Aquatic insects in British Columbia: 100 years of study

GEOFFREY G.E. SCUDDER, KAREN M. NEEDHAM, REX D. KENNER

SPENCER ENTOMOLOGICAL MUSEUM, DEPARTMENT OF ZOOLOGY, UNIVERSITY OF BRITISH COLUMBIA, VANCOUVER, BC, CANADA V6T 1Z4

ROBERT A. CANNINGS

ROYAL BRITISH COLUMBIA MUSEUM, 675 BELLEVILLE STREET, VICTORIA, BC, CANADA V8W 9W2

and SYDNEY G. CANNINGS

BRITISH COLUMBIA CONSERVATION DATA CENTRE, MINISTRY OF SUSTAINABLE RESOURCE MANAGEMENT, PO BOX 9344 STN PROV GOVT, VICTORIA, BC, CANADA V8W 9M1

INTRODUCTION

Aquatic habitats in British Columbia are diverse and numerous. BC is home to large rivers, small ponds, and lakes which vary tremendously in size, depth, and chemical composition (Northcote and Larkin 1963), as well as a variety of fens, marshes, and bogs (Rosenberg and Danks 1987). Not surprisingly, studies in aquatic insects have a long history in our Province. The status of entomological knowledge from 1901 to 1951 in BC was summarized by Spencer (1952), including short paragraphs on each of the aquatic orders. The history of many of the entomologists involved and their collections are highlighted in Hatch's (1949) charming summary of a century of entomology (1835-1948) in the Pacific Northwest.

In the past, provincial studies have emphasized the importance of freshwater fisheries, and these have been accompanied by benthic invertebrate surveys. In recent years, forestry-fisheries interactions have come to the fore. The role of insects in this interaction is creating a new interest in aquatic entomology. The current concerns over water quality and groundwater pollution will undoubtedly involve more study of aquatic insects as environmental indicators.

EPHEMEROPTERA

Since the outstanding and prolific work of J. McDunnough in the 1920s and 1930s on the mayflies of Canada, the only BC-wide survey of Ephemeroptera was conducted by Filmer (1964). Most records since then have been obtained incidentally during other faunal studies. A checklist of BC species was produced by Scudder (1976). McCafferty and Randolph (1998) published a Canadian mayfly compendium that added seven new species to Scudder's 1976 list, as well as containing two species that Scudder (1976) omitted as probable erroneous records, for a total of 92 species in BC. Since this new list was compiled without examining specimens from the Royal British Columbia Museum, the Spencer Entomological Museum, or the Fisheries Branch of the Ministry of Water, Land and Air Protection, these collections may contain more new records for the Province.

Locally, Wigle and Thommasen (1990) collected and recorded ecological notes on 26 species of mayflies in the Bella Coola and Owikeno Lake watersheds of mid-coastal BC.

One of these, *Epeorus nitidus* Eaton, was a new record for the Province. Another new record for BC, *Acentrella turbida* (McDunnough), was found there later (McCafferty *et al.* 1994). Zloty (1996) and Zloty and Pritchard (1997) collected at various southwestern BC locales in search of *Ameletus* species, and to date have found one, *Ameletus pritchardi* Zloty, new to the Province and to science. S. Salter (pers. comm.) recently collected a new mayfly species for the Province, *Caenis youngi* Roemhild, during some invertebrate surveys at Liard Hot Springs in northern BC. In their comparison of the macroinvertebrate assemblages of coastal and continental streams and large rivers in southwestern British Columbia, Reece and Richardson (2000) found that *Paraleptophlebia temporalis* McDunnough predominated in coastal streams.

Heise (no date) in a study of the effect of logging on the fauna of streams in the Penticton Creek and Sicamous Creek watersheds found that mayflies were very sensitive to logging. Richardson and Kiffney (2000) studied the response to metal pollutants of macroinvertebrate fauna in experimental streams off Mayfly Creek in the UBC Research Forest near Maple Ridge, and found that *Ameletus*, *Baetis*, and *Paraleptophlebia* (mainly *P. temporalis*) were very sensitive to Cu, Zn, Mn, and Pb, typical components of urban runoff. Rempel *et al.* (2000) in a study of the macroinvertebrates along gradients of hydraulic and sedimentary conditions in a 10-km reach of the Fraser River near Agassiz, found that the distribution of several genera of mayflies was correlated with hydraulic conditions. Rempel *et al.* (1999) also showed that the densities of *Baetis* and *Rhithrogena* were highest at a depth of 1.5 m before flooding, but shifted to depths of 0.2-0.5 m at peak flow.

Keys to genera of BC mayflies can be found in Edmunds *et al.* (1976), Merritt and Cummins (1996), and Needham (1996). Keys to species have only been completed for a few genera (e.g. *Ameletus*, Zloty (1996), Zloty and Pritchard (1997); *Caenis*, Provonsha (1990); *Tricorythodes*, Alba-Tercedor and Flannagan (1995)).

ODONATA

Spencer (1952) in his brief summary of the status of the knowledge of Odonata in British Columbia did not cite what is perhaps the most significant work of the period, Whitehouse's (1941) delightful and detailed treatment of the provincial fauna. He also neglected Walker's important monographs on two of our most speciose genera, *Aeshna* (Walker 1912) and *Somatochlora* (Walker 1925); although these dealt with the entire North American fauna of these genera, they included much information on the species in British Columbia.

Walker's major opus on the Odonata of Canada and Alaska (Walker 1953, 1958) led off the second half of the century and was completed by the international Odonata expert P. Corbet (Walker and Corbet 1975). It listed many of the locality records known to this time and summarized ecological information.

Since the mid 1970s the study of the Odonata in BC has been continuous. It has been helped by work in adjacent areas, particularly the Biological Survey of Canada's Yukon insect project (S.G. Cannings and R.A. Cannings 1997; S.G. Cannings *et al.* 1991) and the extensive studies of Paulson (e.g. 1997, 1999) to the south in Washington State. This followed the annotated checklist produced by Scudder *et al.* (1976) and the book written by R.A. Cannings and Stuart (1977). The latter published the first distribution maps for the species of the Province.

Robert and Sydney Cannings, periodically helped by their brother Richard, have been the driving force in odonatology in the Province during the past 25 years. They organized numerous dragonfly inventories across the Province, from the Brooks Peninsula on the outer coast of Vancouver Island (R.A. Cannings and S.G. Cannings 1983), to the grasslands of the Chilcotin (R.A. Cannings and S.G. Cannings 1987), to the Rocky



F.C. Whitehouse, a pioneering odonatologist, collecting specimens from his caravan at Harrison and Cultus Lakes in the summer of 1936.

Mountains (R.A. Cannings *et al.* 2000) and the North (R.A. Cannings *et al.* 2001). Others who have made significant contributions to these collections and inventories include G. Hutchings, L. Ramsay, C. Guppy, R. Kenner, D. Blades, and H. Nadel. In addition, the Cannings, along with their colleagues, have documented new species to the Province (R.A. Cannings 1988, 1997; Kenner 2000a) and published much faunistic (R.A. Cannings 1978, 1996; R.A. Cannings *et al.* 1980; S.G. Cannings 1980; S.G. Cannings and R.A. Cannings 1994) and ecological work (R.A. Cannings 1980, 1982a; R.A. Cannings *et al.* 1980; Paulson and R.A. Cannings 1980). Significant in the taxonomic work done on the Odonata in British Columbia and Yukon over the past 25 years is the description of four previously unknown larvae (R.A. Cannings 1981; S.G. Cannings and R.A. Cannings 1980; R.A. Cannings and Doerksen 1979; Kenner *et al.* 2000) and the redescription of several others, along with improved keys to this important life stage (R.A. Cannings 1982b; Kenner 2001).

G.P. Doerksen had begun to examine local dragonflies intensively (Doerksen 1980) when he was killed by a Grizzly Bear while on a research trip to Liard River Hot Springs in 1981. His wonderful dragonfly photographs, willed to the Royal BC Museum, are a valuable research and interpretative resource. Peters (1998), while on a visit from Germany, published a useful study on variability in *Aeshna*. R. Kenner (Kenner 1996, 2000b, 2000c; Kenner and Lane 1997; Kenner and R.A. Cannings 2001) and I. Lane (Lane 2000) have improved our knowledge of the fauna of the Lower Mainland, including the documentation of the first Canadian breeding site of *Tanypteryx hageni* Selys.

Few experimental studies on the Odonata have been undertaken in the Province. G. Pritchard, University of Calgary, has studied the ecology and development of Odonata, especially *Argia vivida* Hagen, of warm springs in British Columbia and adjacent regions (Pritchard 1989, 1991). At the University of BC, P. Pearlstone (1973) examined the food

of larval *Enallagma boreale* Selys and R. Baker (1983) studied the larval competition and feeding behaviour of *Ischnura cervula* Selys.

An important recent development has been the listing of species of management concern by the BC Conservation Data Centre (Ramsay and S.G. Cannings 2000; R.A. Cannings 2001). At the end of the 2001 field season, 23 species were listed. This highlighting of rare species spurred research into their status and habitats, and stimulated regional inventories.

Odonata are now the best known aquatics insects in the Province. Of course, there is still much to learn, especially regarding the ecology of the fauna and the distribution of northern species. Spencer noted 78 species in 1952, but the most accurate published record up to that time was from Whitehouse (1941), who recognized 74 species in 23 genera. By 1977, R.A. Cannings and Stuart could report 80 species and 23 genera. In 2001, 87 species in 27 genera are known from the Province (there are 201 recorded in Canada). Perhaps the most striking addition to the provincial list in the past 50 years was the discovery of *Calopteryx aequabilis* Say at Christina Creek in 1998 (R.A. Cannings *et al.* 2000). This added a new family to British Columbia, the Calopterygidae, making a total of 10.

All available records for the Odonata in BC are databased, georeferenced, and mapped, ready to serve as baseline data for the faunal changes of the new millennium. Useful works for identification, in addition to Walker (1953, 1958), Walker and Corbet (1975), and R.A. Cannings and Stuart (1977) are Westfall and May (1996), Needham *et al.* (2000), and Dunkle (2000).

PLECOPTERA

Ricker (e.g. 1943, 1954) conducted early systematic and distributional studies on stoneflies. An annotated checklist of the Plecoptera of BC was published by Ricker and Scudder (1976). S.G. Cannings (1989) also provided a number of new records, especially for capniids. An up-to-date checklist can be extracted from the North American stonefly list provided on the internet by Stark (2001). Currently, 132 species are known from the Province. More detailed systematic studies that are relevant include Nelson and Baumann's (1989) work on *Capnia*, Stanger and Baumann's (1993) work on *Taenionema*, and Stark and Nelson's (1994) work on *Yoraperla*. Kenneth Stewart (University of North Texas) and Mark Oswood are actively writing "Stoneflies of Alaska and Northwestern Canada," which will include history, keys, illustrations, new locality records, maps, species accounts, and biological notes on the species documented for Alaska, British Columbia, Yukon, and Northwest Territories; publication is anticipated in 2003.

D.B. Donald and R.S. Anderson of the Canadian Wildlife Service (Edmonton) surveyed the stoneflies of the Rocky Mountain National Parks. The lentic stoneflies of these collections were summarized in Donald and Anderson (1980). Donald and Patriquin (1983) related the wing length of Rocky Mountain lentic capniids to their inferred postglacial recolonization history.

A number of studies investigating stonefly population dynamics, foraging ecology, species interactions, and life history in coastal streams have been undertaken by J. Richardson and his colleagues at UBC (Reece and Richardson 2000; Rempel et al. 2000; Richardson 2002; Soluk and Richardson 1997). Muchow and Richardson (2000) reported the occurrence of Plecoptera in small headwater streams in the UBC Research Forest near Maple Ridge. They found the fauna differed in intermittent and continuous flow streams. While Paraleuctra vershina Gautin and Ricker and Visoka cataractae (Neave) occurred only in continuous flow streams, Alloperla pilosa Needham and Claassen, Despaxia augusta (Banks), Moselia infuscata (Claassen), Ostracerca foesteri (Ricker), Pteronarcys californica Newport, Soyedina producta (Claassen), Zapada cinctipes (Banks), and Z. oregonensis (Claassen) occurred in both. Even in small streams (less than half a metre wide) with intermittent flow, the univoltine Moselia infuscata, Soyedina producta, and

Zapada cinctipes were found to emerge in periods when no flow was perceptible. Despaxia augusta, with a 2-year life cycle, was also able to complete its development in the periodically 'dry' channels and reached its highest densities in intermittent streams. The authors suggest that suitable refugia exist for this species and others in the wet sediments of these habitats despite the periodic disappearance of detectable surface flows.

All available, reliably identified records are now databased, georeferenced, and mapped. References useful for identification include Baumann *et al.* (1977), Harper and Stewart (1984), Jewett (1959), Ricker (1943), Stark *et al.* (1986), and Stewart and Stark (1988).

HEMIPTERA

In addition to records in the early literature of Hemiptera in British Columbia, Scudder (1977) published an annotated checklist of the aquatic and semi-aquatic bugs in the Province. In the recent checklist for Canada (Maw *et al.* 2000), a total of 46 species of aquatics (Infraorder Nepomorpha: Families Belostomatidae, Nepidae, Gelastocoridae, Corixidae, Notonectidae) and 14 species of semi-aquatics (Infraorder Gerromorpha: Families Mesoveliidae, Hebridae, Hydrometridae, Gerridae, Veliidae) are recorded.

Over the past 40 years, detailed studies of the biology of both Corixidae and Gerridae have been undertaken, much of this associated with a study of the saline lakes of the British Columbia interior. Scudder (1965a, 1969a, 1969b) investigated the distribution of two closely related species of *Cenocorixa* in these lakes, and found that while *C. bifida* (Hung.) was evidently a freshwater species, *C. expleta* (Uhler) was more saline tolerant.

Extensive study of the osmotic and ionic balance in these two corixid species (Scudder 1971a; Scudder *et al.* 1972; Szibbo and Scudder 1979; Needham 1990) and an investigation of their cuticular permeability (Oloffs and Scudder 1966; S.G. Cannings 1981; S.G. Cannings *et al.* 1988) was accompanied by detailed histological and ultrastructural studies of their excretory organs (Jarial and Scudder 1970) and other organs that were evidently involved in osmotic and ionic regulation (Jarial *et al.*1969; Lo and Acton 1969; Jarial and Scudder 1971). Although the two species differed in their osmotic and ionic regulatory abilities at high salinities, both were able to regulate equally well in low salinity waters. Indeed, the more saline tolerant *C. expleta*, which in the field does not live in freshwater lakes, was successfully reared in freshwater (S.G. Cannings 1978). These studies subsequently led to much more detailed research on the coastal *C. blaisdelli* (Hung.) (Cooper *et al.* 1987, 1988, 1989) and other corixid species (Scudder 1987).

Both of the interior species of *Cenocorixa*, and other Corixidae, were found to be predaceous (Jansson and Scudder 1972; Reynolds 1975), which permitted laboratory rearing and led to other studies. Once species had been reared and the immature stages of both *C. bifida* and *C. expleta* described (Scudder 1966a), studies were carried out on their life cycle (Jansson and Scudder 1974), flight muscle development (Scudder 1971b), and flight muscle polymorphism (Scudder 1964; Acton and Scudder 1969; Scudder and Meredith 1972; Scudder 1975).

Jansson (1972, 1973, 1974a, 1974b), in his extensive study of stridulation in these *Cenocorixa* species, found species-specific mating signals and hence an effective premating isolating mechanism. Further, in an intensive study of their feeding biology, using serological and other techniques, Reynolds and Scudder (1987a, 1987b) studied both the fundamental and realized feeding niches of *C. bifida* and *C. expleta*.

In a review of the factors governing the distribution of *C. bifida* and *C. expleta*, Scudder (1983), following studies on mite parasitism of these species (Smith 1977), suggested that *C. expleta* was excluded from freshwater lakes by mite parasitism. This suggestion has been substantiated by more research (Bennett and Scudder 1998), which showed that for

C. expleta saline lakes are enemy-free space. This research has been cited as an example of a parasite-structured animal community (Minchella and Scott 1991).

In the Gerridae, several species were found to coexist in BC lakes (Maynard 1969; Scudder 1971c). Following the rearing and description of the immature stages of these (Scudder and Jamieson 1972; Spence and Scudder 1978), detailed studies were undertaken of their food consumption and predatory behaviour (Jamieson and Scudder 1977, 1979), growth patterns (Spence *et al.* 1980a), life cycles (Spence and Scudder 1980; Rowe and Scudder 1990), mating and other behaviours (Spence *et al.* 1980b; Rowe 1992, 1994). Spence (1981, 1983, 1989) was then able to undertake a detailed analysis of habitat selection, life cycle strategy, species-packing, and coexistence in these pond skaters. Subsequently, Spence (1990) discovered introgressive hybridization in two species of *Limnoporus* within British Columbia and Alberta, and has gone on to look at the mating system of these (Spence and Wilcox 1986; Wilcox and Spence 1986), and some of the genetic factors accompanying this hybridization between non-sister species (Spence and Maddison 1986; Sperling and Spence 1990, 1991; Sperling *et al.* 1997).

Seven species of Notonectidae occur in BC (Scudder 1965b, 1977). *Notonecta borealis* Hussey was discovered to be primarily a flightless species (Scudder 1966b). Ellis and Borden (1969) have investigated the effect of temperature and other environmental factors on *N. undulata* Say.

MEGALOPTERA

Spencer (1942) treated the Megaloptera, which includes the dobsonflies and the alderflies, within his listing of the Neuroptera, and recorded 4 species from British Columbia. A systematic review of the Sialidae by Ross (1937) gives a key to the species of *Sialis*; 5 species are now know to occur in the Province. Munroe (1951, 1953) sorted out the identity of material from British Columbia that Spencer (1942) reported as *Neohermes disjunctus*, and now 3 species of Corydalidae are known from BC.

While *Dysmicohermes disjunctus* (Walker) is widely distributed, both *Chauliodes pecticornis* L. and *Protochauliodes spenceri* Munroe may be at risk, as they have a restricted distribution in areas of the Province subject to heavy human impact. *Chauliodes pecticornis* is known from Cloverdale and Cowichan, while *Protochauliodes spenceri* is restricted to south-east Vancouver Island in Canada. All known records of Megaloptera in the Province are databased, georeferenced, and mapped.

NEUROPTERA

Of the 8 families of Neuroptera reported from British Columbia, only the family Sisyridae has aquatic larvae. In the Sisyridae, although Spencer (1942) recorded only Sisyra vicaria (Walker) from BC, based upon a specimen from Agassiz determined by F.M. Carpenter, it is now known that another species of spongilla fly, Sisyra fuscata (Fab.), also occurs in the Province. While S. vicaria is widely distributed, S. fuscata is only known from Kaslo and Seton Lake. A key to the species of Sisyridae is given in Parfin and Gurney (1956). All known records of aquatic Neuroptera in BC are now databased, georeferenced, and mapped.

TRICHOPTERA

Some of the earliest records of Trichoptera from British Columbia come from N. Banks, who worked on the group from the early 1900s to the early 1940s. H.H. Ross also contributed significantly to these early records, collecting in the 1930s, 1940s, and 1950s throughout North America. The first attempt to pull all of these scattered records together

into one publication was made by Ross and Spencer (1952), who created a preliminary list of the Trichoptera of BC. This list was added to significantly by Nimmo and Scudder (1978) when they published their annotated checklist containing 248 species, 43 of which were new records for BC. At this time, they stated that "there has been no concerted Trichoptera collecting in British Columbia as a whole, so the fauna must still be regarded as incompletely known."

To partially rectify this, A. Nimmo spent the spring, mid-summer, and fall of 1979 exploring much of the Province in search of caddisflies (Nimmo and Scudder 1983). He added many range extensions to known species, and also recorded 36 new species for BC (Nimmo and Scudder 1983), thus bringing the provincial total to 279 species (they removed 5 species from the 1978 list). However, Nimmo admitted that the northern half of the Province, the Queen Charlotte Islands, and many alpine areas still remain uncollected (Nimmo and Scudder 1983).

Also in the 1970s, G. Wiggins published his invaluable and beautifully illustrated identification guide to the larval caddisflies of North America (Wiggins 1977). A second edition in 1996 recognized some 1400 species of Trichoptera in North America by the end of 1993 (Wiggins 1996). More specific to our region are the keys provided by Schmid (1980) to the genera of Trichoptera in Canada and adjacent States. An English version of this Insects and Arachnids of Canada (Part 7) publication has also been recently made available (Schmid 1998). Unfortunately, keys to caddisflies of BC at the species level are still lacking.

Collections of caddisflies from specific areas of our Province can be found in Clemens *et al.* (1939) for Okanagan Lake, Hardy (1955) for the Forbidden Plateau area of Vancouver Island, Nimmo (1971, 1974, 1977) for eastern BC, Rawson (1934) for the Kamloops region, Schmid and Guppy (1952) for southern Vancouver Island, Scudder (1969b) for the Fraser Plateau, and Winterbourn (1971a,b) for Marion Lake, BC.

On the biology of caddisflies, Richardson (1991) found *Lepidostoma roafi* (Milne) to be univoltine. In a study contrasting the fauna of coastal and continental streams and large rivers in southwestern BC, Reece and Richardson (2000) found that *Onocosmoecus unicolor* (Banks) was unique to coastal streams, while *Brachycentrus occidentalis* Banks was unique to larger rivers. *B. americanus* (Banks) was unique to continental streams in the Merritt area. In Marion Lake, Trichoptera larvae, in particular *Banksiola crotchi* Banks, were the most important food item of rainbow trout (Efford and Tsumura 1973). The effects of the mosquito larvicide *Bacillus thuringiensis* on caddisflies was reported by Duckitt (1986).

Rempel *et al.* (1999), in an investigation of the effect of flooding on benthic invertebrates in the Fraser River near Agassiz, noted that *Hydropsyche* was most abundant at 1.5 m in all months of the years, but the location shifted laterally over a distance of 30 m through the flood cycle. They evidently migrated to the shore zone with the rise in water level, so maintaining a suitable hydraulic microhabitat. Heise (no date), in a study of the effect of logging on the fauna of streams in Penticton Creek and Sicamous Creek watersheds, found that while some caddisfly larvae showed a constant pattern of distribution in response to logging, *Psychoglypha*, a shredder, declined after logging and *Ecclisocosmoecus*, an algal feeder, increased after logging.

Caira and Scudder (1985) reported parasitism of *Psychoglypha alascensis* Banks (Trichoptera: Limnephilidae) by *Pseudoallocreadium alloneotenicum* (Wootton) (Digenea: Allocreadiidae). Caira (1981) investigated parasitism of Trichoptera by *Bunodera mediovitellata* Zimbaluk & Roytman (Digenea: Allocreadiidae) and the encapsulation response. This hemocyte encapsulation response in *P. alascensis* was studied later using Epon implants (Caira and Scudder 1987).

COLEOPTERA

British Columbia has a very rich aquatic beetle fauna. For example, BC has more species of Dytiscidae, Amphizoidae, Haliplidae, and Hydraenidae than any other Province (Larson *et al.* 2000; Bousquet 1991). Yet, beetles appear to be one of the more neglected groups of aquatic insects in BC. Early lists of Coleoptera from various parts of the Province (e.g. Keen 1895, 1905; Stace-Smith 1929, 1930) do contain some aquatic species, but there has been no published provincial checklist, although a preliminary list was developed by Scudder (unpublished). Most of the works dealing with aquatic beetles in BC have been as parts of studies of particular taxa over larger geographical areas. References to keys for aquatic beetles are in Bousquet (1991) and Arnett and Thomas (2001). Species lists for BC are in Bousquet (1991) and Larson *et al.* (2000).

The most important person to study aquatic beetles in BC was H.B. Leech. Leech was born in Kamloops, received much of his early education in Vernon, and graduated from UBC in 1933. From 1930-1947, he worked at the Forest Entomology Laboratory in Vernon where he collaborated with R. Hopping. In 1947, he joined the California Academy of Sciences. He described his first new species in 1937, *Agabus vancouverensis* Leech (Leech 1937), and subsequently described over 50 beetle taxa (Kavanaugh and Arnaud 1981). His collection of over 30,000 specimens of aquatic beetles, many from BC, was donated to the California Academy of Sciences in 1947. Several species of aquatic beetles found in BC are named after Leech: *Haliplus leechi* Wallis, *Helophorus leechi* McCorkle, and *Cymbiodyta leechi* Miller, which is known from Washington and probably occurs in BC (Smetana 1988).

Several other people are associated with aquatic beetles in BC mostly as collectors; for example, G.J. Spencer, R. Hopping, and G. Stace-Smith. M.H. Hatch described several species of aquatic beetles found in BC and is best known for his "Beetles of the Pacific Northwest" (Hatch 1953-1971). Each of them has at least one aquatic beetle from BC named in his honor.

In more recent times, Scudder (1969b) reported some species from interior saline lakes, and he, his students, and associates have collected aquatic beetles as part of more general surveys and added to our knowledge of the distribution of various species, especially in the Gulf Islands and in the northern part of the Province. In addition, J. Lancaster has conducted an ecological study of aquatic beetles in a comparison of the community structure in a series of saline lakes on the Chilcotin Plateau (Lancaster and Scudder 1987). Kenner (2000d) described the distribution of two species of gyrinids in BC, the Yukon, and Alaska.

DIPTERA

The Manual of Nearctic Diptera (McAlpine 1981, 1987) is a wonderful resource for information on systematics and biology of North American Diptera. Illustrated keys identify immature and adult specimens to family and genus. The taxonomic and distributional status, to the early 1960s, of many British Columbia species is outlined in Stone *et al.* (1965).

The Mountain Midges (Deuterophlebiidae) are peculiar, little-known flies found in streams in the western mountains. Courtney (1990) documented the systematics of the Nearctic species, including those known from BC.

In the Chaoboridae, Northcote (1964) and Teraguchi and Northcote (1966) studied the vertical distribution and vertical migration of *Chaoborus* larvae in BC lakes. Taxonomic works on the Phantom Midges that relate to the provincial fauna include Saether (1970) and Borkent (1979, 1993).

Early work on the Culicidae in BC includes that of Hearle (1926, 1927) and Curtis (1967). Belton (1978) studied the mosquitoes of Burnaby Lake, and more recently produced a monograph on the 46 species known in BC (Belton 1983). This work, together with Wood *et al.* (1979), can be used to identify these species.

In his study of the fauna of saline lakes on the Fraser Plateau, Scudder (1969b) found that *Aedes campestris* Dyas and Knab occurred in the most saline of them. The osmotic and ionic regulation in the larvae of this mosquito is therefore of interest; it has been studied by Phillips and Meredith (1969a). They also investigated the active transport of sodium and chloride by the anal papillae of the larvae (Phillips and Meredith 1969b) and the electron microscopic structure of these organs (Meredith and Phillips 1973a, 1973b). Regulation and active transport of magnesium by the Malphighian tubules of these larvae was described by Kiceniuk and Phillips (1974) and Phillips and Maddrell (1974). They also discovered that these tubules could actively transport sulphate ions (Maddrell and Phillips 1975). This work led to comparative studies on other saline-water mosquito larvae including *Aedes dorsalis* (Meigen) and *A. togoi* (Theobald) (Meredith and Phillips 1973c; Strange *et al.* 1982, 1984; Strange and Phillips 1984), both of which occur in the Province. Important reviews resulted from this research (Bradley and Phillips 1977; Phillips *et al.* 1978; Phillips and Bradley 1978; Strange and Phillips 1985; Ng and Phillips 1985).

Gammarid predation on *Aedes togoi* at Horseshoe Bay was reported by Hossack and Costello (1979). Oviposition of *Culex pipiens* L. in water at different temperatures was described by Gillespie and Belton (1980). Ishii and Belton (1984) provided evidence for autogenous egg development in this species and Belton (1982) described the cuticular vestiture of *Aedes communes* (DeGeer) and *A. nevadensis* Chapman and Burr.

The comprehensive treatment of the Black Flies (Simuliidae) of North America by P. Adler, D. Currie, and D.M. Wood is nearing completion; when published, this work will deal with all aspects of the systematics of BC species. Early studies by Curtis (1954) and Shewell (1957, 1959) were followed by research by Peterson (1970), Mahrt (1982), Currie and Adler (1986), and Corkum and Currie (1987). Currie's work in Alberta (1986) and the Yukon (1997) has direct application to the BC fauna. Studies on *Parasimulium* (Borkent 1992; Borkent and Currie 2001) have led to a better understanding of the phylogenetic origins of the Simuliidae. Currie and Walker (1992) documented the use of fossil black fly larvae in paleoecological studies. Cytological research into the giant chromosomes of simuliids has been undertaken in the genus *Prosimulium* (Basrur 1962), in *Stegopterna* (Madahar 1969), in the *Simulium (Eusimulium) vernum* ģroup (Hunter and Connolly 1986), and in the *S. (E.) aureum* group (Leonhardt 1985).

McMullen (1978) surveyed Ceratopogonidae in the Okanagan area of BC. Light trap catches of *Culicoides* in the Fraser Valley were described by Costello (1982). Anderson and Belton (1993) examined populations of *Culicoides obsoletus* Meigen in the lower mainland of BC and hypersensitivity of horses to *Culicoides* bites was reported (Anderson *et al.* 1988, 1991, 1993, 1996). A. Borkent of Enderby is a world authority on Ceratopogonidae and some of his systematic studies directly relate to BC (Borkent and Grogan 1995; Borkent 1998).

Both freshwater and saline-tolerant species of the Chironomidae inhabit saline lakes in the BC interior (Scudder 1969b). At the University of Victoria, Morley and Ring (1972a, 1972b) studied the life histories, ecology, and identification of the intertidal chironomids *Paraclunio alaskensis* Coquillett, *Saunderia clavicornis* (Saunders), *S. marinus* (Saunders), and *S. pacificus* (Saunders). The detailed study of the occurrence of midges in the littoral zone (R.A. Cannings and Scudder 1978) resulted in the discovery of a new species of *Chironomus* (R.A. Cannings 1975a) and many species new to BC and Canada (R.A Cannings 1975b). Subsequently, the physiology of this and other *Chironomus* species was investigated (Sargent 1978) and the phenology compared (R.A. Cannings and Scudder

1979). The ecology of one of these, *C. tentans* Fab., which has distinct chromosomal races in the Province (Acton and Scudder 1971), was researched by Topping (1971, 1972) and, experimentally, Topping (1969) and Topping and Acton (1976) examined the influence of environmental factors on the frequency of certain chromosomal inversions. Eastern Brook Trout were used as predators in this research. The chironomids of Marion Lake in the Fraser Valley were studied by Hamilton (1965); Schultze and Northcote (1972) documented chironomids as fish food in another coastal lake. Mundie (1971) studied their diel drift in Robertson Creek, an artificial spawning channel and secondary outflow of Great Central Lake on Vancouver Island, and found that larval drift rates increased almost two-fold in darkness.

Brillia retifinis Saether is a multivoltine species, able to track shifts in resource abundance in its habitat by virtue of its short generation time (Richardson 1991). The influence of Brillia on the decomposition of conifer leaves in a coastal stream was reported by Summerbell and R.A. Cannings (1981). Richardson and Kiffney (2000), in their study of the response of aquatic insects to metal pollutants, found that chironomids (mainly B. retifinis) showed no significant decrease in densities with increasing doses of copper, zinc, and manganese, typical urban pollutants. Parkinson and Ring (1983) examined more physiological adaptations of P. alaskensis to the marine environment. As part of a provincial government attempt to control the introduced aquatic weed, Myriophyllum spicatum L., in warm lakes and waterways, potential biological control agents were screened. The chironomids found in this study were documented by Kangasniemi and Oliver (1983). One of them, an unnamed, native species that feeds on the plant's apical buds, was subsequently described as Cricotopus myriophylli by Oliver (1984). Borkent's (1984) systematic work on the Stenochironomus complex relates to the BC fauna. Ian Walker and his students and colleagues (Walker et al. 1991, 1993; Heinrichs et al. 1999; Rück et al. 1998; Palmer 1998) have used chironomid fossils in lake sediments to reconstruct paleoenvironments in British Columbia. The larvae of Canadian chironomids can be identified to genus using Oliver and Roussel (1983).

CONCLUSION

The above clearly documents that there has been a dramatic increase in our knowledge of the aquatic insects in British Columbia over the past century. However, much remains to be done, with the Ephemeroptera in particular needing more attention. Additionally, many areas of the province remain to be surveyed, such as the far North and the numerous islands off the west coast. Many more interesting discoveries can be expected during the next 100 years.

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