25. In R. Reardon and B. Onken [eds.], Proceedings: Hemlock Woolly Adelgid Biological Control Committee Meeting, Jan. 13, 2004, Annapolis, MD. USDA Forest Service, FHTET-2004-08.
- Grant, J.F., D. Palmer, J.R. Rhea, G. Taylor, P.L. Lambdin, and I. Deal. 2005.** Assessment of egg releases for establishment of *Sasajiscymnus tsugae* on eastern hemlock, pp. 297-303. In B. Onken and R. Reardon [eds.], Third Symposium on Hemlock Woolly Adelgid in the Eastern United States, Feb. 1-3, 2005, Asheville, NC. USDA Forest Service, Morgantown, WV, FHTET-2005-01.
- Greathead, D.J. 1995.** The *Leucopis* spp. (Diptera: Chamaemyiidae) introduced for biological control of *Pineus* sp. (Homoptera: Adelgidae) in Hawaii: implications for biological control of *Pineus ?boernerii* in Africa. *The Entomologist* **114**: 83-90.
- Harris, J.W.E., and A.F. Dawson. 1979.** Predator release program for balsam woolly aphid, *Adelges piceae* (Homoptera: Adelgidae), in British Columbia, 1960-1969. *J. Entomol. Soc. Brit. Columbia* **76**: 21-26.
- Harris, K.M. 1973.** Aphidophagous Cecidomyiidae (Diptera): taxonomy, biology and assessments of field populations. *Bull. Entomol. Res.* **63**: 305-325.

- Havill, N.P., M.E. Montgomery, G. Yu, S. Shiyake, and A. Caccone. 2006.** Mitochondrial DNA from hemlock woolly adelgid (Hemiptera: Adelgidae) suggests cryptic speciation and pinpoints the source of the introduction to eastern North America. *Ann. Entomol. Soc. Amer.* **99**: 195-203.
- Humble, L.M. 1994.** Recovery of additional exotic predators of balsam woolly adelgid, *Adelges piceae* (Ratzeburg) (Homoptera: Adelgidae), in British Columbia. *Can. Entomol.* **126**: 1101-1103.
- Humble, L.M., and L. Mavin. 2005.** Preliminary assessment of the cold tolerance of *Laricobius nigrinus*, a winter-active predator of the hemlock woolly adelgid from western Canada, p.304. *In* B. Onken and R. Reardon [eds.], Third Symposium on Hemlock Woolly Adelgid in the Eastern United States, Feb. 1-3, 2005, Asheville, NC. USDA Forest Service, Morgantown, WV, FHTET-2005-01.
- Jenkins, J.C., J.D. Aber, and C.D. Canham. 1999.** Hemlock woolly adelgid impacts on community structure and N cycling tares in eastern hemlock forests. *Can. J. For. Res.* **29**: 630-645.
- Kimberling, D.N. 2004.** Lessons from history: predicting successes and risks of intentional introductions for arthropod biological control. *Biological Invasions* **6**: 301-318.
- Kizlinski, M.L., D.A. Orwig, R.C. Cobb, and D.R. Foster. 2002.** Direct and indirect ecosystem consequences of an invasive pest on forests dominated by eastern hemlock. *J. Biogeography* **29**: 1489-1503.
- Koch, R.L. 2003.** The multicolored Asian lady beetle, *Harmonia axyridis*, a review of its biology, uses in biological control, and non-target impacts. *J. Insect Science* **3**: 1-16.
- Kohler, G.R., and D.A. St. Clair. 2005.** Variation for resistance to aphids (Homoptera: Aphididae) among tomato inbred backcross lines derived from wild *Lycopersicon* species. *J. Econ. Entomol.* **98**: 988-995.
- Kruskal, J.B. 1964.** Nonmetric multidimensional scaling: a numerical method. *Psychometrika* **29**: 115-129.
- Lamb, A. 2004.** *Laricobius nigrinus* rearing and field evaluation, pp. 14-15. *In* R. Reardon and B. Onken [eds.], Proceedings: Hemlock Woolly Adelgid Biological Control Committee Meeting, Jan. 13, 2004, Annapolis, MD. USDA Forest Service, FHTET-2004-08.

- Lamb, A.B., S.M. Salom, and L.T. Kok. 2005.** Survival and reproduction of *Laricobius nigrinus* Fender (Coleoptera: Derodontidae), a predator of hemlock woolly adelgid, *Adelges tsugae* Annand (Homoptera: Adelgidae) in field cages. *Biological Control* **32**: 200-207.
- Lamb, A.B., S.M. Salom, L.T. Kok, and D.L. Mausel, 2006.** Confined field release of *Laricobius nigrinus* (Coleoptera: Derodontidae), a predator of the hemlock woolly adelgid, *Adelges tsugae* (Homoptera: Adelgidae), in Virginia. *Can. J. For. Res.* **36**: 369-375.
- Lattin, J.D. 2003.** The Anthocoridae and Miridae (Hemiptera: Heteroptera) on whitebark pine (*Pinus albicaulis*). *Pan-Pacific Entomol.* **79**: 79-89.
- Lattin, J.D., and K. Wetherill. 2001.** Five species of *Empicoris* Wolff from *Corylus cornuta* and *Corylus avellana* in Oregon (Hemiptera: Reduviidae). *Pan.-Pac. Entomol.* **77**: 275-276.
- Lu, W., and M.E. Montgomery. 2001.** Oviposition, development, and feeding of *Scymnus (Neopullus) sinuanodulus* (Coleoptera: Coccinellidae): a predator of *Adelges tsugae* (Homoptera: Adelgidae). *Ann. Entomol. Soc. Am.* **94**: 64-70.
- Mausel, D.L., S.M. Salom, and L.T. Kok. 2005.** Experimental releases of *Laricobius nigrinus* for biological control of hemlock woolly adelgid in the eastern U.S., p. 134. *In* B. Onken, and R. Reardon [eds.], *Third Symposium on Hemlock Woolly Adelgid in the Eastern United States*, Feb. 1-3, 2005, Asheville, NC. USDA Forest Service, Morgantown, WV, FHTET-2005-01.
- McAlpine, J.F., and V.N. Tanasijtshunk. 1972.** Identity of *Leucopis argenticollis* and description of a new species (Diptera: Chamaemyiidae). *Can. Entomol.* **104**: 1865-1875.
- McAvoy, T. 2004.** *Tetraphleps galchanooides* Ghauri, a new predator of hemlock woolly adelgid, pp. 26-28. *In* R. Reardon and B. Onken [eds.], *Proceedings: Hemlock Woolly Adelgid Biological Control Committee Meeting*, Jan. 13, 2004, Annapolis, MD. USDA Forest Service, FHTET-2004-08.
- McClure, M.S. 1987.** Biology and control of hemlock woolly adelgid. *Bull. Conn. Agric. Exp. Stn.* 851, New Haven, CT. 9 pp.
- McClure, M.S. 1989.** Evidence of a polymorphic life cycle in the hemlock woolly adelgid, *Adelges tsugae* (Homoptera: Adelgidae). *Ann. Entomol. Soc. Amer.* **82**: 50-54.

- McClure, M.S. 1990.** Role of wind, birds, deer, and humans in the dispersal of hemlock woolly adelgid (Homoptera: Adelgidae). *Environ. Entomol.* **19**: 36-43.
- McClure, M.S. 1991.** Density-dependent feedback and population cycles in *Adelges tsugae* (Homoptera: Adelgidae) on *Tsuga canadensis*. *Environ. Entomol.* **20**: 258-264.
- McClure, M.S. 1992a.** Effects of implanted and injected pesticides and fertilizers on the survival of *Adelges tsugae* (Homoptera: Adelgidae) and on the growth of *Tsuga canadensis*. *J. Econ. Entomol.* **85**: 468-472.
- McClure, M.S. 1992b.** Hemlock woolly adelgid. *Amer. Nurseryman* **175**: 82-89.
- McClure, M.S., 1995.** *Diapterobates humeralis* (Oribatida: Ceratozetidae): an effective control agent of hemlock woolly adelgid (Homoptera: Adelgidae) in Japan. *Environ. Entomol.* **24**: 1207-1215.
- McClure, M.S., S.M. Salom, and K.S. Shields. 2001.** Hemlock Woolly Adelgid. USDA Forest Service Forest Health Technology Enterprise Team, Technology Transfer, FHTET-2001-03. 14pp.
- McCune, B. 2006.** Nonparametric Multiplicative Regression for Habitat Modeling. <<http://www.pcord.com/NPMRintro.pdf>>.
- McCune, B., and J.B. Grace. 2002.** Analysis of ecological communities. MjM Software Design, Gleneden Beach, OR.
- McCune, B., and M.J. Mefford. 2004.** HyperNiche. Nonparametric multiplicative habitat modeling. Version 1.12. MjM Software, Gleneden Beach, OR.
- McCune, B., and M.J. Mefford. 1999.** PC-ORD. Multivariate analysis of ecological data. Version 5.57 beta. MjM Software, Gleneden Beach, OR.
- McLean, I.F.G. 1992.** Behaviour of larval and adult *Leucopis* (Diptera: Chamaemyiidae). *Br. J. Ent. Nat. Hist.* **5**: 35-36.
- Medina-Gaud, S., A.E. Segarra-Carmona, and R.A. Franqui. 1991.** The citrus blackfly, *Aleurocanthus woglumi* Ashby (Homoptera: Aleyrodidae), in Puerto Rico. *J. Agric. Univ. Puerto Rico* **75**: 301-305.
- Messing R.H., and M.T. Aliniazee. 1985.** Natural enemies of *Myzocallis coryli* (Hom.: Aphididae) in Oregon hazelnut orchards. *J. Entomol. Soc. Brit. Columbia* **82**: 14-18.

- Miliczky, E.R., and D.R. Horton. 2005.** Densities of beneficial arthropods within pear and apple orchards affected by distance from adjacent native habitat and association of natural enemies with extra-orchard host plants. *Biological control* **33**: 249-259.
- Mills, N.J. 1990.** Biological control of forest pests in Africa. *Bulletin of Entomological Research* **80**: 31-36.
- Miller, G.L., J.D. Oswald, and D.R. Miller. 2004.** Lacewings and scale insects: A review of predator/prey associations between the Neuropterida and Coccoidea (Insecta: Neuroptera, Raphidioptera, Hemiptera). *Ann. Entomol. Soc. Am.* **97**: 1103-1125.
- Mitchell, R.G. 1962.** Balsam woolly adelgid predators native to Oregon and Washington. Oregon St. Univ. Agric. Exp. Stn. Tech. Bull. 62, Corvallis, OR. 63 pp.
- Mitchell, R.G., and P.E. Buffam. 2001.** Patterns of long term balsam woolly adelgid infestations and effects in Oregon and Washington. *West. J. App. For.* **16**: 121-126.
- Mitchell, R.G., and J.K. Maksymov. 1977.** Observations of predation on spruce gall aphids within the gall. *Entomophaga* **22**: 179-186.
- Mitchell, R.G., and K.H. Wright. 1967.** Foreign predator introductions for control of the balsam woolly aphid in the Pacific Northwest. *J. Econ. Entomol.* **60**: 140-147.
- Montgomery, M., A.F. Lagalante, and K.S. Shields. 2005.** Resistance of hemlock to *Adelges tsugae*: Promising new developments, p. 179. *In* B. Onken and R. Reardon [eds.], Third Symposium on Hemlock Woolly Adelgid in the Eastern United States, Feb. 1-3, 2005, Asheville, NC. USDA Forest Service, Morgantown, WV, FHTET-2005-01.
- Montgomery, M.E., and S.M. Lyon. 1996.** Natural enemies of adelgids in North America: their prospect for biological control of *Adelges tsugae* (Homoptera: Adelgidae), pp. 89-102. *In* S.M. Salom, T.C. Tigner, and R.C. Reardon [eds.], Proceedings: First Hemlock Woolly Adelgid Review, Oct. 12, 1995, Charlottesville, VA. USDA Forest Service, Morgantown, WV, FHTET-96-10.
- Onken, B. 2005.** Where are we now and where do we need to go?, pp. 240-244. *In* B. Onken and R. Reardon [eds.], Third Symposium on Hemlock Woolly Adelgid in the Eastern United States, Feb. 1-3, 2005, Asheville, NC. USDA Forest Service, Morgantown, WV, FHTET-2005-01.

- Orwig, D.A., and D.R. Foster. 1998.** Forest response to the introduced hemlock woolly adelgid in southern New England, USA. *J. Torrey Bot. Soc.* **125**: 60-73.
- Orwig, D.A., D.R. Foster, and D.L. Mausel. 2002.** Landscape patterns of hemlock decline in New England due to the introduced hemlock woolly adelgid. *Biogeography* **29**: 1475-1487.
- Rao, V.P., and M.A. Ghani. 1972.** Studies on predators of *Adelges* spp. in the Himalayas. Misc. Pub. No. 3, Commonwealth Agricultural Bureau. Farnham Royal, UK. 116 pp.
- Raworth, D.A., and M.C. Robertson. 2002.** Occurrence of the spider mite predator *Stethorus punctillum* (Coleoptera: Coccinellidae) in the Pacific Northwest. *J. Entomol. Soc. Brit. Columbia* **99**: 81-82.
- Reid, W., B.L. Parker, M. Skinner, S. Gouli, and H.B. Teillon. 2002.** Insect-killing fungi for management of hemlock woolly adelgid: a review of progress, pp. 198-204. *In* B. Onken, R. Reardon, and J. Lashomb [eds.], Proceedings: Hemlock Woolly Adelgid in Eastern North America Symposium, Feb. 5-7, 2002, East Brunswick, NJ. USDA Forest Service and State Univ. of N.J. Rutgers, East Brunswick, NJ.
- SAS Institute. 1999.** SAS/STAT user's guide, version 8. SAS Institute, Cary, NC.
- Salom, S.M., L.T. Kok, B.M. Eisenback, J.G. Fidgen, R.W. Flowers, H.A. Gatton, A.B. Lamb, T.J. McAvoy, D.L. Mausel, and G. Zilahi-Balogh. 2005.** Overview of HWA biological control activities with *Laricobius* spp., pp. 131-133. *In* B. Onken and R. Reardon [eds.], Third Symposium on Hemlock Woolly Adelgid in the Eastern United States, Feb. 1-3, 2005, Asheville, NC. USDA Forest Service, Morgantown, WV, FHTET-2005-01.
- Salom, S.M., A.A. Sharov, W.T. Mays, and D.R. Gray. 2002.** Influence of temperature on development of hemlock woolly adelgid (Homoptera : Adelgidae) progrediens. *J. Entomol. Sci.* **37**: 166-176.
- Schooley, H.O., J.W.E. Harris, and B. Pendrel. 1984.** *Adelges piceae* (Ratz.), balsam woolly adelgid (Homoptera: Adelgidae), pp. 229-234. *In* J.S. Kelleher and M.A. Hulme [eds.], Biological control programmes against insects and weeds in Canada 1969-1980. Commonwealth Agricultural Bureau, Farnham Royal, Slough, UK.
- Shields, K.S., and C.A.S.-J. Cheah. 2005.** Winter mortality in *Adelges tsugae* populations in 2003 and 2004, pp. 354-356. *In* B. Onken and R. Reardon [eds.], Third Symposium on Hemlock Woolly Adelgid in the Eastern United States, Feb.

1-3, 2005, Asheville, NC. USDA Forest Service, Morgantown, WV, FHTET-2005-01.

Shields, K.S., and R.T. Hirth. 2005. Bacterial endosymbionts of *Adelges tsugae* Annand: potential targets for biocontrol?, pp. 357-359. In B. Onken and R. Reardon [eds.], Third Symposium on Hemlock Woolly Adelgid in the Eastern United States, Feb. 1-3, 2005, Asheville, NC. USDA Forest Service, Morgantown, WV, FHTET-2005-01.

Skinner, M., B.L. Parker, S. Gouli, and T. Ashikaga. 2003. Regional responses of hemlock woolly adelgid (Homoptera: Adelgidae) to low temperatures. *Environ. Entomol.* **32**: 523-528.

Smith, B.C. 1958. Development, feeding habits, and predator-prey relations of insect predators of the balsam woolly aphid, *Adelges piceae* (Ratz.) (Homoptera: Adelgidae), recently introduced into Canada. *Can. Entomol.* **90**: 441-449.

Smith, B.C., and H.C. Coppel. 1957. Releases in North America and reviews of bionomics in Europe of insect predators of the balsam woolly aphid, *Adelges piceae* (Ratz.) (Homoptera: Adelgidae). *Can. Entomol.* **89**: 410-420.

Snyder, W.E., and E.W. Evans. 2006. Ecological effects of invasive arthropod generalist predators. *Annual Review of Ecology, Evolution, and Systematics* **37**: 95-122.

Stathas, G.J. 2000. *Rhyzobius lophanthae* prey consumption and fecundity. *Phytoparasitica* **28**: 203-211.

Stoetzel, M.B. 2002a. History of the introduction of *Adelges tsugae* based on voucher specimens in the Smithsonian Institute National Collection of Insects, p. 12. In B. Onken, R. Reardon, and J. Lashomb [eds.], Proceedings: Hemlock Woolly Adelgid in Eastern North America Symposium, Feb. 5-7, 2002, East Brunswick, NJ. USDA Forest Service and State Univ. of N.J. Rutgers, East Brunswick, NJ.

Stoetzel, M.B. 2002b. Coniopterygidae (Neuroptera): overlooked predators of *Adelges tsugae*? In B. Onken, R. Reardon, and J. Lashomb [eds.], Proceedings: Hemlock Woolly Adelgid in Eastern North America Symposium, Feb. 5-7, 2002, East Brunswick, NJ. USDA Forest Service and State Univ. of N.J. Rutgers, East Brunswick, NJ.

Tanasijtshuk, V.N. 1992. Morphological differences and phylogenetic relationships between the genera of chamaemyiid flies (Diptera: Chamaemyiidae). *Entomol. Obozr.* **71**: 199-230. (In Russian; translated in *Entomol. Rev.* **72**: 66-100.)

- Tanasijtshuk, V.N. 2002.** Studies on Nearctic species of *Leucopis* (Diptera: Chamaemyiidae). I. The redescription of Nearctic *Leucopis* published before 1965. *Zoosyst. Rossica* **11**: 193-207.
- Teucher, G. 1955.** The outbreak of *Adelges (Gilletteella) cooleyi* in Germany. *NachrBl. Dtsch. PflSch. Dienst.* **9**: 102-108. (In German).
- Tingley, M.W., D.A. Orwig, R. Field, and G. Motzkin. 2002.** Avian response to removal of a forest dominant: consequences of hemlock woolly adelgid infestations. *J. Biogeography* **29**: 1505-1516.
- van Lenteren, J.C., D. Babendreier, F. Bigler, G. Burgio, H.M.T. Hokkanen, S. Kuske, A.J.M. Loomans, I. Menzler-Hokkanen, P.C.J. Van Rijn, M.B. Thomas, M.G. Tommasini, and Q.Q. Zeng. 2003.** Environmental risk assessment of exotic natural enemies used in inundative biological control. *BioControl* **48**: 3-38.
- Waage, J.K., and N.J. Mills. 1992.** Biological control, pp. 412-430. *In*: M.J. Crawley [ed.], *Natural enemies: the population biology of predators, parasites and diseases*. Blackwell Scientific, Oxford, UK.
- Wallace, M.S., and F.P. Hain. 2000.** Field surveys and evaluation of native and established predators of the hemlock woolly adelgid (Homoptera: Adelgidae) in the southeastern United States. *Environ. Entomol.* **29**: 638-644.
- Wang, H., D. Yao, G. Li, C. Zhang, L. Li, H. Guo, and D. Zhao. 1998.** Investigation of hemlock woolly adelgid and its natural enemies in China, pp. 41-46. *In* *Resource Technology 1997: Beijing International Symposium Proceedings*, China Forestry Pub. House, Beijing.
- Ward, J.S. 2002.** Restoration of damaged stands: dealing with the after effects of hemlock woolly adelgid. pp. 118-126. *In* B. Onken, R. Reardon, and J. Lashomb [eds.], *Proceedings: Hemlock Woolly Adelgid in Eastern North America Symposium*, Feb. 5-7, 2002, East Brunswick, NJ. USDA Forest Service and State Univ. of N.J. Rutgers, East Brunswick, NJ.
- Ward, J.S., M.E. Montgomery, C.A.S.-J. Cheah, B.P. Onken, and R.S. Cowles. 2004.** *Eastern Hemlock Forests: Guidelines to Minimize the Impacts of Hemlock Woolly Adelgid*. USDA Forest Service Northeastern Area State & Private Forestry, NA-TP-03-04. 27 pp.
- Webb, R.E., J.R. Frank, and M.J. Raupp. 2003.** Eastern hemlock recovery from hemlock woolly adelgid damage following imidacloprid therapy. *J. Arbor.* **29**: 298-301.

- Wilson, F. 1938.** Notes on the insect enemies of Chermes with particular reference to *Pineus pini*, Koch. and *P. strobi*, Hartig. Bull. Entomol. Res. **29**: 373-389.
- Wilson, F. 1960.** A review of the biological control of insects and weeds in Australia and Australian New Guinea. Commonw. Inst. Biol. Control, Tech. Comm. No. 1, Ottawa. 102 pp.
- Yorks, T.E., D.J. Leopold, and D.J. Raynal. 2003.** Effects of *Tsuga canadensis* mortality on soil water chemistry and understory vegetation: possible consequences of an invasive herbivore. Can. J. For. Res. **33**: 1525-1537.
- Young, R.F., K.S. Shields, and G.P. Berlyn. 1995.** Hemlock woolly adelgid (Homoptera: Adelgidae): stylet bundle insertion and feeding sites. Ann. Entomol. Soc. Amer. **88**: 827-835.
- Yu, G., M.E. Montgomery, and D. Yao. 2000.** Lady beetles (Coleoptera: Coccinellidae) from Chinese hemlocks infested with the hemlock woolly adelgid, *Adelges tsugae* Annand (Homoptera: Adelgidae). Coleopt. Bull. **54**: 154-199.
- Zilahi-Balogh, G.M.G., C.D. Broeckling, L.T. Kok, and S.M. Salom. 2005.** Comparison between a native and exotic adelgid as hosts for *Laricobius rubidus* (Coleoptera: Derodontidae). Biocontrol Sci. and Tech. **15**: 165-171.
- Zilahi-Balogh, G.M.G., L.M. Humble, A.B. Lamb, S.M. Salom, and L.T. Kok. 2003a.** Seasonal abundance and synchrony between *Laricobius nigrinus* (Coleoptera: Derodontidae) and its prey, the hemlock woolly adelgid (Homoptera: Adelgidae). Can. Entomol. **135**: 103-115.
- Zilahi-Balogh, G.M.G., L.T. Kok, and S.M. Salom. 2002a.** Host specificity of *Laricobius nigrinus* Fender (Coleoptera: Derodontidae), a potential biological control agent of the hemlock woolly adelgid, *Adelges tsugae* Annand (Homoptera: Adelgidae). Biol. Contr. **24**: 192-198.
- Zilahi-Balogh, G.M.G., L.T. Kok, and S.M. Salom. 2002b.** A review of world-wide biological control efforts for the family Adelgidae, pp. 129-140. In B. Onken, R. Reardon, and J. Lashomb [eds.], Proceedings: Hemlock Woolly Adelgid in Eastern North America Symposium, Feb. 5-7, 2002, East Brunswick, NJ. USDA Forest Service and State Univ. of N.J. Rutgers, East Brunswick, NJ.
- Zilahi-Balogh, G.M.G., S.M. Salom, and L.T. Kok. 2003b.** Development and reproductive biology of *Laricobius nigrinus*, a potential biological control agent of *Adelges tsugae*. BioControl **48**: 293-306.

Zilahi-Balogh, G.M.G., S.M. Salom, and L.T. Kok. 2003c. Temperature-dependent development of the specialist predator *Laricobius nigrinus* (Coleoptera: Derodontidae). *Environ. Entomol.* **32**: 1322-1328.

Zondag, R., and M.J. Nuttall. 1989. *Pineus laevis* (Maskell), pine twig chermes or pine woolly aphid (Homoptera: Adelgidae), pp. 295-297. *In* P.J. Cameron, R.L. Hill, J. Bain, and W.P. Thomas [eds.], *A Review of Biological Control of Invertebrate Pests and Weeds in New Zealand 1874 to 1987*. Commonwealth Institute of Biological Control, Technical communication No. 10.

APPENDICES

Appendix A. Pacific Northwest locations not included in the survey where hemlock woolly adelgid infestations were observed during 2005 through 2006.

State, County, City	Location
OR, Linn, Hwy. 126	Clearwater Cove Campground
OR, Lincoln, Newport	Oregon Coast Aquarium parking lot
WA, Cowlitz, Castle Rock	Interstate 5 southbound rest area milepost 52
WA, Thurston, Tumwater	Washington Department of Natural Resources Work Center
WA, Thurston, Olympia	Burfoot Park
WA, Mason, Shelton	Dennie Ahl, USDA Forest Service Seed Orchard
WA, Grays Harbor, Taholah	Quinalt Nation Seed Orchard
WA, King, Seattle	Woodland Park Zoo and Washington Park Arboretum
WA, Jefferson, Queets	South Beach campground
WA, Clallam, Port Angeles	Washington Department of Natural Resources Work Center
WA, Clallam, Sequim	Dungeness National Wildlife Refuge
WA, Whatcom, Bellingham	Hampton Tree Farm Seed Orchard

Appendix B. Abundance of adult predatory species identified from *Adelges tsugae* infested *Tsuga heterophylla* in the Pacific Northwest, January 2005 through November 2006.

Order	Species	Total adults ^a	Number of collection sites (n = 16)	Determination credit ^b	OSAC accession ID ^c
Hemiptera	Miridae	(3)			
	<i>Campyloneura virgula</i> (Herrich-Schäffer)	1	1	1	000028839
	<i>Ceratopsus apicatus</i> Van Duzee	57	2	1	000028840
	<i>Deraeocoris brevis</i> (Uhler)	72	11	1	000028841
	<i>Heterotoma planicorne</i> Pallas	2	1	1	000028842
	<i>Phytocoris</i> sp.	24	7	1	000028843
	Nabidae				
	<i>Anaptus major</i> (Costa)	1	1	1	000028844
	<i>Nabis alternatus</i> Parshley	6	4	1	000028845
	<i>Nabis roseipennis</i> Reuter	3	2	1	000028846
	Anthocoridae				
	<i>Anthocoris whitei</i> Reuter	2	1	1	000028847
	<i>Elatophilus pullus</i> Kelton & Anderson	2	1	1	000028848
	<i>Orius minutus</i> (L.)	9	5	1	000028849
	<i>Tetrableps latipennis</i> Van Duzee	3	2	1	000028850
	Reduviidae				
	<i>Empicoris rubromaculatus</i> (Blackburn)	139	15	1	000028851
	<i>Rhynocoris ventralis</i> (Say)	1	1	1	000028852

Appendix B. (Continued).

Order	Species	Total adults ^a	Number of collection sites (n = 16)	Determination credit ^b	OSAC accession ID ^c
Neuroptera	Raphidiidae				
	<i>Agulla</i> sp.	1	1	2	000028853
	Coniopterygidae	(1)			
	<i>Conwentzia californica</i> Meinander	62	12	3	000028854
	<i>Semidalis angusta</i> (Banks)	8	6	3	000028855
	Hemerobiidae				
	<i>Hemerobius</i> spp.	117 ^d	13		
	<i>Hemerobius bistrigatus</i> Currie	3		3	000028856
	<i>Hemerobius ovalis</i> Carpenter	1		3	000028857
	<i>Hemerobius pacificus</i> Banks	7		3	000028858
	<i>Hemerobius stigma</i> Stephens	1		3	000028859
	Chrysopidae	(1)			
	<i>Chrysoperla downesi</i> (Smith)	4	4	3	000028860
	<i>Chrysoperla plorabunda</i> (Fitch)	3	1	3	000028861
<i>Chrysopodes placita</i> (Banks)	3	3	4	000028862	
Coleoptera	Staphylinidae	(7)			
	<i>Anthobium</i> sp.	1	1	5	000028863
	<i>Bryophacis</i> sp.	3	1	6	000028864
	<i>Carcinocephalus exsculptus</i> (Maklin)	1	1	5	000028865

Appendix B. (Continued).

Order	Species	Total adults ^a	Number of collection sites (n = 16)	Determination credit ^b	OSAC accession ID ^c
Coleoptera	Staphylinidae (Continued)				
	<i>Quedius peltax</i> Smetana	9	3	6	000028866
	<i>Tachyporus nitidulus</i> (Fabricius)	19	3	6	000028867
	<i>Xantholinus linearis</i> (Olivier)	1	1	6	000028868
	Cantharidae	(2)			
	<i>Cultellunguis larvalis</i> (Leconte)	2	1	7	000028869
	<i>Dichelotarsus cavicollis</i> (LeConte)	3	2	7	000028870
	<i>Dichelotarsus piniphilus</i> (Eschscholtz)	399	8	7	000028871
	<i>Malthodes</i> sp.	2	1	7	000028872
	Derodontidae	(1)			
	<i>Laricobius laticollis</i> Fall	1	1	2	000028873
	<i>Laricobius nigrinus</i> Fender	754	16	2	000028874
	Coccinellidae	(1)			
	<i>Coccidophilus atronitens</i> (Casey)	9	4	8	000028875
	<i>Coccinella septempunctata</i> L.	45	6	8	000028876
	<i>Coccinella trifasciata subversa</i> LeConte	2	1	2	000028877
	<i>Cycloneda polita</i> Casey	21	6	8	000028878
	<i>Exochomus quadripustulatus</i> (L.)	8	1	8	000028879
	<i>Harmonia axyridis</i> (Pallas)	7	3	8	000028880

Appendix B. (Continued).

Order	Species	Total adults ^a	Number of collection sites (n = 16)	Determination credit ^b	OSAC accession ID ^c
Coleoptera	Coccinellidae (Continued)				
	<i>Mulsantina picta</i> (Randall)	95	14	9	000028881
	<i>Rhyzobius forestieri</i> (Mulsant)	5	3	8	000028882
	<i>Rhyzobius lophanthae</i> (Blaisdell)	31	9	10	000028883
	<i>Scymnus (Pullus) coniferarum</i> Crotch	1	1	8	000028884
	<i>Scymnus</i> sp.	3	1	2	000028885
	<i>Stethorus punctillum</i> Weise	114	10	10	000028886
	<i>Zilus</i> sp.	24	2	8	000028887
Diptera	Syrphidae	(3)			
	<i>Eupeodes aberrantis</i> Curran	1	1	11	000028888
	<i>Eupeodes luniger</i> (Meigen)	1	1	11	000028889
	<i>Melanostoma mellinum</i> (L.)	1	1	11	000028890
	<i>Syrphus opinator</i> (Osten Sacken)	1	1	11	000028891

Appendix B. (Continued).

Order	Species	Total adults ^a	Number of collection sites (n = 16)	Determination credit ^b	OSAC accession ID ^c
Diptera	Chamaemyiidae	(3)			
	<i>Leucopis argenticollis</i> Zetterstedt	86	13	12	000028892
	<i>Leucopis atrifacies</i> (Aldrich)	13	7	12	000028893

^a Parentheses indicate unidentified adults; underline indicates determination from larvae only.

^b 1. J.D. Lattin, Oregon State Univ.; 2. G.R. Kohler, Oregon State Univ.; 3. N.D. Penny, California Acad. Sci.; 4. C.A. Tauber, Univ. California, Davis; 5. M.K. Thayer, Field Museum Nat. Hist.; 6. A.F. Newton, Field Museum Nat. Hist.; 7. A.S. Ramsdale, Montana State Univ.; 8. N.J. Vandenberg, Systematic Entomol. Lab., USDA ARS; 9. D.K. Young, Univ. Wisconsin; 10. S.J. Krauth, Univ. Wisconsin; 11. F.C. Thompson, Systematic Entomol. Lab., USDA ARS; 12. S.D. Gaimari, California Dept. Food & Agric.

^c Voucher specimens deposited at the Oregon State Arthropod Collection (OSAC), Dept. of Zoology, Oregon State University, Corvallis, OR.

^d Adult *Hemerobius* spp. could not be separated into species by the author.

Appendix C. Abundance of predatory species identified from infestations of *Adelges piceae* and *Adelges cooleyi* in the Pacific Northwest, June 2005 through October 2006.

		prey species:	<i>Adelges piceae</i>	<i>Adelges cooleyi</i>	<i>Adelges cooleyi</i>		
		host species:	<i>Abies grandis</i>	<i>Pseudotsuga menziesii</i>	<i>Picea engelmannii</i>		
		# samples:	16	19	9		
Order	Species	Number of adults and (immatures)			OSAC accession ID ^a		
Hemiptera	Miridae		(1)	(16)			
	<i>Ceratocapsus apicatus</i> Van Duzee		2	5		000028966	
	<i>Deraeocoris brevis</i> (Uhler)		2	3		000028967	
	Nabidae						
	<i>Nabis alternatus</i> Parshley				1	000028968	
Hemiptera	Reduviidae	(1)	(3)				
	<i>Empicoris rubromaculatus</i> (Blackburn)	1	(1)	5 (5)		000028969	
	Coniopterygidae		(3)				
	<i>Conwentzia californica</i> Meinander		2			000028970	
	<i>Semidalis angusta</i> (Banks)		1			000028971	
Hemiptera	Hemerobiidae		(5)	(1)			
	<i>Hemerobius</i> spp.		1	1		000028972	
Neuroptera	Chrysopidae			(2)			

Appendix C. (Continued).

Order	Species	Number of adults and (immatures)	OSAC accession ID ^a
	prey species:	<i>Adelges piceae</i>	<i>Adelges cooleyi</i>
	host species:	<i>Abies grandis</i>	<i>Pseudotsuga menziesii</i>
	# samples:	16	19
			9
Coleoptera	Coccinellidae	(2)	
	<i>Harmonia axyridis</i> (Pallas)		(2) 000028973
	<i>Mulsantina picta</i> (Randall)	5	000028974
	<i>Rhyzobius lophanthae</i> (Blaisdell)	2	000028975
	<i>Stethorus punctillum</i> Weise	4	000028976
Diptera	Syrphidae	(4)	(2)
	Chamaemyiidae	(21)	(1)
	<i>Neoleucopis tapiae</i> (Blanchard) ^b	1	000028977

^a Voucher specimens deposited at the Oregon State Arthropod Collection (OSAC), Dept. of Zoology, Oregon State University, Corvallis, OR.

^b Determined by S.D. Gaimari, Calif. Dept. Food & Agric.

Appendix D. Adult Hymenoptera identified from *Tsuga heterophylla* beat samples in the Pacific Northwest, January 2005 through November 2006.

Species	Determination credit ^a	OSAC accession ID ^b	<i>Adelges tsugae</i> predator host ^c
Megaspilidae			
unkown		000028894	
Ceraphronidae			
<i>Ceraphron</i> sp.	1	000028895	
Braconidae			
<i>Alysia</i> sp.	2	000028896	
<i>Aphidius</i> sp.-a	2	000028897	
<i>Aphidius</i> sp.-b	2	000028898	
<i>Bracon</i> sp.	2	000028899	
<i>Dinotrema</i> sp.	3	000028900	
<i>Hormius</i> sp.	2	000028901	
<i>Lysiphlebus</i> sp.	2	000028902	
<i>Monoctonus</i> sp.	2	000028903	
<i>Opius</i> sp.	2	000028904	
<i>Orgilus</i> sp.	2	000028905	
<i>Pauesia</i> sp.	2	000028906	
<i>Phenocarpus</i> sp.	2	000028907	

Appendix D. (Continued).

Species	Determination credit ^a	OSAC accession ID ^b	<i>Adelges tsugae</i> predator host ^c
Ichneumonidae			
<i>Aclastus</i> sp-a	2	000028908	
<i>Aclastus</i> sp-b	2	000028909	
<i>Aperileptus</i> sp.	2	000028910	
<i>Apotemnus truncatus</i> Cushman	2	000028911	
<i>Campoletis septentrionalis</i> Viereck	2	000028912	
<i>Charitopes gastricus</i> (Holmgren)	2	000028913	
<i>Cymodusa</i> sp.	2	000028914	
<i>Dichrogaster oregona</i> Townes	2	000028915	
<i>Endasys hesperus</i> Luhman	2	000028916	
<i>Gelis</i> sp.	2	000028917	
<i>Gelis tenellus</i> (Say)	2	000028918	
<i>Grypocentrus</i> sp.	2	000028919	
<i>Ichneumon</i> sp.	2	000028920	
<i>Ischnus inquisitorius atriceps</i> (Cresson)	2	000028921	
<i>Mastrus</i> sp.	2	000028922	
<i>Megastylus</i> sp.	2	000028923	
<i>Ophion</i> sp.	2	000028924	
<i>Orthocentrus</i> sp.	2	000028925	
<i>Phobocampe</i> sp.	2	000028926	

Appendix D. (Continued).

Species	Determination credit ^a	OSAC accession ID ^b	<i>Adelges tsugae</i> predator host ^c
Ichneumonidae (Continued)			
<i>Picrostigeus</i> sp.	2	000028927	
<i>Plectiscidea</i> sp-a	2	000028928	
<i>Plectiscidea</i> sp-b	2	000028929	
<i>Stenomacrus</i> sp.	2	000028930	
<i>Syrphoctonus pallipes</i> (Gravenhorst)	2	000028931	Syrphidae pupae
<i>Transonema</i> sp.	2	000028932	
<i>Woldstedtius flavolineatus</i> (Gravenhorst)	2	000028933	Syrphidae pupae
<i>Zoophthorus (Mastrus)</i> sp.	2	000028934	
Mymaridae			
unknown		000028935	
Eulophidae			
<i>Aprostocetus</i> sp.	1	000028936	
<i>Chrysocharis</i> sp.	1	000028937	
<i>Diglyphus begini</i> (Ashmead)	1	000028938	
Aphelinidae			
unknown		000028939	
Encyrtidae			
<i>Ericydnus</i> sp.	1	000028940	
<i>Lamennaisia</i> sp.	1	000028941	

Appendix D. (Continued).

Species	Determination credit ^a	OSAC accession ID ^b	<i>Adelges tsugae</i> predator host ^c
Encyrtidae (Continued)			
<i>Syrphophagus</i> sp.	1	000028942	Syrphidae pupae
Eupelmidae			
unknown		000028943	
Torymidae			
<i>Megastigmus</i> sp.	1	000028944	
<i>Torymus</i> sp.	1	000028945	
Pteromalidae			
<i>Coelopisthia</i> sp.	1	000028946	
<i>Gastrancistrus</i> sp.	1	000028947	
<i>Mesopolobus</i> sp.	1	000028948	
<i>Pachyneuron albutius</i> Walker	1	000028949	Syrphidae pupae
<i>Pachyneuron</i> n. sp.	1	000028950	<i>Leucopis</i> spp. pupae (Chamaemyiidae)
<i>Pachyneuron</i> sp.-a	1	000028951	<i>Leucopis</i> spp. pupae (Chamaemyiidae)
<i>Trichomalopsis</i> sp.	1	000028952	
Eurytomidae			
<i>Tetramesa</i> sp.	1	000028953	
Figitidae			
<i>Melanips</i> sp.	4	000028954	<i>Leucopis</i> spp. pupae (Chamaemyiidae)

Appendix D. (Continued).

Species	Determination credit ^a	OSAC accession ID ^b	<i>Adelges tsugae</i> predator host ^c
Eucoilidae			
unknown		000028955	
Heloridae			
<i>Helorus</i> sp.	5	000028956	Chrysopidae pupae
Proctotrupidae			
unknown		000028957	
Diapriidae			
<i>Aclista</i> sp.-a	6	000028958	
<i>Aclista</i> sp.-b	6	000028959	
<i>Camptopsilus</i> sp.	6	000028960	
<i>Trichopria</i> sp.	6	000028961	
Scelionidae			
<i>Idris</i> sp.	1	000028962	
<i>Telenomus</i> sp.	1	000028963	
<i>Trissolcus</i> sp.	1	000028964	

Appendix D. (Continued).

Species	Determination credit^a	OSAC accession ID^b	<i>Adelges tsugae</i> predator host^c
Platygastridae			
<i>Platygaster</i> sp. (prob.)	6	000028965	

^a 1. S.L. Heydon, Univ. California, Davis; 2. J.C. Luhman, Minnesota Dept. Agric.; 3. R.A. Wharton, Texas A&M Univ.; 4. M.L. Buffington, Systematic Entomol. Lab., USDA ARS; 5. G.R. Kohler, Oregon State Univ., 6. M.J. Yoder, Texas A&M Univ.

^b Voucher specimens deposited at the Oregon State Arthropod Collection (OSAC), Dept. of Zoology, Oregon State University, Corvallis, OR.

^c Parasitic taxa determined from specimens reared on predator hosts in the laboratory.

