15. The aquatic insects: biogeographic considerations

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Introduction

Islands hold a special appeal. Having sharply circumscribed physical limits, many of their attributes can be defined and treated as closed systems. This has certain advantages for compared to continental situations, islands provide a simplified milieu in which to investigate the relationships between the biota and island habitats as well as the colonization process itself both in its historical and dynamic aspects. In fact, the study of the effects of insularity on colonization and subsequent development of island faunas has been a fruitful line of investigation in evolutionary biology.

Islands vary greatly in their size and isolation both in physical terms as well as relative ease of access and colonization between groups of organisms. For example, what we as free ranging terrestrial creatures regard as the single island of Newfoundland is in fact an archipelago to many organisms, especially freshwater forms. For them, insularity is twofold, produced first by the oceanic barriers and secondly by barriers within the island's landmass itself, namely terrestrial sites, flowing water for lentic species and lentic sites for lotic species. In this way island populations of certain species face similar problems to those experienced by continental populations with, in the case of Newfoundland, the oceanic barriers not even being of a larger scale than intracontinental disjunctions in habitat.

Freshwater habitats, especially in areas subjected to glaciation, are unstable, changing with major climatic and geological events. However, even under constant conditions, erosion and deposition change stream profiles and standing water passes through successional stages leading to its disappearance. The net result is that in high latitudes aquatic insect species must disperse to persist and thus must be good island colonizers. This places a premium on possession of either high vagility or a range of environmental

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tolerance, or both. For this reason we might expect aquatic insects to show less diversity, wider ranges and greater ability to cross barriers than forms living in more stable or less insular environments.

Working from these premises, this study is developed not from the point of historical biogeography but rather from a more ecological perspective. It has been assumed that the fauna of adjacent source areas is likely to be able to disperse to the Island of Newfoundland and that factors determining deviation in the island's fauna should be looked for in the present physical and biological environment of the island itself. Our concern has been to describe the overall environment and relate this to characteristics of the organisms. It is only when inadequacies in this approach are discovered that historical explanations can be sought.

The physical environment

Hydrology

The interplay of climate and geology produces the hydrological setting in which aquatic insects occur. Newfoundland's climate is cool and humid resulting in an excess of precipitation over evapotranspiration across the entire island. The quantity and distribution of the excess precipitation, in the form of runoff, is indicated in Fig. 1. There is no strongly marked seasonality in the annual distribution of precipitation, however the summer months tend to be the driest (Fig. 2). This reduced precipitation acts in concert with raised summer evapotranspiration levels to produce what is typically the annual low in water levels. Excess of precipitation prohibits development of endorheic basins, thus all drainage basins are open and subject to flushing.

Compared with continental drainage basins, most of the island's systems are small for no part of the island lies more than 130 km from a coast. However, a few extensive basins dominate parts of the western and central island where the gentle northeast declination of the surface produces several large systems which arise close to the southern shore and drain towards the north and east. Table 1 presents some drainage basin parameters for Newfoundland's seven largest rivers.

Table 2 shows the relationship between basin size and frequency of occurrence of streams on the island. Basin relief varies greatly but in general the greatest relief, hence steepest stream gradients, occurs along the mountainous portions of the west coast and the south coast while much of the remainder of the island is a low plateau of rolling relief. Obviously gradient

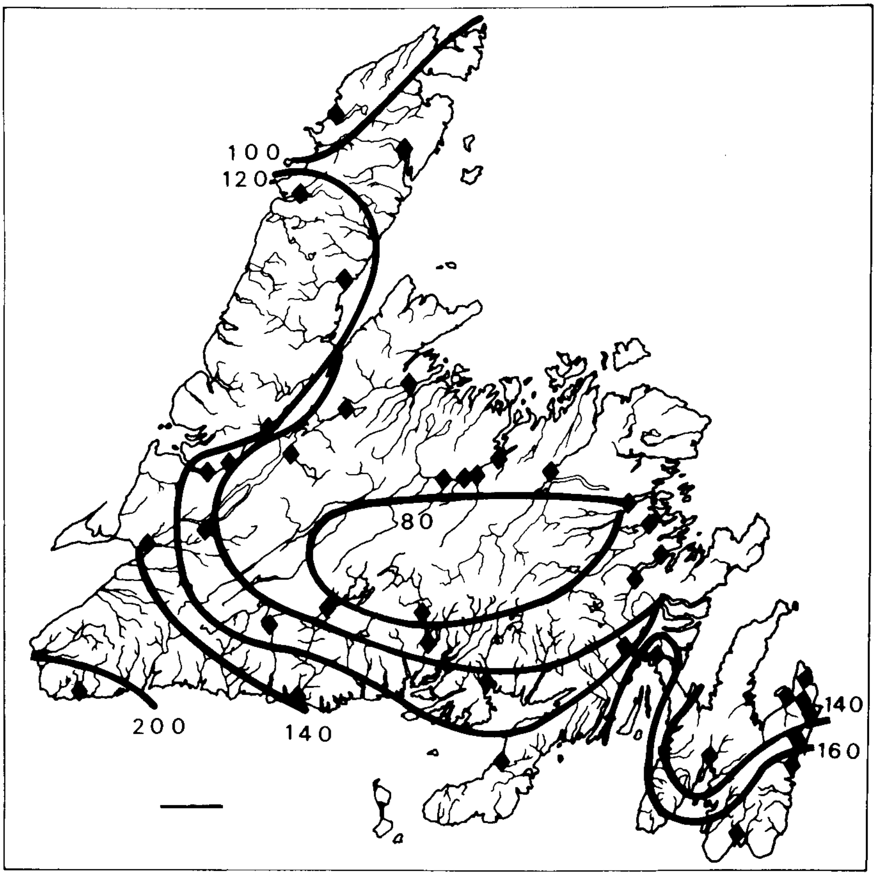


Fig. 1 Water runoff, in cm, from the island of Newfoundland. Diamonds indicate location of gauging stations. (Data courtesy Water Survey of Canada, St. John's and from Yoxall 1980).

varies greatly over short distances along a stream course as well as generally decreasing in mean value as stream length increases (Table 2) so that streams, with increasing length, tend to acquire the concave profile of a classical graded stream (Fig. 3). However, surficial features of the island are of a glacial-fluvial morphology, dominated by recent glacial features superimposed on a resistant lithology. Stream development does not follow the classical fluvial morphological patterns and probabilistic patterns of stream basin organization are highly modified by nonfluvial features. For example, the island's land mass exists as a plateau elevated sharply along much of its coastline. Many streams, which may be of low gradient over much of their length, plunge precipitiously off this plateau a short distance from their

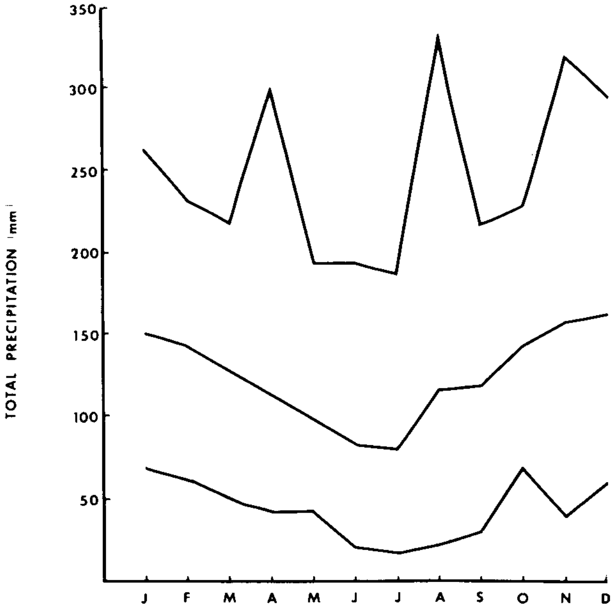


Fig. 2 Monthly precipitation recorded at St. John's airport. Lines indicate, from top to bottom, monthly maximum, mean and minimum.

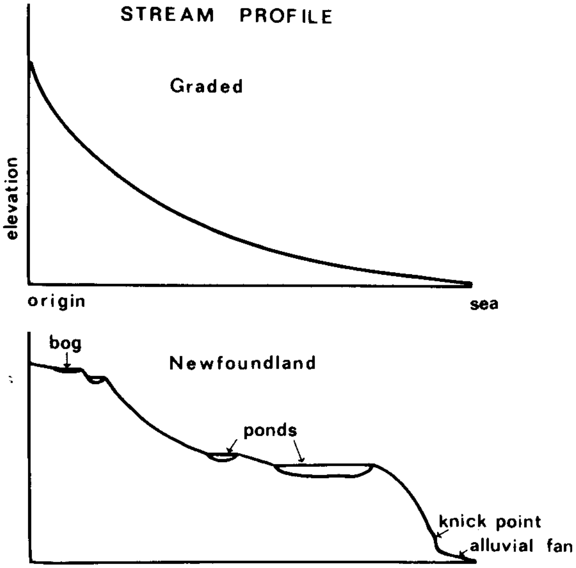


Fig. 3 Generalized profile of a classical graded stream and a hypothetical Newfoundland stream.

Table 1 Selected drainage basin parameters for the seven largest rivers on the Island of Newfoundland (data from Porter *et al.* 1974)

River	Basin area (km²)	Perimeter (km)	Max. basin relief (m)	Axial length (km)	x̄ gradient
Exploits	11 272	978	655.3	237	0.0027
Humber	7 679	734	659.3	122	0.0054
Gander	6 398	564	426.7	156.7	0.0027
Salmon*	2 708	362	381	83.2	0.0045
Grey*	2 394	343	469.4	102.2	0.0045
White Bear*	2 027	340	634.9	86.9	0.0073
Terra Nova	1 883	319	376.1	105.4	0.0035

* The drainage basins of these rivers have been extensively modified and interconnected through diversion for the Bay d'Espoir hydroelectric development. Headwater portions of the Exploits river have also been captured in this project (Murray & Harmon 1969).

Table 2 Size distribution of drainage basins on the Island of Newfoundland (data from Murray & Harmon 1969)

Drainage basin area	No. of basins	x̄ relief/axial length
< 25 km²	4109	0.038*
25–249	237	0.021
250–1299	51	0.011
1300–2599	3	0.005
> 2600	4	0.004

* Based on measurements on 52 larger streams of this group.

mouths. Isostatic fluctuations in land elevation and Pleistocene sea level variations have had mixed effects on stream outwash zones. Thus streams exist which have deeply incised channels cut through alluvial deltas while on the other hand certain streams drain into what appears to be flooded valleys. Along stream courses, features producing ponds and bogs exert flow and erosional control complexing the stream profile. Bogs may be important sites of water storage. The slow passage of water through denser peat layers means that bogs may be important transducer elements in drainge basins acting as major regulators of base flow. The effects of these features on the stream profile are indicated in a generalized way in Fig. 3.

In addition to local topography, stream characteristics are also modified by regional substrate types and climates. However, there are hydrographic features common to most if not all island streams. The annual hydrograph tends to be bimodal. Highest flows are typically related to the period of snow melt and occur during late April and May. Summer is a period of falling water levels with minimal annual flows usually occurring from late July to early September. Seasonal variation in precipiation greatly modifies this pattern and in some years high water levels occur throughout the summer. Cyclonic storms in the fall produce the highest seasonal precipitation resulting in increased stream flow in autumn and early winter. Discharge rates drop in mid- to late winter as soils freeze and precipitation accumulates as snow and ice although mid-winter melts and periods of rain frequently produce winter flooding. The averaged hydrograph for the Exploits River shows this annual pattern (Fig. 4).

Climatic variation as well as basin characteristics modify the generalized hydrograph both from one year to the next and from basin to basin. Hydrographs for the same year are presented in Fig. 5 for two streams with differing basin characteristics. Isle aux Morts River occupies a small basin (214.2 km^2) with high relief, thus giving the relatively steep gradient of 0.0178 over its axial basin length. Lakes in the basin are small and few and bog development

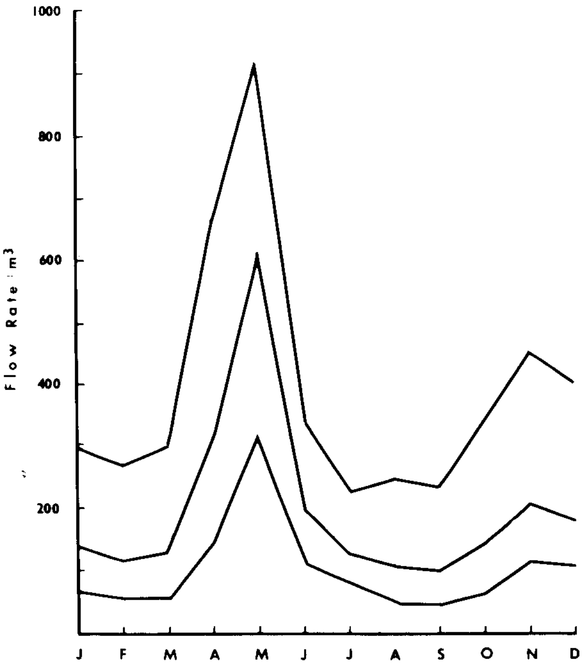


Fig. 4 Hydrograph of mean monthly runoff and 95% confidence limits for Exploits River, Newfoundland, 1913–1959 (redrawn from Murray and Harmon 1969).

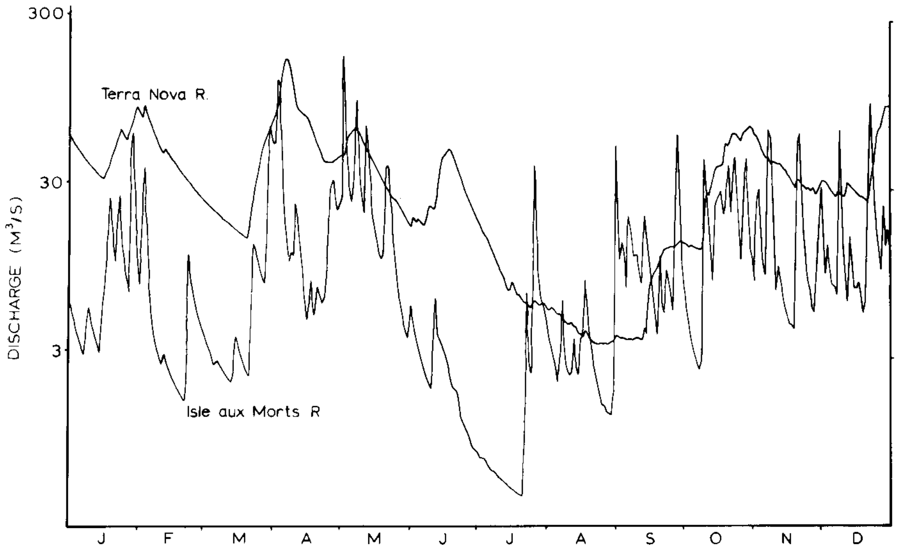


Fig. 5 Hydrographs for Isle aux Morts and Terra Nova Rivers, Newfoundland, 1976. (Data courtesy Water Survey of Canada, St. John's).

limited. Precipitation quickly enters the stream and, with little opportunity for within basin storage, is rapidly transported out. Consequently the hydrograph shows a highly erratic pattern of spates followed by rapid return to base flow. This pattern is characteristic of many streams on the south and west coasts. On the other hand, the Terra Nova River shows a much smoother hydrograph with short-term fluctuations highly dampened. In this basin lower relief enhances pond and bog development and provides sites for within basin storage retarding the passage of water. Internal flow controls in a basin also control the extent and distribution of erosional forces. An uncontrolled river, such as the Isle aux Morts River, tends to have unstable, scoured substrate of coarse size while Terra Nova River substrates are much more stable and varied as erosional and depositional zones are intermixed for each area of standing or pooled water forms a lower base level controlling erosion in that stream segment.

In many portions of the island, low relief and the irregularly glaciated topography produce a landscape dominated by an abundance of bodies of standing water. The terminology applied to these water bodies is somewhat confused. Most are locally termed ponds while only those bodies of water of surface areas greater than 100 km^2 are generally called lakes. Pools (any small, shallow lentic habitat lacking defined inflows and outflows), bogs and fens are abundant. These lentic habitats, together with streams, cover approximately one third of the island's area (Murray & Harmon 1969).

The variety of lentic habitats precludes much generalization. Kerekes (1974, 1978) investigated limnological features of ponds in Gros Morne and Terra Nova National Parks and Davis (1972, 1976) investigated lakes on the Avalon Peninsula. Characteristics and productivity of these habitats are influenced by edaphic features of the drainage basin, flushing rates and position of the water body in the system. Kerekes (1974) found that planktonic primary production is low, limited by low levels of nutrients, low light conditions brought about by reduced solar radiation as well as high water color of many ponds, and often suboptimal water renewal rates (Kerekes 1973). The volume of a pond relative to the size of its catchment basin determines the flushing rate with the smaller the ratio the faster the renewal rate in the pond. Kerekes (1974) developed a morphometric index relating primary production to flushing rate. Low rates of water renewal limit production through consumptive depletion of nutrients by plants. At the other extreme, high rates of water renewal dilute nutrient levels and, in addition, displace phytoplankton and seston regardless of nutrient supply.

Substrates vary considerably in lentic sites. Ponds may occupy depressions in bedrock or be in tills which vary in coarseness from fine clays and sands to huge boulders which protrude above the surface over much of the pond. Larger ponds and lakes with water surfaces broadly exposed to wind have wave-washed shorelines of mineral materials while smaller ponds or protected bays often have shorelines overgrown by vegetation. This vegetation zone may be rooted or form a mat either suspended by shoreline boulders or largely floating. In fact, all stages of pond-bog-peatland succession can be observed in most regions. The low fertility of most waters plus low temperatures contribute to slow decomposition and rapid accumulation of organic material in aquatic systems. Depositional areas typically possess deposits of peat or a fine semifluid ooze derived from peat and other fine debris. Dense layers of peat may be very resistant to water flow and small ponds and pools are often found perched above the water table on peat beds. Although the ponds may be shallow, macrophytes are generally limited, either by nutrients, low light penetration in colored waters or by substrates which are either too coarse or too fine and soft.

Water temperatures

The cold Labrador Current bathing the island maintains a cool climate with a strong seasonal lag in temperature. Frequently cloud cover or fog reduces insolation and opportunities for daily warming, especially along windward coastal areas such as the South Coast and Avalon Peninsula. Temperatures in most aquatic habitats are low and probably exceed 25°C in only the shallowest pools and streams and for only short periods of time. Maximum summer surface temperatures of lakes and ponds tend to range between 13° and 23°C depending upon location and size of the water body (Kerekes 1974, 1978) while the range of summer stream temperatures in Gros Morne Park is 9–22°C (Kerekes 1978). A seasonal thermograph is presented for a small Avalon Peninsula stream in Fig. 6. This is a small exposed stream draining a shallow pond and thus probably reflects some of the warmest temperatures to be found in regional streams.

Even in sun-warmed ponds and streams, the influence of groundwater or bog drainage produces localized cool zones. Groundwater, hyporheic water and water standing in bogs and fens below the living vegetation mat remain

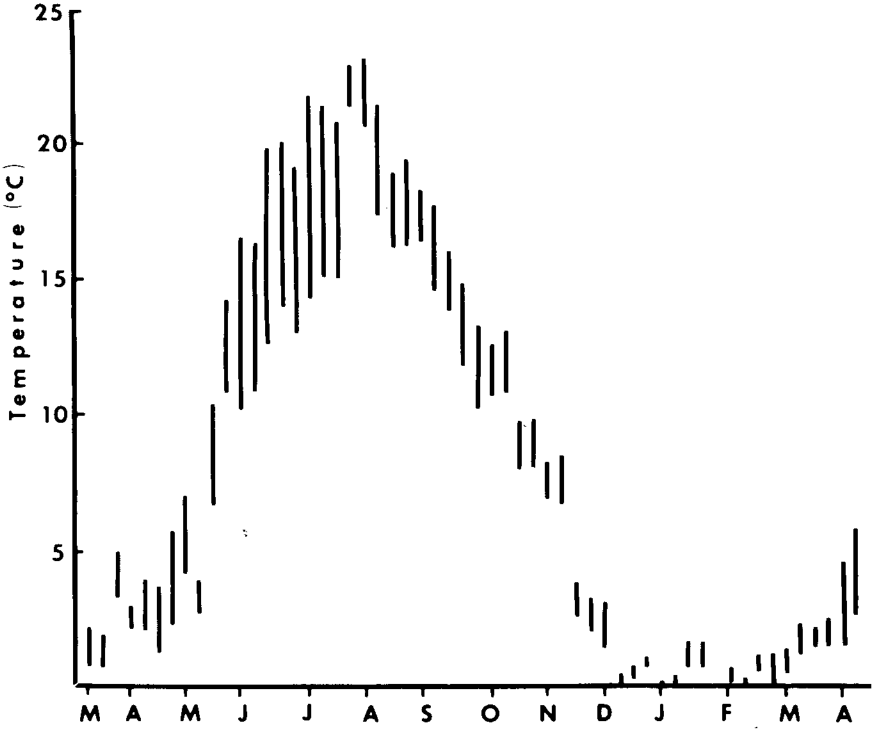


Fig. 6 Weekly mean maximum – minimum temperature range in Broad Cove River, Avalon Peninsula, 1979–1980.

cold throughout the season. These sources may provide water to the surface, often at considerable volume, that remains at a uniformly cool temperature throughout the year. In winter, these sources may have a converse effect on temperatures and may slightly warm small aquatic habitats preventing complete freezing.

Deeper ponds and lakes become thermally stratified in summer but many ponds are polymictic, being shallow and exposed to wind.

Water chemistry

The water chemistry of Newfoundland streams has been reviewed by Jamieson (1974a, b), while Kerekes (1974, 1978) provides a summary of chemical conditions affecting productivity of lakes in Gros Morne and Terra Nova Parks. In general, waters are acidic with low levels of dissolved materials. Figure 7 indicates the geographical pattern in pH, alkalinity, conductivity and chlorides in the lower reaches of Newfoundland streams. These parameters are influenced by regional geology for the values of each are highest in areas of sedimentary deposits, especially limestones and dolomites. The figures show only the most general trends for local exceptions to regional conditions abound. For example, *Sphagnum* bog may be found occupying depressions of limestone felsenmeer so that localized habitats of low pH and low conductance can be found overlying or within the geological formation producing the island's most basic and mineral-rich waters.

Kerekes (1977) found evidence to indicate that low phosphorus levels limit primary production in Newfoundland lakes. Basins lying on ingneous or metamorphic rock receive their major source of phosphorus through precipitation, which supplies only very low quantities. Phosphorus concentrations in Gros Morne Park, for example, range from less than 4.1 mg P/m^3 to 32 mg P/m^3 in lakes and 0.9 to 30.4 mg P/m^3 in streams. The higher levels were found in waters of sedimentary basins and for the highest values, human enrichment could not be ruled out. On the basis of phosphorous concentrations, Newfoundland's waters are oligotrophic ($[P] < 10$ mg/m^3) or mesotrophic ([P] 10–20 mg/m^3), with only culturally enriched sites or a very few natural sites classified as eutrophic (Vollenweider 1968).

Water also varies in transparency and color. Transparent color, when present, is produced by humic acids as well as complexed soluble iron, and results from bog conditions within the drainage basin. Streams and lakes with small, well-drained basins or basins with little bog development are clear, while with increasing input of bog waters the water becomes transparent

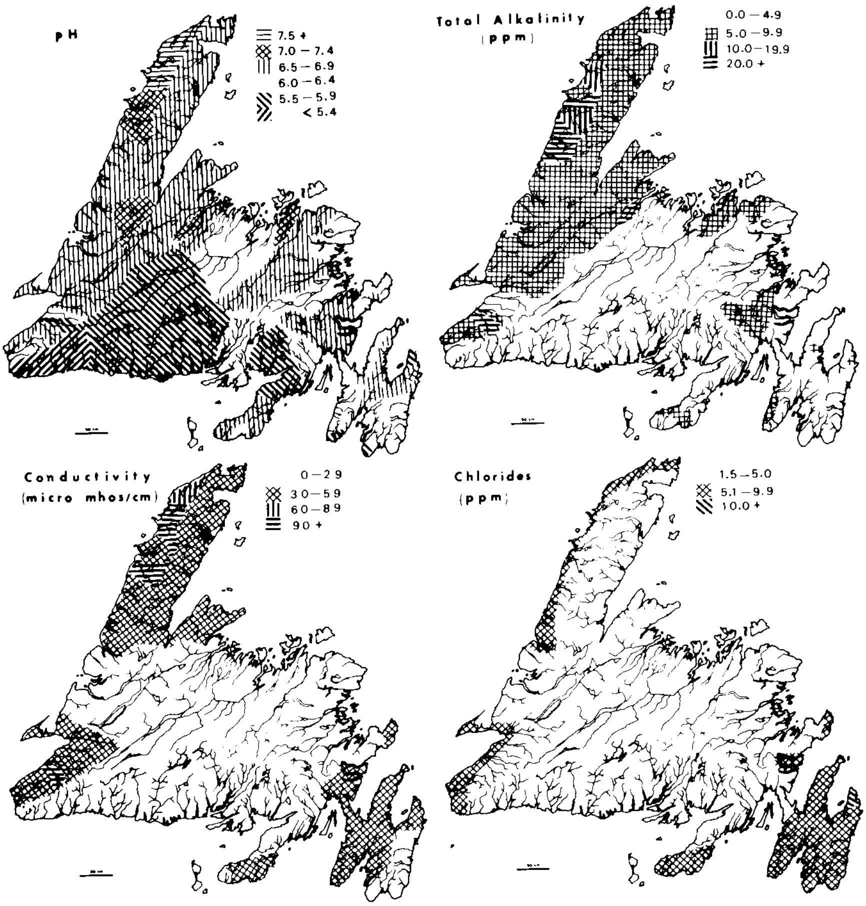


Fig. 7 Geographical variation in pH, alkalinity, conductivity and chlorides in the lower sections of Newfoundland streams. (Data from Jamieson 1974a, b, Porter *et al.* 1974 and independent measurement).

brown. Kerekes (1978) recorded colored water of up to 250 Hazen Units. Colored water reduces light penetration limiting the depth of the photosynthetic zone. A high correlation exists between water color and dissolved organic carbon in the water (Forsberg 1967). This material is available to algae and bacteria and can be important in primary production within a water system (Allen 1971).

The combination of low pH, low levels of dissolved nutrients and frequent occurrence of highly colored water contribute to the generally low productivity of Newfoundland's lentic waters. This is supported by the low fish production of most ponds and lakes (Wiseman 1973; Wiseman & Whelan 1974; Bruce 1976) for the fish can be taken as integrators of the total range of environmental conditions.

Although Newfoundland has an abundance of freshwater and a relatively low human population, the island's waters have not escaped the impact of human activity. To date, man's activities have had mainly local effects. For example, road salting may cause significant increases in conductance of a drainage basin (Kerekes 1974). The high pH and conductance of streams of the northeastern Avalon Peninsula are certainly the result of cultural activities. Settlements are usually situated at stream mouths where domestic sewage,fish plant and industrial effluent affect the lower reaches. Many barachois have been built up with resulting pollution. Water from many streams and ponds has been diverted for domestic and industrial use. Hydroelectric projects, both large such as Bay d'Espoir, Hinds Lake and Upper Salmon as well as many much smaller plants, have changed water levels and flow regimes in a number of drainage basins.

Forestry has had diverse impacts in addition to the hydrological effects of clearcutting drainage basins. Although not as commonly practised as previously, log driving occurs in some streams and lakes giving rise to accumulations and decomposition of bark, slash and logs in many systems. Diversion rivers and water control structures to aid in log driving were built on many streams although most are not now used. The resort to aerial spraying of insecticides to control forest pests means that water in much of the most productive portions of the province is now regulalrly subjected to some insecticide dosage.

During the present period of concern over acid rain, this problem must be seen as a very real threat to Newfoundland's freshwaters. The already low pH and the limited buffering capacity of the water makes the aquatic systems especially suspectable to degradation by even light amounts of pollution.

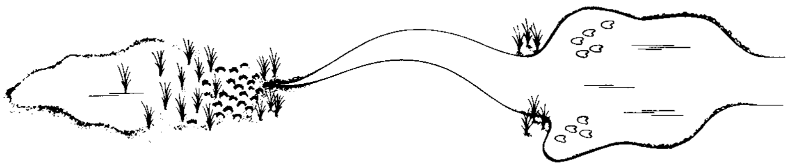
Aquatic habitats

Williams (1979) reviewed aquatic habitats of Canadian insects. He presented some of the detailed and often complex terminology that has been applied to aquatic habitats and characterized many of the important habitat types in terms of physical conditions and composition and attributes of their faunas. William's overview applies well to Newfoundland within the context of the regional hydrometeorological and geological setting described above. However, the features defining habitats form a continuum so that delimitation of most habitats, except a few highly specialized forms such as pitcher plant leaves, is rather arbitrary. For this reason, the continuum approach of Vannote *et al.* (1980) has much to recommend it.

Figure 8 represents an attempt to indicate the major habitat types occupied by Newfoundland aquatic insects, to indicate some of the principal characteristics of each habitat and to show the pattern and direction of variation in habitat characteristics. This is presented as a model, recognizably oversimplified in certain ways, which is hoped will have heuristic value for plotting and describing the range of conditions affecting the distribution of various insect groups.

Left to right in Fig. 8 represents movement from upper to lower regions of a drainage system and from small to larger bodies of water. A series of descriptors are included to indicate qualitatively the nature of conditions at each segment of the system.

In general, headwater portions of Newfoundland drainage systems have a relative paucity of temporary pools. Precipitation is adequate to keep larger impermeable basins filled while those basins that are sufficiently permeable to permit total water loss or are so small that evaporation over a short time can deplete the contained water, are too unstable to support populations of most insects. Fluctuating margins of permanent habitats produce conditions approaching those of temporary pools but usually with significant differ-



Description	New + temporary ponds	Marsh	Bog & fen seep springs	Stream order 1 2 3 4+	Ponds & Lakes emergents mineral shoreline	Outflow
Flow	lentic----------/lotic			----------/lentic	----------/lotic wave action	
Temperature	warm varied ↔		cool stable ↔	warm varied ↔	polymictic to stratified	warm
Water level	unstable		stable	fluctuating	stabilized	buffered
Substrate	inorganic clay-rock shallow	organic	deep organic iron ppte.	varied mineral erosional zone mineral, depositional organic rich	varied, flocculant organic through to coarse mineral	mineral
pH	various ↔		acidic →	higher pH →		
Distribution	usually artificial, man-made and beaver ponds	successional stages	size,	gradient & substrate determined by local topography	least common in areas of high relief abundant elsewhere	

Fig. 8 Generalized diagram of Newfoundland aquatic habitats indicating variation in selected characteristics.

ences in nutrient regime and faunal composition. Within bogs, rising and lowering water levels may produce temporary pond conditions with a distinct seasonality and a temporal duration adequate to permit the development of distinctive faunas. However such habitats suffer from very low nutrient levels in the water, low pH, loose peaty substrates and only limited allochthonus input resulting in low production. Such temporary bog pools may possess characteristic associations of species but generally the density and diversity of the insect fauna is low.

Pools within bogs and fens, whether they be temporary or permanent, are obvious aquatic habitats. However, much of the area of many bogs lacks visible water but water can be found on depression of the living vegetation mat. The shading provided by the vegetation keeps this water cold throughout the summer. In addition, low pH (3.5 to 4.5) and very low dissolved nutrient levels contribute to make this a habitat of low productivity (Williams 1979). Although impoverished in terms of insect density, a diverse fauna can be found in this habitat, consisting of hygrophilic terrestrial, more or less amphibious and truely aquatic species.

Shallow pools with an abundance of emergent monocotyledonous plants tend to be the richest lentic habitats. These are generally minerotrophic sites in which the vegetation is a reflection of nutritional enrichment. The terrestrial portions of these plants die back annually providing a rich food source for detritivores and saprivores, and the associated insect fauna is generally abundant and diverse. With an increase in abundance of *Sphagnum* and ericaceous shrubs, productivity falls off.

Streams form a continuum just as do lentic habitat types, thus definition of habitat units within a drainage system is always somewhat arbitrary. The classification of streams on the basis of an ordering system is useful in many regions but less applicable in the Newfoundland setting where difficulties are encountered in defining basin limits and stream channels in boggy regions. Nevertheless, it does provide a useful representational system for denoting relative sizes of streams in a system. Headwater (1st order) streams are varied depending upon water source. The fauna of streams originating from bogs may be indistinguishable from the fauna of the bog pools but with increase in flow rates and increase in the amount of mineral substrate, more characteristic stream biotas develop. Iron rich springs form an interesting and common class of headwater stream. Water coming to the surface is rich in dissolved iron which either oxidizes or precipitates out in response to changing conditions of water chemistry so that deposits of reddish iron precipitate occur near the stream source. The fauna of such sites is generally limited but does contain a few unusual elements.

Downstream changes occur in many habitat parameters which in turn determine the relative importance of sources of energy input, types of nutrients, trophic strategies of the members of the fauna, and faunal diversity. Patterns of variation in these features have been discussed by Vannote *et al.* (1980). Although the general trends outlined by Vannote *et al.* (1980) are probably applicable to Newfoundland streams, certain factors such as low temperatures throughout aquatic systems, low nutrient levels, substrates frequently unsuitable for vascular hydrophytes, bog water which contributes fine particulate organic material and abundant dissolved organic material but little coarse particulate organic material, and irregularity in stream profiles are all factors that contribute to deviation from the stream continuum model.

In Newfoundland, most drainage system have various forms of flow control punctuating the stream profile. Such controls may produce a series of lentic or near lentic depositional habitats which vary from steadies (a section of stream with very light laminar flow, generally slightly wider and deeper than the regular channel) and gullies (a narrow, elongate pond consisting of a widening and deepening of the channel, usually without discernible flow) with high flushing rates to ponds and lakes in which the water turnover rate may be measured in weeks, months or years. Such lentic habitats can act as depositional areas for entrained materials as well as form nutrient sinks. On the other hand, if water turnover rates are low enough, a plankton population can develop which can be transported into the outflow and become available to the stream trophic system.

Characteristically stream outlets from ponds and lakes are densely populated by filter feeding Trichoptera and Diptera, certain species of which are restricted to this site. These areas generally possess the highest biomass of insects of any portion of the drainage system. Although planktonic production in lake may be low, the passive feeding mechanism of filter feeders effectively concentrates this production in a localized region in the initial few meters of the outlet stream.

The insect fauna

Knowledge of the Newfoundland insect fauna is very uneven. Lindroth's (1955, 1963) classical studies of the island's ground beetles are among the best faunal studies available on any group of Canadian insects. At the other extreme, many major taxonomic groups of Newfoundland insects have not received even cursory attention. Morris (1980, 1982) provides a historical overview of the exploration of Newfoundland's insect fauna. This general patchiness in knowledge is also displayed in the understanding of the aquatic fauna.

The state of knowledge of each of Newfoundland's aquatic insect orders is described in the following sections. Aquatic species recorded from the island or now known to occur on the island are listed and thus a number of new records are included. Also, an overview of select aspects of the ecology, distribution and other peculiarities of each order is presented. The objective is to focus on those features most likely responsible for shaping the composition and ecological and geographical distribution of the island's aquatic insect fauna.

The checklists of species include the following information: species name, reference for Newfoundland records, Newfoundland distribution and range. Newfoundland distributions are indicated with alphabetical symbols representing island subdivisions or faunal regions as indicated in Fig. 9. Geographical ranges are highly simplified and consist of the following patterns: transcontinental (H = Holarctic); east of the Rocky Mountains; east of the Great Plains; northern Appalachian; and eastern coastal.

Order Odonata – damselflies and dragonflies

The order Odonata is the best known order of aquatic insects in the fauna. Williamson (1906), Whitehouse (1948) and Valle (1955) provided lists of Newfoundland dragonflies while Walker (1953, 1958) and Walker & Corbet (1975) treated the Newfoundland fauna in a monograph of the Odonata of Canada and Alaska. A checklist of the island's dragonflies is presented in Table 3. The list includes 35 species, two of which are new records. Of these species, *Pantala flavescens* is, without doubt, only in the fauna as a vagrant while the remaining 34 species are resident.

Dragonflies form a conspicuous component of the island's insect fauna. During the warm summer season, from mid-June to mid-September, adults abound near all water bodies and the larger, strong flying species are found even in sites remote from water. However, the distribution of the aquatic nymphs is much more restricted (Fig. 10). Nymphs develop in shallow, almost always permanent habitats such as pools, margins of ponds and lakes, ditches, small streams and the edges of rivers. Nymphs of most species are found in lentic sites, usually associated with rooted vegetation or accumulations of plant debris. Many *Aeshna* nymphs are found in both lentic and marginal lotic sites while the nymphs of *Calopteryx aequabilis* and *Somatochlora walshii* are typically in depositional lotic habitats. Only the nymphs of *Ophiogomphus colubrinus* is found in riffle areas of swift streams.

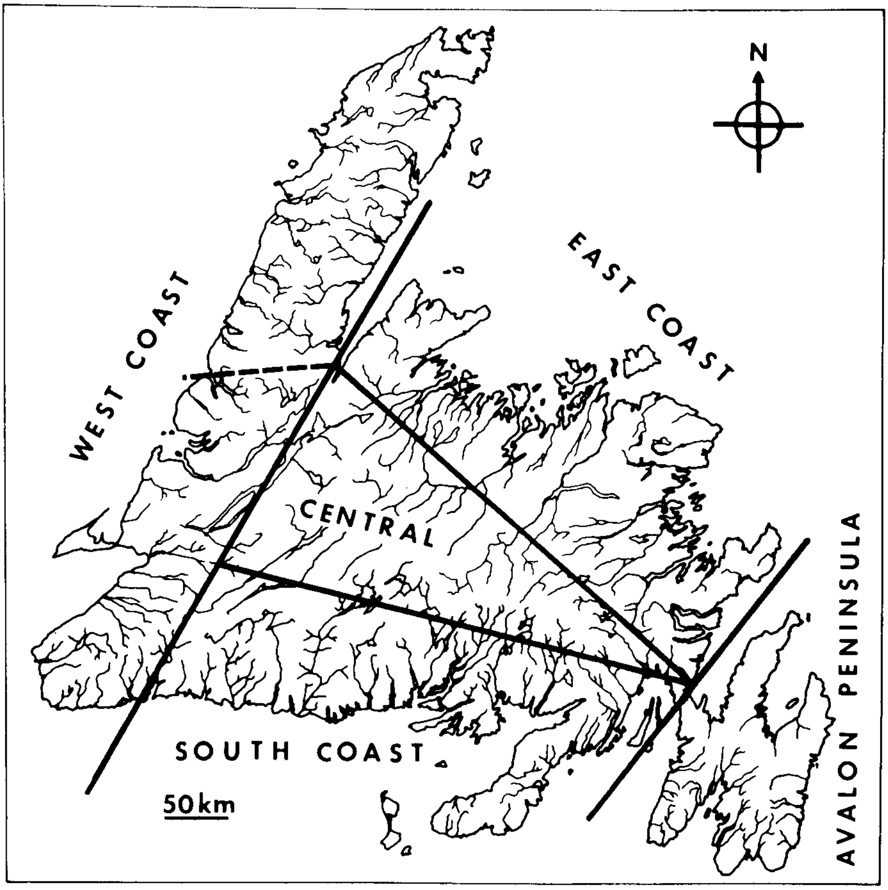


Fig. 9 Faunal regions of Newfoundland. These are arbitrary regions used in a descriptive sense in both text and checklists to indicate island ranges. West Coast region is subdivided into southern and northern subregions.

There is no published study on the biology of any Newfoundland dragonfly population. Corbet (1980) cites references showing that the period of nymphal development of many species is extended by low temperatures or diminished food supply. It is expected that many of the island's species will prove to have protracted life cycles extending through two or more years. This is indicated by the observation that the nymphs of *Aeshna* species, *Ophiogomphus colubrinus, Calopteryx aequabilis* as well as unidentified corduliid and libellulid nymphs can be collected in a range of size classes throughout the year. In contrast, the Lestidae and Coenagriidae generally

Table 3 Checklist of the Odonata of insular Newfoundland

Species	Recorded by	Newfoundland distribution	Range
CALOPTERYGIDAE			
Calopteryx aequabilis Say	Morris 1969; Bowers 1980	general	E. of Rocky Mtns. boreal*
LESTIDAE			
Lestes d. disjunctus Selys	Walker 1953; Valle 1955	general	transcontinental, boreal
COENAGRIIDAE			
Nehalennia irene Hagen	Valle 1955	W, C, E	transcontinental, boreal
Coenagrion resolutum Hagen	Walker 1953; Valle 1955	general	transcontinental, boreal
C. interrogatum Hagen	Walker 1953	W, C, E	E. of Rocky Mtns. boreal
Enallagma boreale Selys	Walker 1953; Valle 1955	general	transcontinental, boreal
E. civile Hagen	new record	E, S, A	transcontinental, southern
E. cyathigerum Charpentier	Walker 1953; Valle 1955	general	transcontinental, boreal
E. ebrium Hagen	Walker 1953	general	transcontinental, boreal
Ischnura posita Hagen	new record	C	E. of Gt. Plains, southern
I. verticalis Say	Walker 1953; Valle 1955	general	E. of Gt. Plains, boreal
AESHNIDAE			
Aeshna canadensis Walker	Walker 1958	general	transcontinental, boreal
A. eremita Scudder	Valle 1955; Walker 1958	general	transcontinental, boreal
A. interrupta Walker	Valle 1955; Walker 1958	general	transcontinental, boreal
A. juncea L.	Walker 1958	general	holarctic, boreal
A. septentrionalis Burm.	Walker 1958	W	transcontinental, boreal
A. sitchensis Hagen	Walker 1958	general	transcontinental, boreal
A. subarctica Walker	Walker 1958	W	transcontinental, boreal
A. umbrosa Walker	Valle 1955; Walker 1958	general	transcontinental, boreal
GOMPHIDAE			
Ophiogomphus colubrinus Selys	Walker 1958	general	transcontinental, boreal
CORDULIIDAE			
Cordulia shurtleffi Scudder	Walker & Corbet 1975	general	transcontinental, boreal
Somatochlora albicincta Burm.	Walker & Corbet 1975	W	transcontinental, boreal
S. cingulata Selys	Valle 1955; Walker & Corbet 1975	general	transcontinental, boreal
S. forcipata Scudder	Walker & Corbet 1975	W, C	E. of Rocky Mtns. boreal
S. franklini Selys	Whitehouse 1948	W	transcontinental, boreal
S. septentrionalis Hagen	Valle 1955; Walker & Corbet 1975	W, C	transcontinental, boreal
S. walshii Scudder	Walker & Corbet 1975	general	transcontinental, boreal

Table 3 (continued)

Species	Recorded by	Newfoundland distribution	Range
LIBELLULIDAE			
Leucorrhinia glacialis Hagen	Walker & Corbet 1975	general	transcontinental, boreal
L. hudsonica Selys	Valle 1955; Walker & Corbet 1975	general	transcontinental, boreal
L. proxima Calvert	new record	general	transcontinental boreal
Libellula quadrimaculata L.	Valle 1955; Walker & Corbet 1975	general	holarctic, general
Pantala flavescens Fab.	Valle 1975	vagrant	cosmopolitan, southern
Sympetrum costiferum Hagen	Walker & Corbet 1975	general	transcontinental, boreal
S. danae Sulzer	Valle 1955; Walker & Corbet 1975	general	transcontinental, boreal
S. internum Montgomery	Walker & Corbet 1975	W, C, E	transcontinental, boreal

* The term boreal is used if the species occurs widely within the boreal zone. Many of these species have distributions that extend to varying degrees beyond this region.

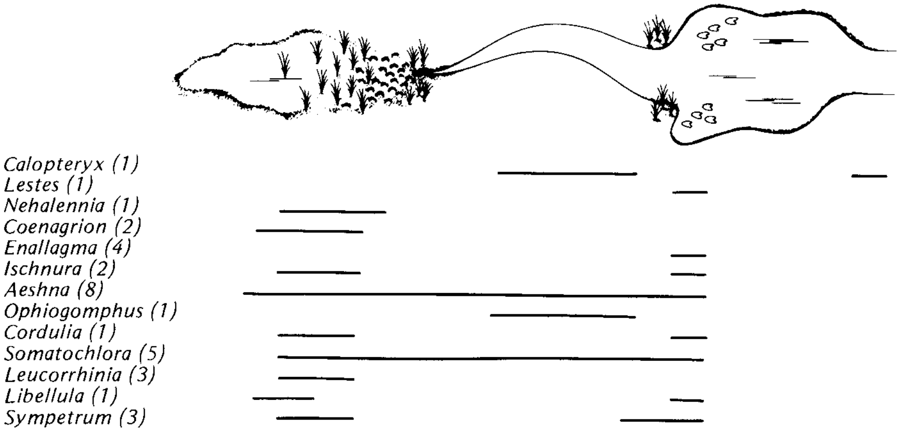


Fig. 10 Ecological distribution of nymphs of Newfoundland Odonata.

show synchronous nymphal development and adult emergence indicating a univoltine cycle.

Even in bog pools of low productivity, dragonfly nymphs may be abundant and constitute a major portion of the arthropod standing crop, although this has not been measured locally. Because of their high assimilation efficiency (Lawton 1970), low metabolic activity as well as the protracted life cycle of many species, dragonfly nymphs elsewhere have been found to constitute a dominant portion of the animal biomass of suitable habitats (Benke 1976).

All dragonflies are predators both as larvae and adults. Larval predation stategies vary from those which stalk or more in search of prey to those which sprawl on the bottom lying in wait. Larvae of both forms occur in lentic and marginal lotic habitats but the only larvae in strongly flowing waters are sprawlers. Larvae prey on a variety of organisms with selection based chiefly on size and availability (Corbet 1962, 1980). Dragonfly larvae tend to be in deeper, more permanent and less densely vegetated sites than are dysticid beetles, the other major group of general predators in shallow lentic sites. This separation may be due in part to competition and differing predation strategies but is likely reinforced by predation of the larger dragonfly larvae on the generally smaller and more active dytiscid larvae. Adults feed on other insects, usually captured in flight, with the range of prey taken apparently related to prey availability as well as the size and flight abilities of the dragonfly species (Pritchard 1964).

The flight activity of adult dragonflies is governed by light and temperature. High levels of adult activity are observed only under conditions of sunlight, warm temperatures and light winds. Because of the cool summers, frequent cloudy or foggy periods and windy conditions, Newfoundland may be unsuitable or marginal for the adult stages of many dragonflies, as was suggested by Valle (1955). Semivoltine or especially longer indeterminate life cycles may provide island populations with the flexibility to survive cold or inclement summers.

Range patterns of Newfoundland dragonflies are summarized in Table 4. Eighty-five percent of the species are transcontinental in the boreal zone while the remaining 15 percent have wide ranges in the eastern portion of the continent. Compared to the Maritime Provinces, which have about 86 species

Table 4 Summary of the range patterns of Newfoundland species of Odonata. Non-breeding species omitted

Distribution pattern	No. of species	% of species
Holarctic, transcontinental	5	15
Nearctic, transcontinental	24	70
East of Rocky Mountains	3	9
East of Great Plains	2	6
Appalachian and East coast	0	0
Total	34	100

(Walker 1953; Walker and Corbet 1975), Newfoundland's fauna is impoverished. Species present in the Maritimes but lacking in Newfoundland are generally those that occur south of, or just enter the southern boreal region. On the other hand, the faunas of Newfoundland and Labrador are similar and differ in only a few species (*Somatochlora franklini* Selys and *S. minor* Calvert occur in Labrador but not on the island. Several species have been recorded from Newfoundland and northern Quebec but not Labrador. On the basis of such distribution patterns these absences from Labrador are probably collection artifacts). Most of the species occurring in nearby boreal regions are present on the island; thus the island's fauna is derived from the impoverished, widely distributed, cool adapted boreal fauna.

As adult dragonflies are strong fliers and relatively long lived, the sea barriers separating Newfoundland from the mainland would be expected to be less effective in limiting dragonfly dispersal than the dispersal of most other aquatic insects. The occasional occurrence of the non-breeding, southern *Pantalla flavescens* demonstrates the ability of at least some species to disperse long distances. It could be postulated that the faunal reduction between the Maritime Provinces and Newfoundland is more likely due to habitat unsuitability on the island than inability of species to cross the Cabot Strait. However, there may be other factors influencing dragonfly dispersal. Being strong fliers and orienting by visual cues, dragonflies may not normally move beyond visual contact with the shore to which they are usually capable of returning. Long-range dispersal by wind drift, an energetically undemanding dispersal strategy, may not be used by many dragonflies in which case their effective flight range would be limited to distances covered in active flight. However, high elevation dispersal flight has been recorded for at least certain migratory species so that long-range wind-assisted dispersal cannot be ruled out (Corbet 1974, 1980). In addition, dragonfly dispersal generally precedes reproduction in the phenology of the adult life (Corbet 1980). Mating immediately precedes oviposition and occurs at the breeding site. As the most probable founders would be single, unmated individuals, establishment of a new population would depend upon the dual probabilities of their discovering a mate and a suitable breeding site.

There is little evidence of endemism in island populations. Walker (1958) remarked that female specimens of *Aeshna i. interrupta* from the Magdalen Islands and Newfoundland differed from Nova Scotia and western Ontario specimens in the shape of abdominal segment 3 and the tendency of spots on the thorax to coalesce but as he had seen too few specimens from the region he chose not to give these populations formal recognition. However, Cannings & Stuart (1977) noted that *A. interrupta* is the most variable species of

Aeshna in British Columbia and that the three subspecies recognized by Walker do not show a definite geographical separation. Because the pattern of variation in this species is complex and at least part of this is thought to be environmentally induced (e.g. female anal appendages, Walker 1958), it is probably best at this time not to put much zoogeographic weighing on the occurrence of recognizable local populations.

In summary, the island's fauna is comprised of widespread boreal species, just those that might be expected on the basis of the climate and geographical setting of the island. The oddity in the fauna is the absence of a few widespread boreal forms that also occur in Labrador (e.g. *Somatochlora minor, S. whitehousei*) suggesting that either the island is environmentally unsuitable for even a portion of the boreal fauna or that the combined coastal barrens and narrow straits between Newfoundland and Labrador are effective barriers to even such aerially adept insects as certain dragonfly species.

Order Ephemeroptera – mayflies

Mayflies are among the most poorly known of Newfoundland's aquatic insects. The only paper dealing specifically with the island's fauna is by Berner (1959) who recorded eight taxa, four identified to species and four to genus only. The lack of knowledge of the fauna stems from from two major problems: the taxonomy is based on the imaginal stage which is short lived, difficult to collect and for several species not yet associated with the nymphs; also, taxonomy of many genera is confused. Modern revisions are available for only a few of the major genera but where published they have revealed a great deal of synonymy (e.g. Allen & Edmunds 1962–1965; Morihara & McCafferty 1979; Bednarik & McCafferty 1979). In spite of these limitations, a list of the mayfly species taken on the island is presented in Table 5. The taxa so listed appear valid but the nomenclature is certainly subject to further revision. Compared to the 301 species estimated to be present in Canada (Lehmkuhl 1979), Newfoundland's fauna is indeed poor.

The ecological distributions of the island's taxa are indicated diagrammatically in Fig. 11. The majority of species are inhabitants of flowing water, found principally in permanent streams of second order or larger and usually on mineral substrates.

The lentic fauna is rather limited. *Stenonema fermoratum* and some populations of *Heptagenia pulla*, while catagorized as lentic species, have been found along stony, exposed shores of larger ponds and lakes or at the months of lake outlets and thus are actually living in habitats with water movement and substrate scouring. *Siphlonurus alternatus* is also in this habitat but may occur in more protected sites as well. *Caenis simulans* occurs in eutrophic situations such as windrows of decaying vegetation along lake shores, the emergent zone of nonpeaty ponds and on the clay marl of limestone ponds. Burks (1953) noted *C. similans* is pollution tolerant and in fact the species abounds in polluted ponds in the St. John's area but is infrequently encountered elsewhere. Burrowing mayflies of the genus *Hexagenia* are local in distribution and have been collected only infrequently. Their distribution is probably restricted to ponds with tracts of suitable sandy or gravelly bottoms into which the larvae may burrow (Edmunds *et al.* 1976) although in at least one pond, nymphs were found in loose peat substrates (P. Ryan, pers. com.).

Leptophlebia cupida, while essentially a lentic species, is the most abundant and widely distributed mayfly. Nymphs occupy a variety of habitats ranging from newly formed pools, beaver ponds, bog pools, carex marshes, shorelines of larger ponds and lakes, including both emergent and rocky shores, as well as along backwaters and margins of slower streams. The seasonal migration of nymphs described by Neave (1930) and Clifford (1969) has not been observed in Newfoundland. As winter freezing is not as severe in Newfoundland as in much of the continental range of the species, complete freezing of bog and headwater habitats is unlikely and the species may not be forced to evacuate these portions of its habitat in winter. However, if population movements do occur, the prolonged melt and warming period in the spring may extend migrations over a long period of time making them diffuse and not obvious.

The lotic fauna contains ecologically diverse species ranging from *Baetis* spp, *Epeorus pleuralis* and *Rithrogena undulata* which may be found on the upper side of rocks in even very swift water, to *Ameletus* sp. found along the margins of streams in eddies, backwaters and flooded areas. Many of the lotic species occur under cover (e.g. most of the Heptageniidae), well down in the substrate (hyporheic, e.g. *Habrophlebia vibrans*), in protected sites (*Paraleptophlebia* spp., *Drunella cornuta, Eurylophella* spp.), or sprawling on the surface of substrates or in attached vegetation (*Ephemerella* spp. and *Baetis* spp.). Few mayflies enter the smallest seepages and springs, the most notable are *Baetis* spp. in fast flows and mineral substrates and *Leptophlebia cupida* and *Siphlonurus quebecensis* in organically rich sites. The richest faunas are in turbulent streams of second order or larger. However, in larger streams with unstable substrates, faunal density falls off. Few species occur in polluted waters but *Ephemerella invaria* has been collected in a polluted stream in St. John's.

Table 5 Checklist of the Ephemeroptera of insular Newfoundland

Species	Recorded by	Newfoundland distribution	Range
SIPHLONURIDAE			
Ameletus sp.	new record	general	?
Siphlonurus alternatus Say	new record	general	transcontinental
S. quebecensis Prov.	new record	general	E. of Gt. Plains
BAETIDAE			
Baetis flavistriga McD.	new record	general	E. of Gt. Plains & Arctic (Cobb & Flannagan 1980)
B. macdunnoughi Ide	new record	general	N.E.
B. pygmaeus Hagen	new record	general	E. of Gt. Plains & Arctic (Cobb & Flannagan 1980)
B. tricaudatus Dodds	new record	general	transcontinental
Baetis sp.	Berner 1959		
Callibaetis skokianus Needham?	Berner 1959	SW	E. of Gt. Plains
Centroptilum convexum Ide	new record	A	E. of Gt. Plains
HEPTAGENIIDAE			
Epeorus pleuralis Banks	Berner 1959 (as *Epeorus* sp.); Dance 1979	general	E. of Gt. Plains
Heptagenia pulla Clemens	new record	general	E. of Gt. Plains
Heptagenia spp.	new record	general	?
Rhithrogena undulata Banks	Dance 1979	W	transcontinental
Stenonema femoratum Say	Bednarik & McCafferty 1979	general	E. of Rocky Mnts.
S. vicarium Walker	new record	general	E. of Rocky Mnts.
LEPTOPHLEBIIDAE			
Habrophlebia vibrans Needham	new record	general	E. of Gt. Plains
Leptophlebia cupida Say	Walker 1853 (as *Ephemera hebes* Walker); Berner 1959	general	transcontinental
Paraleptophlebia adoptiva McD.	new record	general	E. of Rocky Mnts.
P. debilis Walker	new record	general	transcontinental
EPHEMERELLIDAE*			
Drunella cornuta Morgan	Berner 1959 (as *Ephemerella cornutella* McD); Dance 1979	general	E. Appalachian

Table 5 (continued)

Species	Recorded by	Newfoundland distribution	Range
Ephemerella aurivillii Bengts.	Berner 1959	general	transcontinental, Holarctic
E. subvaria McD.	new record	general	E. of Gt. Plains
Eurylophella funeralis McD.	new record	general	E. of Gt. Plains
E. prudentalis McD.	Berner 1959	general	E. Appalachian
TRICORYTHIDAE			
Tricorythodes atratus McD.	Berner 1959	S, A	E. of Gt. Plains
CAENIDAE			
Caenis simulans McD.	new record	general	transcontinental
EPHEMERIDAE			
Hexagenia sp.	new record	general	?

* Generic classification of Allen 1980.

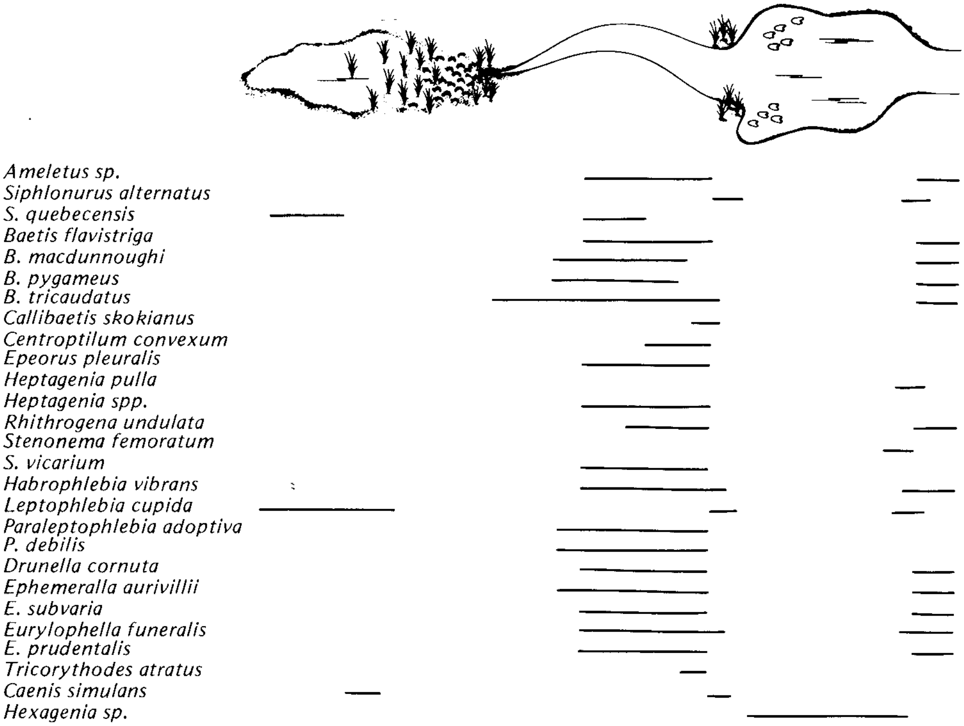


Fig. 11 Ecological distribution of nymphs of Newfoundland species of Ephemeroptera.

In the species poor Newfoundland fauna, there are generally only one or two species of each major adaptive (ecological) type (usually represented at the genus or subgenus level). With the exception of the members of the genera *Ameletus, Baetis* and *Heptagenia*, which are poorly understood taxonomically, when two or more species of the same genus are found locally, there are usually obvious factors isolating the species. For example, two species of *Stenonema* occur on the island, *S.* (s. str.) *femoratum* in lentic sites, *S. (Mccaffertium) vicarium* in streams; *Ephemerella invaria* is in warm streams while its congener, *E. aurivillii*, is in cold streams (in the very few observed instances of co-occurrence one species is much the dominant). *Eurylophella funeralis* and *E. prudentalis* often occur in the same stream but *funeralis* is in slower water with more silt and accumulated debris than *prudentalis*. McDunnough (1931) has also reported *E. prudentalis* from lakes. The two Newfoundland species of *Paraleptophlebia* occur in similar habitats in the same streams, however they are temporally separated for *P. adoptiva* is a winter species with spring adult emergence while *P. debilis* is a summer species with fall emergence. Clifford (1969) commented on the temporal separation of *Leptophlebia cupida* and *P. adoptiva* as a mechanism reducing competition between these two ecologically similar species. *Siphlonurus alternatus* is a lentic species usually found on mineral substrates while *S. quebecensis* occurs among emergent vegetation in marginal lotic sites.

Because of the large discontinuity in ecological zones occupied by the various species, it seems unlikely that the distributions of most species are markedly modified by interspecific competition. It is possible that the range of habitats occupied by *Ephemerella* and *Eurylophella* species might be broader in the absence of congeners than presently observed. In fact, the reduced fauna of the island suggests that interspecific competition would be reduced and that in the absence of competitors niche widths might be broader than in continental faunas. Associated with an increase in niche width, might be increased intraspecific variability. *Leptophlebia cupida* might be a case in point for it is eurytopic and highly variable in size. However, this suggestion will require considerably more detailed field studies, both in Newfoundland and elsewhere, coupled with experimental studies before a definitive conclusion can be reached.

Nymphal mayflies can be found throughout the year although lowest densities and diversity exist in mid- to late summer. Most species are univoltine. The most common life-history pattern is for the eggs to hatch in late summer or fall with the nymphs being found until adult emergence the following spring or early summer. In these forms, egg hatch and nymphal growth rates are staggered so that a range of nymphal size classes may be present at any one time although final adult emergence may be restricted to a time frame of several weeks to a month or more (e.g. *Leptophlebia cupida*). However, *Epeorus pleuralis, Drunella cornuta,* and perhaps the two *Siphlonurus* species are present as nymphs for only short periods of the year, in spring and early summer, while *Paraleptophlebia debilis* nymphs are found only during the summer. *Baetis tricaudatus* is at least bivoltine with considerable overlap of generations while the life histories of the other *Baetis* species are not known at present. There is some evidence, based on size differences among spring and winter collected nymphs, that *Eurylophella* species may take more than one year to develop.

The winged subimaginal and imaginal stages constitute the terrestrial portion of the mayfly life cycle. Although effective fliers, these stages must have limited flight duration and range for they are nonfeeding, short-lived, exclusively reproductive, dispersal stages. Berner (1959) cites this, along with the disjunct distribution of suitable nymphal habitats, as deterrents to dispersal and thus as the significant factors producing limited ranges of mayfly species. Limitations on the dispersal abilities of mayflies may have been important in shaping the composition of the present fauna. Although the relationships between the faunas of Newfoundland and the adjacent mainland, e.g. Labrador and Nova Scotia, are not known, it is certain that the Newfoundland fauna is impoverished. McDunnough (1930, 1932) recorded 30 species from the north shore of the Gulf of St. Lawrence, of which only seven or eight occur in Newfoundland. This low level of similarity results from a mixture of incomplete collection and undiscovered synonymy but the indication of faunal reduction on the island is certainly real.

The island's limited fauna could result from dispersal difficulties experienced by the adults but this explanation is not entirely satisfactory. Probably dispersal ability does not vary a great deal between mayfly species or if it does there seems to be no imbalance in the island fauna towards species with particular sets of adult attributes that would enhance dispersal abilities, e.g. large size, and relative longevity. In terms of the range of habitats occupied by mayflies, the Newfoundland fauna is fairly well balanced lacking primarily filter feeding and burrowing forms. If dispersal limitations were the principal factors shaping the composition of the island's fauna, it would seem likely that the fauna would be more imbalanced – i.e. some genera would be represented by the full range of species occurring on the adjacent mainland while other genera would be lacking. Waters (1961), Gyselman (1980) and others have found nymphal intraspecific competition to be important in regulating densities of populations of some mayfly species. Interspecific competition between ecologically similar species is also likely and in fact such interspecific interactions have been postulated as shaping the mayfly fauna of harsh environments elsewhere (e.g. Brittain 1980). Stability in water levels, temperatures and nutrient input in Newfoundland streams, especially over the fall to spring period when most nymphs are found, would reduce the opportunities for faunal enrichment due to differing colonization or exploitation abilities of species in fluctuating environments (Southwood 1978). Low productivity of aquatic environments and limited types of nutrient input into streams reduce the number and types of habitats available. Perhaps Newfoundland habitat diversity or, more likely, productivity is inadequate to support a diverse fauna over prolonged periods. Thus it is postulated that the present fauna is shaped by distributional and ecological interactions to produce a 'balanced' species-poor fauna.

Perhaps also supporting this argument is the lack of regionality in the island's fauna. All but two or three species have wide distribution on the island and will probably be found in suitable habitats in all regions. An exception to this is *Rhithrogena undulata* which has been found only in streams draining the Long Range Mountains. Nymphs are found only on smooth, scoured boulders in fast water and their distribution reflects the distribution of suitable rock habitats. Elsewhere, stones tend to be coarse textured or encrusted with epilithic plants or minerals and are probably unsuitable.

Table 6 summarizes the North American range patterns of Newfoundland mayflies. As the taxonomy of the group is clarified, changes will be required but their effect should be minimal. The majority of species occur in the eastern deciduous forest biome, east of the Great Plains, and extend up into the eastern boreal regions or even well into the arctic (Cobb & Flannagan 1980). A few species extend through the boreal region to the eastern slopes of

Table 6 Summary of the range patterns of Newfoundland species of Ephemeroptera*

Distribution pattern	No. of species	% of species
Holarctic, transcontinental	1	4
Nearctic, transcontinental	6	24
East of Rocky Mountains	2	8
East of Great Plains	13	52
Appalachian and East Coast	3	12
Total	25	100

* An additional 4 or 5 unidentified species are known from Newfoundland. These belong to genera whose eastern North American species are largely limited to the area east of the Great Plains.

the Rocky Mountains. The majority of lotic species do not cross the Great Plains and their main axis of distribution is north-south, principally along the Appalachian mountains but also extending, in various degrees, beyond this into neighboring forested areas.

The transcontinental assemblage of species is ecologically diverse: three are lentic *(S. alternatus, L. cupida* and *C. simulans)*, one is warm water lotic *(P. debilis)* and three are cold water lotic (boreal to subarctic) *(R. undulata, B. tricaudatus* and *E. aurivillii)*.

In summary the island's mayfly fauna has the majority of its lotic forms derived from a northward extension of species whose distribution is centered in the eastern deciduous biome. The lentic species are mainly transcontinental in the boreal zone. The few transcontinental lotic species tend to be ecological specialists, in specialized habitats of wide distribution.

Order Plecoptera – stoneflies

Although the order Plecoptera is represented on the island by only twelve species (Table 7), several species are widely distributed and abundant. Nymphal stoneflies are common inhabitants of almost all lotic habitats as well as being found along exposed, stoney margins of larger, deeper lakes were water temperatures remain low. The habitat distribution of Newfoundland species is indicated in Fig. 12. Of the various orders of aquatic insects, the Plecoptera are the most restricted to cool, clean, well-oxygenated water (Hynes 1976; Wiggins & Mackay 1978). Nymphs occur in protected sites such as in debris, in clumps of rooted vegetation or, most commonly, under stones. At least one species, *Leuctra ferruginea,* is a regular member of the hyporheic fauna, penetrating considerable depths into streambed gravels. The most diverse faunas occur in second order or larger streams but *L. ferruginea* nymphs may be found in the smallest springs and seepages so long as silt or iron precipitates are not so deep as to smother inorganic substrates. Larvae of *Nemoura macdunnoughi* may be very abundant locally on and among rooted macrophytes.

Trophically, members of the families Leuctridae, Capniidae and Nemouridae (the island's smaller stoneflies) are shredders, herbivores or detritivores while the larger forms belonging to the families Chloroperlidae, Perlidae and Perlodidae are primarily carnivores feeding on Diptera, Trichoptera, Ephemeroptera and Plecoptera larvae (Harper 1978). Smaller species have wide distributions throughout stream systems while the larger forms tend to be mainly in larger streams.

Table 7 Checklist of the Plecoptera of insular Newfoundland

Species	Recorded by	Newfoundland distribution	Range
LEUCTRIDAE			
Leuctra ferruginea Walker	Brinck 1958	general	W. to Sask.
L. truncata Claassen*	Dance 1979	W	Que., New England
CAPNIIDAE			
Allocapnia minima Newport	Ricker 1947; Brinck 1958	W, C, E	E. of Gt. Plains
Paracapnia angulata Hanson	new record	W	W. to Sask.
P. opis Newman	Newman 1839; Ricker 1947; Brinck 1958	general	northeastern
NEMOURIDAE			
Nemoura macdunnoughi Ricker	Ricker 1947; Brinck 1958	general	northeastern
CHLOROPERLIDAE			
Alloperla caudata Frison	Brinck 1958	W, C	E. of Gt. Plains
A. concolor Ricker	Brinck 1958 (as *A. neglecta*)	general	northeastern
A. naica Provancher	Brinck 1958; Ricker 1964	W	northeastern
PERLIDAE			
Acroneuria abnormis Newman	Brinck 1958	N. Pen.	W. to Sask.
PERLODIDAE			
Isogenus frontalis Newman	Ricker 1947, 1952, 1964; Brinck 1958	general	W. to Sask.
Isoperla bilineata Say	Dosdall & Lehmkuhl 1979	W	W. to Rocky Mnts.
I. transmarina Newman	Ricker 1947; Brinck 1958	general	transcontinental

* Very similar to *L. ferruginea*, status unclear.

No life history or ecological studies have been published on any island population of stoneflies, thus ecological information presented below has been obtained from literature sources or collection observations.

Nymphs of three size classes were represented in a single collection of *Acroneuria abnormis* made in July, suggesting that two – or perhaps three – year classes of nymphs were present. Hitchcock (1974) states that the species

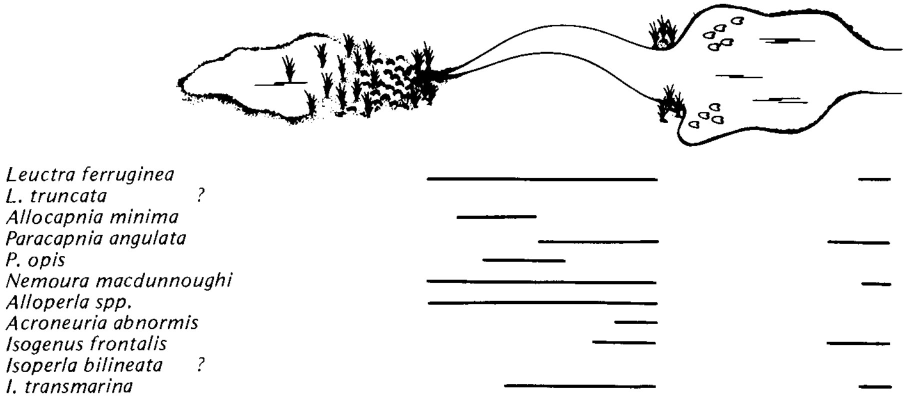


Fig. 12 Ecological distribution of nymphs of Newfoundland species of Plecoptera.

probably requires more than a year to complete development in lower latitudes thus a two-year plus life cycle in northern Newfoundland is likely. *Leuctra ferruginea* adults have been collected from June 14 to September 23 while larvae in various size classes have been found in streams continuously throughout the year. Early summer collections of adults contain both males and females while late summer and fall collections contain only females. It is not known if larval growth, maturity and reproduction occur continuously throughout the year, whenever temperatures are suitable, or if asynchronous egg hatching or slow development rates are responsible for the staggered pattern of temporal distribution. These observations agree with the results of Harper's (1973) studies in Quebec where he noted an extended period of adult emergence and a life cycle of variable duration, from univoltine to semivoltine, depending upon stream temperatures. All other Newfoundland species are probably univoltine for there is generally synchronization of larval development with well-defined periods of adult emergence.

Few stonefly nymphs, with the exception of the above two species, are to be found in streams over the summer, while the greatest nymphal populations and presumably most growth occur in the winter and spring months. Adults of most species emerge in spring to early summer (late May to early July). The earliest emerging adults are those of *Allocapnia minima* and *Paracapnia opis* which regularly appear in March and April when stream margins are still frozen and snow covers the ground. Adult stoneflies tend to be retiring. Those of most species can be found under cover along stream banks. These can often be collected effectively by throwing water up onto the bank which forces the stoneflies out from under cover to run up the bank. At night several species come to light or can be found running actively over streamside rocks. The green *Alloperla* adults are more active during the day than most adult stoneflies and are frequently found in flight over streams or sitting on stream side vegetation where their green color renders them inconspicuous.

The island's fauna is very impoverished in species compared with the faunas of Labrador or Nova Scotia. Apparently salt water presents an effective barrier to the dispersal of many species. For example, compared to the island's 12 species, 20 occur in Labrador and 58 in Nova Scotia (Ricker 1947, Hitchcock 1974, Brinck 1958). All 12 Newfoundland species have been recorded (or are strongly suspected of occurring on the basis of distribution pattern) from Nova Scotia while ten of these species have also been recorded from Labrador. *Alloperla concolor,* while not recorded from Labrador, has been reported from the Ungava region of Quebec (Ricker *et al.* 1968) and thus is almost certainly in Labrador. Only *Alloperla caudata* occurs in western Newfoundland and Nova Scotia but is absent from Labrador, suggesting *A. caudata* colonized Newfoundland by crossing the Cabot Strait. The other species in the fauna probably entered by crossing the Strait of Belle Isle although the alternative route cannot be discounted, especially for the relatively actively flying species of the genus *Alloperla*. However, if colonization was via the Cabot Strait, a higher percentage of non-Labrador forms would likely exist in the fauna considering the diverse potential source fauna in Nova Scotia. The pattern of distribution of species on the island strongly suggests the Strait of Belle Isle route for *Paracapnia angulata* and *Acroneuria abnormis* as their present distribution is restricted to the vicinity of the Strait. All other species have wide distributions on the west coast. It is noteworthy that from west to east across the island, there is a progressive diminution in species number so that on the eastern Avalon Peninsula only five species are known while a sixth reaches the central Avalon (Fig. 13). Some of these range limits do not show any obvious correlation with physiographic or climatological features but faunal diversity decreases with increasing distance from the postulated source area.

Brachyptery occurs in two island species: *Paracapnia opis* and *P. angulata.* In *P. opis,* all 27 females examined had full wings while 52 males had wings ranging in size from one-third the length of the abdomen to fully developed with most specimens showing some degree of brachyptery. One of the 80 *P. angulata* females seen was macropterous and the 9 males were micropterous with the wings reduced to tiny stubs. In both of these species, long-winged forms exist (albeit at very low frequencies in *P. angulata*), especially among females, suggesting flight as the mechanism of colonization of the island. It is interesting to note the presence of brachypterous endemic stoneflies in the

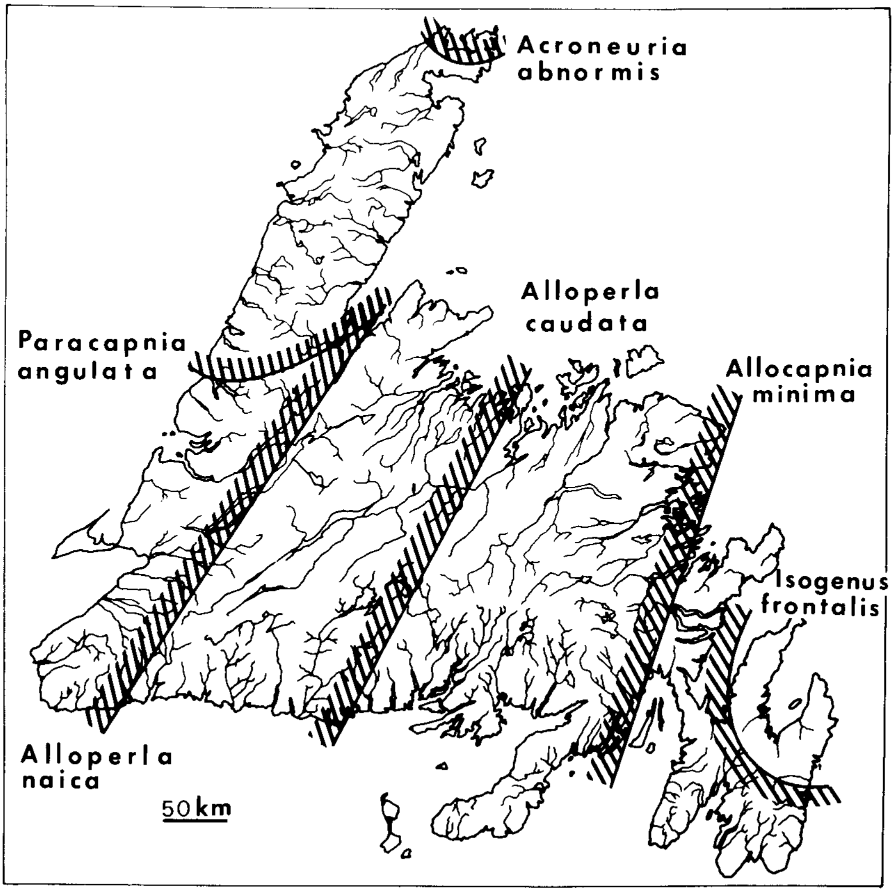


Fig. 13 Approximate eastern limits of distribution of six Newfoundland species of stonefly. The remaining species occur throughout the island.

eastern arctic, namely *Capnia sugluka* Richer and *C. labradora* Ricker, but no similar instances have been noted from Newfoundland (Ricker 1964).

Table 8 summarizes the known range patterns of the Newfoundland species. There is only a small Holarctic element in the Nearctic Plecopteran fauna. All Newfoundland species are Nearctic (Ricker 1944) while only one species, *Isoperla transmarina*, is transcontinental. Five species occur in the boreal zone west to at least Saskatchewan (Dosdal & Lehmhul 1979) while the remaining six species are eastern or northeastern in distribution. The occurrence of species with these patterns of distribution is not surprising for this parallels the distribution of the lotic mayfly fauna. What is surprising is

Table 8 Summary of the range patterns of Newfoundland species of Plecoptera

Distribution pattern	No. of species	% of species
Holarctic, transcontinental	0	0
Nearctic, transcontinental	1	8
East of Rocky Mountains	5	42
East of Great Plains	2	17
Appalachian and East Coast	4	33
Total	12	100

the absence of certain wide ranging species which are represented in northern Quebec and Labrador, for example *Alloperla mediana* Banks, *Brachyptera pacifica* Banks, *Capnia vernalis* Newport, *Nemoura linda* Ricker, *Pteronarcys dorsata* Say, and *Taeniopteryx nivalis* Fitch (Ricker 1964; Hitchcock 1974; Ricker & Ross 1968; Dosdall & Lehmkuhl 1979). These species are lotic but rather eurytopic, thus it would seem that barriers to dispersal rather than absence of suitable habitats on the island are the principal factors responsible for their absence. However, as these are mainly detritivores or phytophagus (Harper 1978), the low productivity of Newfoundland streams may be limiting to at least some of these species.

Order Hemiptera – true bugs

The order Hemiptera is comprised primarily of terrestrial insects with aquatic forms constituting a numerically small portion of the included species. Within the order is a gradation of ecological types, ranging from the terrestrial to the truely aquatic. However, it is recognized that these ecological series are not phyletic (Usinger 1963). The distribution of Newfoundland hemipteran families in this ecocline is indicated in Table 9. Also, the ecologically analogous coleopteran families are included for comparison.

These insects are primarily air breathing and are thus tied to the atmosphere or submerged air stores. However, adaptations such as the ability to carry air stores in or on the body while submerged, physical gills or the use of plastron respiration give these insects variable degrees of independence from the surface. Small corixid nymphs, which have a closed tracheal system, seldom if ever surface to renew tracheal air supplies and it is assumed that they respire cutaneously (Scudder 1976).

Most species possess a feeding, long-lived adult which exists in the same

Table 9 Comparison of the ecological distribution of the Newfoundland families of Hemiptera and Coleoptera

Habitat		Families of	
		Hemiptera	Coleoptera
A.	Species completely terrestrial and not associated with free water	majority of families	majority of families
B.	Species found at edge of free water, essentially terrestrial	Saldidae	many Carabidae and Staphylinidae. Hydrophilidae in part.
C.	Species feeding and living on or in the surface film	Gerridae, Mesoveliidae, Veliidae	Gyrinidae (adult stage only, larvae aquatic)
D.	Immature stages aquatic, adults terrestrial	none	Chrysomelidae (Donaciinea) Helodidae
E.	Larvae and adults aquatic	Belostomatidae Corixidae Notonectidae	Dytiscidae Elmidae Haliplidae Hydrophilidae

habitat as the larva and which may be as important trophically, or perhaps even more important, than the larva. This is in opposition to mayflies, stoneflies, caddisflies and most Diptera where adults are terrestrial and usually nonfeeding, short-lived dispersal and reproductive stages. The larvae, however, have narrower ecological ranges and are less tolerant of environmental change than adults. The adult stage can often disperse to new habitats if conditions change, or is at least better able to withstand periods of water level fluctuation, drying or freezing. Thus by possessing a relatively short, vulnerable larval period, these insects are able to take advantage of fluctuating or temporary habitats not colonized by many other aquatic insects.

The aquatic Hemiptera, being hemimetabolous, do not require terrestrial pupation sites as do the ecologically similar beetles and thus can exist in deeper water, farther from banks and under more unstable water level conditions (e.g. broad expanses of marsh, large rivers, rock pools, deep *Sphagnum* pools, etc.) than many beetles. Atmospheric respiration limits aquatic Hemiptera to shallow waters but absence of a pupal stage frees the life cycle from the proximity of land or dependence upon nonflooded sites.

Although life history studies of Newfoundland Hemiptera have not been undertaken, the seasonal distribution of adults suggests most, if not all, overwinter as adults as is the case with most temperate species (Brooks &

Kelton 1967; Usinger 1963). Most species are univoltine. However, Spence & Scudder (1980) have shown *Gerris buenoi* and *G. comatus* to be bivoltine in British Columbia and this seems to be the rule for most north temperate species of the subgenus *Gerris*. Certain populations of corixids are known to have more than one generation in a summer but nymphs that do not mature by late fall die at freeze-up (Jansson & Scudder 1974).

The taxa of semiaquatic and aquatic Hemiptera known from Newfoundland are listed in Table 10 and their ecological distribution is indicated in Fig. 14. This fauna is discussed below on the basis of ecological groupings.

a) *Water margin inhabitants*: This is the habitat occupied by most members of the family Saldidae. These are active, running or leaping bugs, the adults of which readily take flight for short distances. These insects are predators or scavengers on dead insects (Schuh 1967). Many beetles (e.g. *Bembidion* species in Carabidae, *Stenus* species in Staphylinidae) are ecologically similar but saldids, probably due to their higher mobility, especially in the nymphal stage, and lack of the pupal stage, are more successful in occupying open shoreline habitats, floating vegetation mats, rocky sites and sites with fluctuating water levels. Most species occur on dark mud or peat at the margins of pools but some are in dense emergent vegetation, or floating vegetation mats. At least one species, *Pentacora ligata*, is found on rocks protruding from stream channels. These are actually terrestrial insects that are associated with the water's edge probably because of the abundance of prey in these sites.

b) *Surface film inhabitants – skaters*: Three hemipteran families occur in this habitat, ranging from the large species of *Gerris* (Gerridae) which occur on open protected waters and small *Mesovelia* (Mesoveliidae) usually around lily pads, or floating *Potamogeton* leaves, to minute *Microvelia* (Veliidae) which occur on mats of floating vegetation debris or in dense emergent vegetation at the edge of water bodies. These are essentially terrestrial insects which skate on the water surface and prey on insects trapped in or sitting on the surface film. However, at least specimens of *Gerris* have been observed entering the water and remaining submerged for various lengths of time. This is apparently an adaptation that allows the insects to escape low air temperatures, especially in spring, when this behaviour hastens the rate of sexual maturation (Spence *et al.* 1980). Living on the surface film restricts these species to relatively smooth surfaces such as small pools, protected shorelines of ponds and lakes, among emergent vegetation, and slow areas at the margins of streams. Calabrese (1977) characterized the habitats of ten Connecticut species of *Gerris*, a group which includes the four Newfoundland species. She concluded that *G. remigis* is a species of cool flowing water, the species *G. comatus* and *G. buenoi*, which show a high frequency of co-occurrence, are lentic species associated with floating vegetation and that *G. dissortis* is a eurytopic species that 'uses a high fecundity to achieve a numerical advantage over the other *Gerris*' species with which it coexists. Spence & Scudder (1980) also concluded that interspecific competition resulted in evolution towards specialized habitat use by British Columbia gerrid species. These authors found *G. buenoi* to prefer grass/sedge habitat while *G. comatus* was found more frequently with floating vegetation. These predaceous insects make use of water surface disturbances or ripples in location of struggling prey, and species of *Gerris* have been shown to use surface waves in communication (Jamieson & Scudder 1979; Wilcox 1980).

c) *Fully aquatic species:* The only truly aquatic Hemiptera in the fauna are the members of the families Corixidae, Notonectidae and Belostomatidae. The largest and most ecologically diverse family of aquatic Hemiptera is the Corixidae. Corixids occur in a variety of habitats but most are found in sites where substrates are firm and plant debris not too dense. For example, specimens of *Arctocorisa* spp. are usually found on bare mineral substrates in newly formed ponds as well as on sandy bottomed ponds on limestone barrens. However, species such as *Sigara penniensis, S. signata, Callicorixa audeni* and *Hesperocorixa minorella* occur on firm substrates, among emergent vegetation as well as in small peat pools in which the bottom is covered with loose peaty-silt. In dry continental regions, certain species of corixids are halophilous and form a characteristic fauna of saline ponds (Scudder 1976; Tones 1975). As saline habitats such as estuarine and salt splash pools are poorly developed on the island, it is not surprising that saline pool corixids are poorly represented in the fauna. *Trichocorixa sexcincta* and *T. verticalis fenestrata* have been found only in barachois and estuarine ponds, sites usually well-flushed by fresh water but subject to occasional salt water inundation. The only lotic species in the fauna are *Sigara trilineata* and *Palmacorixa buenoi* which occur along quiet margins of larger rivers in depositional areas of very low current, clay to sandy substrates and sparse rooted emergent vegetation.

Corixids are trophically diverse. Some are known to feed on the cell contents of filamentous algae (Hungerford 1948; Reynolds 1975) and bottom oozes containing diatoms, protozoa and rotifers but evidence suggests that most are predaceous (Merritt & Cummins 1978; Pajunen 1977; Scudder 1976).

Two species of the family Notonectidae are known from the island. Both are strong, actively swimming predators which frequent the open waters of pools and small ponds. *Notonecta insulata* is found most frequently along the abrupt peaty banks of deep bog pools, while *N. undulata* is rather widely

Table 10 Checklist of the aquatic and semiaquatic Hemiptera of insular Newfoundland

Species	Recorded by	Newfoundland distribution	Range
CORIXIDAE			
Arctocorisa convexa Fieb.	Hungerford 1948	N	transcontinental
A. chanceae Hung.	Hungerford 1948	N	transcontinental
A. planifrons Kirby	Hungerford 1948	A	transcontinental
Callicorixa audeni Hung.	Hungerford 1948	general	transcontinental
C. alaskensis Hung.	Hungerford 1948	general	transcontinental
Dasycorixa sp.	new record	S	?
Glaenocorisa quadrata Walley	Hungerford 1948	E	?, transcontinental, H
Hesperocorixa minorella Hung.	Hungerford 1948	general	E. of Gt. Plains
H. atopodonta Hung.	new record	W	transcontinental
Palmacorixa buenoi Abbott	new record	W	E. of Rocky Mnts.
Sigara compressoidea Hung.	new record	general	E. of Gt. Plains
S. conocephala Hung.	new record	S, E, W, A	E. of Rocky Mnts.
S. decoratella Hung.	new record	general	transcontinental
S. dolabra H. & S.	new record	E, A	E. of Gt. Plains
S. macropala Hung.	new record	A	E. of Gt. Plains
S. mathesoni Hung.	new record	W	E. of Rocky Mnts.
S. penniensis Hung.	Hungerford 1948	general	transcontinental
S. signata Fieber	Hungerford 1948	general	E. of Gt. Plains
S. trilineata Prov.	new record	W, S, C, E	E. of Rocky Mnts.
Trichocorixa sexcincta Ch.	new record	A, W	E. of Rocky Mnts.
T. verticalis fenestrata Wl.	new record	W, A, E	NE
NOTONECTIDAE			
Notonecta insulata Kirby	Lindberg 1958	general	E. of Gt. Plains
N. undulata Say	Lindberg 1958	general	E. of Gt. Plains
BELOSTOMATIDAE			
Lethocerus americanus Leidy	new record	general	transcontinental
MESOVELIIDAE			
Mesovelia mulsanti White	new record	general	transcontinental
VELIIDAE			
Microvelia buenoi Drake	new record	general	transcontinental
M. pulchella Westwood	new record	general	transcontinental
GERRIDAE			
Gerris buenoi Kirkaldy	new record	general	transcontinental
G. comatus D & H	new record	general	transcontinental
G. dissortis D & H	Lindberg 1958	general	transcontinental
G. nyctalis D & H	Drake & Harris 1934 (in error?)	?	W. North America

Table 10 (continued)

Species	Recorded by	Newfoundland distribution	Range
G. remigis Say	Lindberg 1958	general	transcontinental
SALDIDAE			
Pentacora sphacelata Uhl.	Lindberg 1958	W	Atlantic coast
P. ligata Say	Lindberg 1958	E	E. of Gt. Plains
Salda bouchervillei Prov.	Lindberg 1958	general	transcontinental
S. crassicornis Uhl	Lindberg 1958	general	E. of Rocky Mnts.
S. buenoi McD.	Lindberg 1958	W, N, E, C	transcontinental
S. lugubris Say	Brooks & Kelton 1967	?	transcontinental
S. obscura Prov.	Lindberg 1958	W, S, E, N	transcontinental
Saldula nigrita Parsch.	Lindberg 1958	general	transcontinental
S. opacula Zett.	Lindberg 1958	general	transcontinental H.
S. orbiculata Uhl	Lindberg 1958	n	transcontinental
S. pallipes – palustris complex	Lindberg 1958 (as *S. pallipes* F. & *S. fernaldi* Drake)	general	transcontinental H.
S. saltatoria L.	new record	general	transcontinental H.
S. separata Uhl.	Lindberg 1958 (as *S. illinoiensis*)	general	E. of Rocky Mnts.

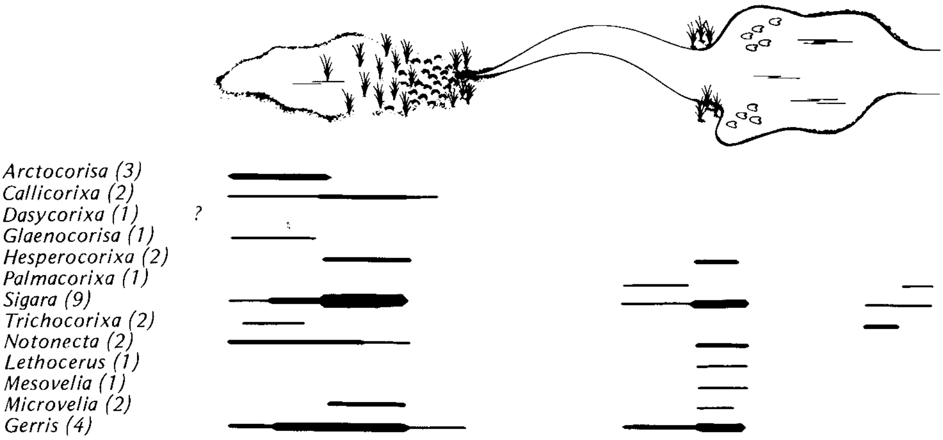


Fig. 14 Ecological distribution of Newfoundland aquatic Hemiptera.

Table 11 Range patterns of Newfoundland species of aquatic and semi-aquatic Hemiptera

	Transcontinental		East of Rocky Mountains	East of Great Plains	Appalachian and East Coast
	Holarctic	Nearctic			
Corixidae	1	8	5	5	1
Notonectidae		1		1	
Belostomatidae		1			
Veliidae		2			
Mesoveliidae		1			
Gerridae		4			
Saldidae	3	6	1	2	1
Total	4	23	6	8	2
Percentage	9	53	14	19	5

distributed in both bog and nonbog habitats. *Lethocerus americanus*, a predaceous bug of the family Belostomatidae, is the largest aquatic insect in the fauna. The species is apparently uncommon and is known from only a few widely scattered marshes.

The majority of Newfoundland's hemipteran fauna is comprised of species with broad ranges (Table 11). For example, *Lethocerus americanus, Notonecta undulata, Gerris remigis* and *Microvelia pulchella* have almost continent-wide distributions south of the arctic. A few species have ranges best described as subarctic, namely *Glaenocorisa quadrata, Arctocorisa chanceae* and *A. convexa*. Most other species are boreal and transcontinental but a few have ranges variously limited in the west. The few species not extending west of the eastern boundary of the Great Plains still have broad ranges, generally centered in the eastern deciduous forest zone and extending north, to various degrees, into the eastern boreal region.

The two taxa with restricted eastern distributions are of interest. *Trichocorixa verticalis* has a continent-wide distribution south of the boreal zone within which several geographical subspecies have been recognized. In the Gulf of St. Lawrence area, including Newfoundland, the species is represented by *T.v. fenestrata*. Sailer (1948) considered that *T.v. fenestrata* was derived from *T.v. interiores* Sailer, the subspecies that occupies the north central portion of the continent and not the Atlantic seaboard subspecies *T.v. sellaris* Abbott which occurs from Maine south. Thus, even for this regional endemic, the affinities are with the boreal or subboreal region. The saldid *Pentacora sphacelata* has a limited coastal distribution, occurring along the Atlantic coast from western Newfoundland to the Carribean.

The continental pattern of distribution of various species is reflected, at least in part, in their island distributions. For example, the subarctic species tend to be restricted to the Northern Peninsula (e.g. *Arctocorisa convexa)* or to the regions of coastal barrens (e.g. *Arctocorisa planifrons, Callicorixa alaskensis, Glaenocorisa quadrata),* while the widespread boreal species occur throughout the island. Although the two island species of *Callicorixa* show range overlap in both their continental and island distributions, partial geographical segregation exists on the island where *C. alaskensis* is coastal or on barrens, while *C. audeni* is generally distributed but most abundant in forested regions (Fig. 15).

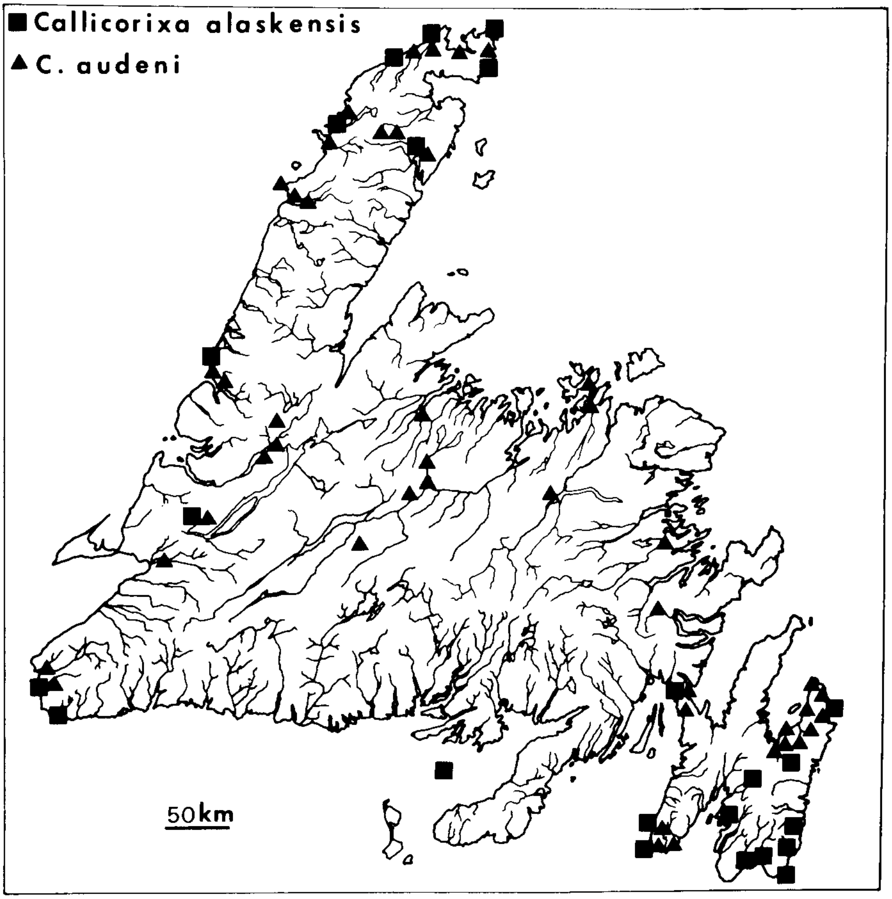


Fig. 15 Collection localities for Newfoundland species of *Callicorixa* (Hemiptera: Corixidae).

There is some relationship between habitat and distribution pattern. For example, all surface film inhabiting species are transcontinental. The species of *Gerris* are generally distributed across the island while members of the other two families have been collected only from ponds within forested regions. The species *Gerris dissortis* and *G. comatus* are constantly fully winged within the fauna while all other surface film inhabiting bugs are dimorphic with the apterous form predominating. Vepsäläinen (1974) argues that frequency of wing dimorphism in water striders is related to habitat permanency. Although aquatic habitats tend to be permanent and relatively stable in Newfoundland, the existence of at least one constantly macropterous gerrid, *G. dissortis,* might be due to its being a relatively r-selected species that persists in a competitive situation with its congeners through possessing greater vagility and fecundity (Calabrese 1977).

In the single collection of *Palmacorixa buenoi* seen from the island, all specimens (22) were brachypterous. However, aside from the surface dwelling species, all other Newfoundland aquatic and semiaquatic Hemiptera are macropterous. Macroptery does not necessarily imply the insect is capable of flight. Young (1965a & b) and Scudder (1975) have shown that flight muscle polymorphism may exist in macropterous species. Young (1965a & b) concluded that most corixids showed a tendency towards flightlessness but that this was strongly modified by habitat stability. Species living in temporary or impermanent habitats were the most vagile. On the other hand, Scudder (1975) could not find a relationship between habitat stability and degree of flightlessness in British Columbia, but he did note that low temperatures during development of certain corixids resulted in an accumulation of nonflying morphs in populations. High temperatures brought about a release of developmental arrest and resulted in muscle development (Scudder & Meredith 1972).

Flying corixids, and presumably other flying aquatic Hemiptera, are attracted by shiny surfaces and do not appear capable of selecting suitable water bodies before alighting (Popham 1964). In an island environment considerable mortality could result through loss of flying individuals into the ocean, and this could act as a strong selection factor against flight.

Three aspects of Newfoundland's geography and climate, namely the proximity of the sea, relatively stable freshwater habitats, and cool temperatures, have been demonstrated as contributing to increased flightlessness in aquatic Hemiptera elsewhere. Wing reduction in Newfoundland populations is not higher than in continental boreal faunas but less readily observed flight muscle polymorphism may be common. This has not been investigated locally but principles established in other population studies would support the prediction of high incidence of loss of flight capabilities in Newfoundland water bugs. Circumstantial support is provided by the absence of flight records, even from light traps, for any Newfoundland aquatic species. Clearly flight dispersal must occur but swarms of corixids in rain pools or at electric light have not been seen nor have any specimens of *Lethocerus americanus*, in places called the electric light bug because of its propensity to fly to light, been seen at light.

The Newfoundland fauna is not especially rich in species compared with other temperate faunas (Table 12), reflecting the relative lack of habitat diversity in Newfoundland and adjacent faunal source areas. There is little evidence to suggest significant faunal reduction between Newfoundland and the adjacent regions of Quebec and Labrador. For example, Walley (1930, 1932) recorded 23 species from the Quebec North Shore, of which all but two, *Notonecta borealis* and *Rhagovelia* sp., have been found on the island. Newfoundland contains a relatively complete boreal fauna comprised of mainly predaceous, lentic species with extensive east-west distributions in the boreal and subboreal regions.

Table 12 Comparison of the number of families and species of aquatic and semiaquatic Hemiptera in selected temperate faunas

Region	No. of families	No. of species
British Isles (Usinger 1963)	13	85
California (Usinger 1963)	15	113
Canada (Scudder 1979)	12	165
British Columbia (Scudder 1977)	9	54
Prairie Provinces (Brooks & Kelton 1967)	12	95
Newfoundland	7	44

Order Coleoptera – beetles

The order Coleoptera is often singled out for special comment because of its unsurpassed species diversity. However, this diversity is much reduced at higher latitudes (Campbell 1979) as well as in aquatic habitats. With slightly over one hundred aquatic species (Table 13), the order Coleoptera is the third largest order of aquatic insects in the Newfoundland fauna, containing fewer species than either Diptera or Trichoptera.

Most Newfoundland aquatic beetle diversity is contributed by the families Dytiscidae (62 species), Hydrophilidae (15 species) and Gyrinidae (9 species)

Table 13 Checklist of aquatic Coleoptera of insular Newfoundland

Species	Recorded by	Newfoundland distribution	Range
HALIPLIDAE			
Haliplus immaculicollis Harris	Balfour-Browne 1948	general	transcontinental
H. cribarius LeC.	Balfour-Browne 1948	general	transcontinental
H. subguttatus Roberts	Balfour-Browne 1948	W	transcontinental
DYTISCIDAE			
Liodessus affinis (Say)	Balfour-Browne 1948; Bistrom 1978	general	transcontinental
Hygrotus sayi B.-B.	Balfour-Browne 1948; Anderson 1971	general	transcontinental
H. canadensis Fall	new record (= *compar* of Bistrom 1978?)	N. Pen.	E. of Rocky Mtns.
H. suturalis LeC.	Balfour-Browne 1948	W	transcontinental
H. quebecensis Brown	Balfour-Browne 1948 (syn. of *H. borealis* Fall?) (= *H. compar* of Bistrom 1978?)	general	transcontinental
H. picatus Kirby	new record	W, C, E	transcontinental
H. impressopunctatus Schaller	Balfour-Browne 1948	W	transcontinental, H
H. unguicularis Crotch	Balfour-Browne 1948	W	transcontinental
Oreodytes scitulus LeC.	Bistrom 1978; Fall 1923 as *H. septentrionalis;* Balfour-Browne 1948 as *H. rivalis*	general	transcontinental
O. laevis Kirby	Bistrom 1978	W	transcontinental
Deronectes elegans Panzer	Balfour-Browne 1948 as *Potamonectes depressus elegans;* Bistrom 1978 as *P. depressus*	general	transcontinental, H.
D. griseostriatus Degeer	Balfour-Browne 1948; Bistrom 1978	general	transcontinental, H.
Hydroporus carolinus Fall	Balfour-Browne 1948	general	Atlantic coast
H. pulcher LeC.	Bistrom 1978 as *H. ohionis* Fall? new record	general	E. of Gt. Plains
H. undulatus Say	Balfour-Browne 1948; Fall 1923; Bistrom 1978 as *H. consimilis*	general	transcontinental
H. solitarius Sharp	Fall 1923; Balfour-Browne 1948	general	E. of Gt. Plains

Table 13 (continued)

Species	Recorded by	Newfoundland distribution	Range
DYTISCIDAE			
H. paugus Fall	Fall 1923; Bistrom 1978	general	transcontinental
H. acadianus B.-B.	new record	general, coastal	Nova Scotia, Nfld.
H. aequus Fall	Bistrom 1978	W & C	N.E.
H. brevicornis Fall	Fall 1923; Balfour-Browne 1948	general	N.E.
H. notabilis LeC. (including *H. arcticus* Thoms.)	Balfour-Browne 1948 Bistrom 1978	general	transcontinental, H.
H. niger Say	Balfour-Browne 1948	general	E. of Gt. Plains
H. signatus Mann.	Fall 1923; Balfour-Browne 1948 Bistrom 1978	general	transcontinental
H. tristis Paykull	Bistrom 1978	general	transcontinental, H.
H. striola Gyllenhal	Fall 1923; Bistrom 1978	general	transcontinental
H. badiellus Fall	Fall 1923; Bistrom 1978	general	E. of Rocky Mtns.
H. criniticoxis Larson	new record (Bistrom 1978, as *H. fuscipennis* Schaum)	W	transcontinental
H. rectus Fall	Bistrom 1978; Larson 1975	general	E. of Rocky Mtns.
H. morio Aubé	Fall 1923 (as *H. melanocephalus* Gyll.)	coastal	transcontinental, H.
H. tenebrosus LeC.	Bistrom 1978	SW, N	W. to B.C.
Agabus seriatus Say	Fall 1922a; Balfour-Browne 1948 Bistrom 1978	general	Ssp. *s. seriatus* E. of Gt. Plains
A. kenaiensis Fall	Bistrom 1978 (as *A. wagastjernae* SaRlb.)	N. Pen, Avalon	transcontinental, H.?
A. sharpi Jakobs	Bistrom 1978 (identity not known)	W.	Siberia
A. semipunctatus Kirby	Fall 1922a; Bistrom 1978	W, C	transcontinental
A. arcticus Paykull	Bistrom 1978	N. Pen.	transcontinental, H.
A. punctulatus Aubé	(according to Balfour-Browne 1948, previously recorded from Nfld. Authority? No specimens seen)	?	E. of Rocky Mtns.

Table 13 (continued)

Species	Recorded by	Newfoundland distribution	Range
DYTISCIDAE			
A. anthracinus Mann.	Balfour-Browne 1948	general	transcontinental
A. ambiguus Say	Balfour-Browne 1948; Bistrom 1978	general	transcontinental
A. leptapsis LeC.	Bistrom 1978	general	E. of Rocky Mtns, NE. B.C.
A. infuscatus Aubé	Larson 1975	general	transcontinental, E. Palaearctic
A. confinis Gyll.	Bistrom 1978	general	transcontinental, H.
A. erichsoni G. + H.	Balfour-Browne 1948; Bistrom 1978 – both as *A. nigroaeneus* Er.	W, C	transcontinental, H.
A. phaeopterus Kirby	Balfour-Browne 1948; Bistrom 1978; Larson 1975	general	transcontinental
A. congener Thunberg	Larson 1975	N. Pen.	transcontinental, H.
A. sp. nr. *congener*		general	?
Ilybius angustior Gyll.	Balfour-Browne 1948; Bistrom 1978	general	transcontinental, H.
I. discedens Sharp	Balfour-Browne 1948; Larson 1975; Bistrom 1978	general	transcontinental
I. pleuriticus LeC.	Balfour-Browne 1948; Larson 1975; Bistrom 1978	general	transcontinental
I. biguttulus Germ.	Balfour-Browne 1948; Bistrom 1978	W, C, E, A	E. of Gt. Plains
I. subaeneus Er.	Fall 1927 in error		
Copelatus glyphicus Say	Bistrom 1978	C	transcontinental (Leech 1970)
Rhantus binotatus Harris	Balfour-Browne 1948 (as *R. zimmermanni* Wallis); Zimmerman & Smith 1975; Bistrom 1978	general	transcontinental
R. wallisi Hatch	Balfour-Browne 1948 (as *R. suturellus* sensu Wallis)	general	transcontinental
R. suturellus	Zimmerman & Smith 1975	general	transcontinental

Table 13 (continued)

Species	Recorded by	Newfoundland distribution	Range
DYTISCIDAE			
Colymbetes paykulli Er.	Balfour-Browne 1948; Larson 1975 (as *C. longulus* LeC.); Bistrom 1978	W, C	transcontinental, H.
C. dolobratus (Payk.)	Zimmerman 1980	general	transcontinental
Neoscutopterus angustus LeC.	Bistrom 1978	general	transcontinental
Graphoderus liberus Say	Balfour-Browne 1948	C	transcontinental
G. perplexus Sharp	new record	general	transcontinental
Acilius semisulcatus Aubé	Balfour-Browne 1948; Larson 1975	general	transcontinental
A. fraternus Harr.	Balfour-Browne 1948; claims previously recorded from Nfld. Citation? (No doubt in error)		
Dytiscus harrisii Kirby	new record	general	transcontinental
D. dauricus Gebler	new record	general	transcontinental, H.
D. alaskanus B.-B.	Balfour-Browne 1948 (as *D. ooligbuckii* Kirby); Bistrom 1978	W, C	transcontinental
GYRINIDAE			
Gyrinus affinis Aubé	new record	general	transcontinental
G. aquiris LeC.	new record	W	E. of Gt. Plains
G. bifarius Fall	Balfour-Browne 1948	W, C	transcontinental
G. confinis LeC.	Brinck 1960	W, C	transcontinental
G. dubius Wallis	Wallis 1926; Balfour-Browne 1948	Coastal	Nfld., Lab., Que.
G. latilimbus Fall	Balfour-Browne 1948	general	transcontinental
G. sayi Aubé (= *lugens* Fall)	Fall 1922b; Balfour-Browne 1948	general	E. of Gt. Plains
G. minutus L.	Balfour-Browne 1948	general	transcontinental, H.
G. opacus Sahlb.	Brinck 1960	W, N	transcontinental, H.
HYDROPHILIDAE			
Helophorus lineatus Say	Balfour-Browne 1948	?	?
H. sp. 1		general	?
H. sp. 2		W, C	?
H. sp. 3		N	?
Laccobius agilis Rand.?	Balfour-Browne 1948	W, C, E	transcontinental
L. reflexipennis Malcolm	new record	W, C, E	NE

Table 13 (continued)

Species	Recorded by	Newfoundland distribution	Range
HYDROPHILIDAE			
L. spangleri Wilson	new record	W, N	E. of Gt. Plains
L. sp.		N	?
Paracymus subcupreus Say	new record	W, C	transcontinental
Crenitis morata Horn	new record	N. Pen.	transcontinental
Anacaena limbata F.	Balfour-Browne 1948	general	transcontinental, H.
Enochrus hamiltoni Horn	Balfour-Browne 1948	general	E. of Gt. Plains
E. ochraceus Melsh.	new record	general	E. of Gt. Plains
Cymbiodyta vindicata Fall	Balfour-Browne 1948; Smetana 1974	general	transcontinental
Hydrobius fuscipes L.	Balfour-Browne 1948	general	transcontinental, H.
HELODIDAE			
Cyphon 3 + spp.		general	?
ELMIDAE			
Oulimnius latiusculus LeC.	new record	general	Appalachian
Promoresia tardella Fall	new record	general	Appalachian
Stenelmis crenata Say.	new record	general	E. of Gt. Plains
CHRYSOMELIDAE			
Donacia p. proxima Kirby	Marx 1957	general	transcontinental
D. hirticollis Kirby	Marx 1957	general	transcontinental
D. pusilla Say	Schaeffer 1925	SW	transcontinental
D. emarginata Kirby	new record	general	transcontinental
D. fulvipes Lacordaire	new record	general	NE
D. germari Mann.	Schaeffer 1925	general	transcontinental
Galerucella nymphaeae L.	new record	general	transcontinental, H.

while the remaining four families are less diverse and more restricted in distribution and habits. The members of the three largest families are primarily predaceous in the larval stages while adults may be predators, scavengers, or even phytophagus, as it has been suggested for some hydrophilids, although this has seldom been convincingly demonstrated. Members of the remaining four families are mainly phytophagus or detritivores.

The general range of aquatic habitats occupied by the various coleopteran families is indicated in Table 9 in comparison with the distribution of hemipteran families. Species diversity of aquatic Coleoptera in Newfoundland habitats is indicated diagrammatically in Fig. 16. Semiaquatic forms, that is,

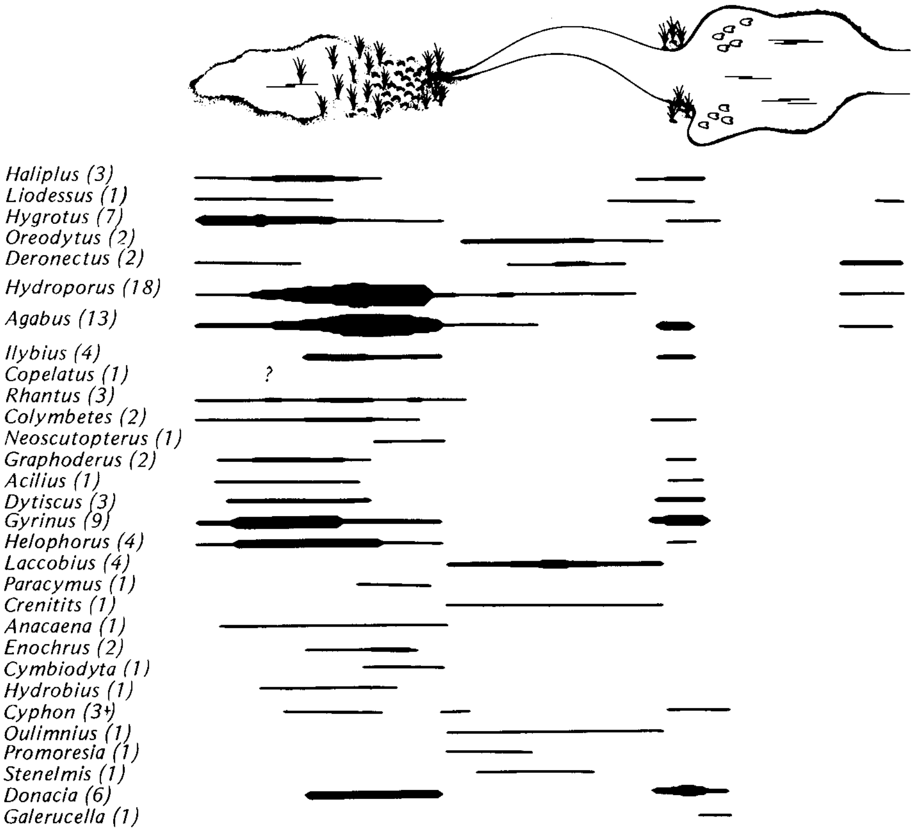


Fig. 16 Ecological distribution of Newfoundland aquatic Coleoptera.

shoreline inhabiting terrestrial species, are usually not treated as aquatic beetles and will not be considered in this discussion.

Water beetles occur in all aquatic habitats except the deeper water of ponds and lakes. However, the greatest diversity exists in small, shallow lentic sites that are densely overgrown with emergent vegetation. With either decreasing vegetation or increasing depth or flow, fewer species are found. Larson (1975) presented observations for adults of many boreal dytiscid species which indicate that species distributions are often correlated with water temperature, habitat permanence, vegetation composition and abundance and substrate characteristics. This supports Galewski's (1971) contention that structural components of the habitat are more important than chemical features in determining dystiscid beetle distribution. In addition, dependence on atmospheric respiration and terrestrial pupation restrict many species to shallow, standing or slowly flowing water in proximity to land.

It is also possible that competition with other insects may limit the distribution of certain beetles. For example, pools or portions of pools with high densities of dragonfly larvae generally have only a few larger dytiscid beetles while adjacent areas lacking dragonfly larvae (because of the density of vegetation, habitat impermanence or complete winter freezing) will often have dense, diverse dytiscid populations. Competition would be expected to exist between these two groups of predators but, in addition, the larger, more energetically efficient dragonfly larvae are possibly predators on beetle larvae.

In spite of high species diversity, aquatic beetles seldom attain the densities or biomass shown by other aquatic insects such as Odonata, Ephemeroptera, Trichoptera or Diptera. Rather than the existence of few species with broad ecological niches, the adaptive strategy shown by coleopteran groups is the development of large numbers of species each with a narrow niche. Because of this, beetle faunas have a potential for providing rather precise information on prevailing aquatic conditions and the distribution of habitat types. To date this has not been exploited, probably because beetle distribution tends to be concentrated in habitats too small to either support fish or to be of economic significance to man and thus inadequately studied or monitored.

The high diversity of beetles in the fauna makes it impossible to provide anything more than a cursory overview of select aspects of their biology and distribution. This will be done on a family basis emphasizing biological characteristics of the family that appear important in determining Newfoundland occurrence and distribution.

The family Dytiscidae is the most diverse aquatic family in the order (Arnett 1963) and this is certainly reflected in the island fauna where two thirds of the water beetle species are dytiscids. Many dytiscid species have broad ranges in the boreal region and certain large genera reach maximum development in north temperate latitudes, especially within the glaciated regions. In this region the glacially sculptured topography abounds in suitable shallow, vegetated, lentic habitats. Much of this region's fauna enters Newfoundland, especially the forms characteristic of bogs, fens, and densely shaded, cold-water marshes. The northern transcontinental elements that tend to be missing from the island fauna are those species of open, sun-warmed pools and temporary vernal ponds. An example showing these distribution patterns is provided by the genus *Rhantus*. There are four transcontinental lentic species in the latitude of southern and central Canada, namely *R. consimilis* Mots., *R. frontalis* Marsh., *R. suturellus* and *R. wallisi*

(Zimmerman & Smith 1975). The species *R. consimilis* and *R. frontalis* occur principally in warm waters and temporary habitats while *R. suturellus* and *R. wallisi* are typically in cold, shaded, permanent pools (Larson 1975). The two warm water species do not occur in Newfoundland while the cold water species are abundant and widely distributed. *Hygrotus picatus* and *H. impressopunctatus* are a pair of morphologically similar species: *H. picatus* in cold, shaded, permanent habitats; *H. impressopunctatus* in exposed, warm, often temporary ponds. The Newfoundland distributions of the two are indicated in Fig. 17. *H. picatus* is widespread on the island while specimens of *H. impressopunctatus* have been found only in shallow, exposed coastal pools along the west side of the island. This distribution suggests that specimens disperse to the island but are limited by scarcity of suitable habitat. This

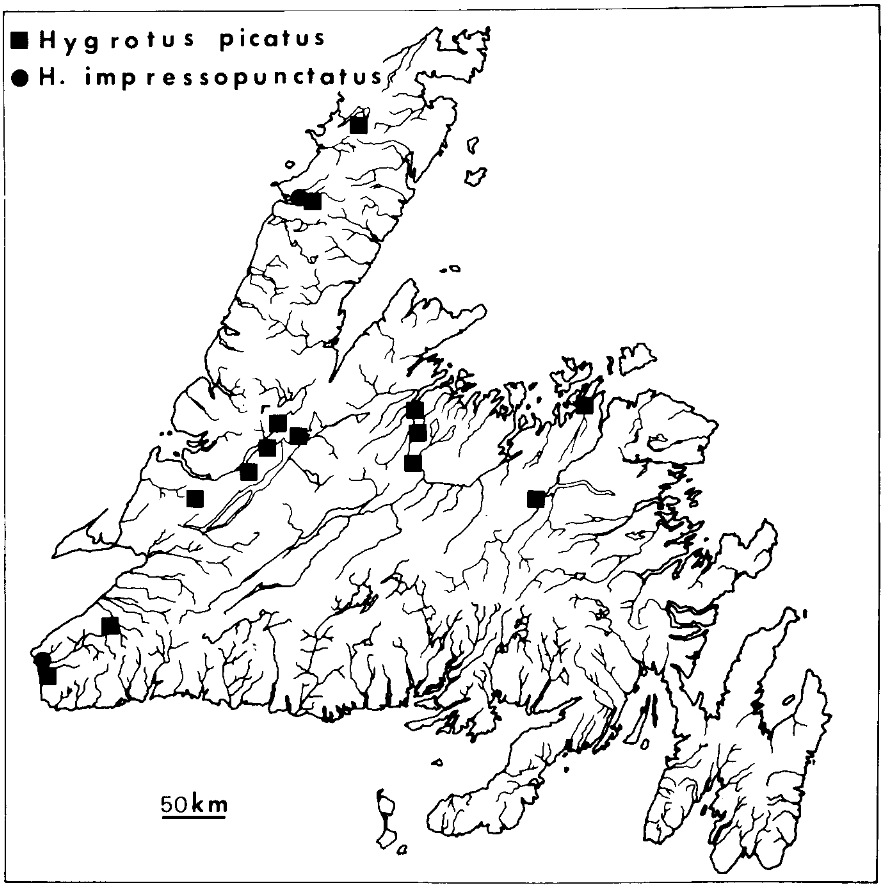


Fig. 17 Collection localities for *Hygrotus impressopunctatus* and *H. picatus*.

pattern is repeated in other genera, with the cold adapted, permanent pond species being the members of each genus represented in the fauna. Human activity that produces shallow, sunwarmed ponds in open areas, such as highway borrow pits, might be expected to increase the available habitat for warm water species and enhance their establishment and distribution on the island. Already, the distribution of *Hygrotus quebecensis*, a species favored by artificial ponds, reflects the distribution of borrow pits.

A few boreal species are rare or absent in Newfoundland. For example *Laccophilus biguttatus* Kirby, *Laccornis conoideus* LeC. and *Rhantus sinuatus* LeC. have broad distributions in the boreal region east of the Rocky Mountains and extend well into the north in at least the prairie region. Yet none have been found in Newfoundland where suitable habitat appears to exist. *Agabus erichsoni*, a holarctic boreal species adapted to temporary ponds, is relatively uncommon.

Few dytiscid species occur in flowing water although in island streams one or more species occur in almost every stream segment. Springs, fingertip tributaries and small headwater pools, especially if they have pockets of dense emergent vegetation, are the habitats of *Agabus ambiguus, A. leptapsis, A. seriatus* (if there are mineral substrates) and *Rhantus binotatus*. These species are transcontinental in such situations. On the island, where some degree of flow or flushing is found in all habitats, these marginal lotic species are almost ubiquitous. *Oreodytes laevis* and *O. scitulus* occur in pools and eddies of large turbulent streams while *Hydroporus pulcher, H. solitarius*, and *Deronectes elegans* are on mineral substrates in sheltered pools and backwaters.

Temperate dytiscids are generally univoltine and this seems to be true for all Newfoundland species. Most species overwinter as adults but there are a few exceptions. *Agabus infuscatus* adults have been collected only in late summer and fall and it appears as though the species overwinters in either the egg or larval stage. Similarly *Hydroporus notabilis* appears to overwinter as a larva. James (1970) found *A. erichsoni* overwinters as both eggs and adults. Unidentified *Agabus* larvae have been taken with *A. ambiguus* adults in winter collections, thus both stages may overwinter.

The family Haliplidae is poorly represented in the fauna. Three species have been discovered in lentic habitats but only one, *Haliplus immaculicollis* is common especially in shallow barachois ponds. These insects are considered to be phytophagus in both larval and adult stages (Doyen & Ulrich 1978), somewhat unusual food habits for beetles of the suborder Adephaga. The insects are univoltine, with adults overwintering and even remaining active under the ice (Wallis 1933).

Nine species of Gyrinidae, all of the genus *Gyrinus*, occur in the fauna. Adults are adapted to life in the surface film while the gill breathing larvae may occur to depths of several meters in ponds. Adults are found in small pools or protected sites of larger ponds as well as still portions of streams. It is not unusual to find aggregations of beetles consisting of several species (Fall 1922b) but there are some specialists in the genus. *Gyrinus minutus* is found almost exclusively in peat-ringed bog pools while *G. opacus* and *G. dubius* are species of coastal barrens and alpine pools. There is one generation per year, with adults overwintering. Pupae are terrestrial and usually occur on the banks, but *G. limbatus* larvae crawl up emergent plant stems and produce an oval pupal case of plant fibers stuck to the plant stem. Five species occur generally throughout the island while the following are more restricted: *G. dubius* – coastal and alpine areas; *G. opacus* – Northern Peninsula; and *G. aquiris* and *G. bifarius* – west coast.

As is usual in the boreal region, the family *Hydrophilidae* is relatively poorly represented although one species, *Anacaena limbata*, is the most widespread and abundant water beetle on the island. This species, like most hydrophilids, occurs in eutrophic sites with large amounts of decaying vegetation. Few species are found in peat bogs although fen sites may possess more diverse faunas. Although most species are lentic, the four *Laccobius* species occur under stones and in debris along the margins of streams. Most species are widely distributed over the island but two species of *Helophorus, Crenitis morata* and *Laccobius spangleri* and *Laccobius* sp. are known only from the Northern Peninsula. *Cercyon litoralis* Gyll., not a true aquatic insect, occurs abundantly wherever wrack accumulates along coastal beaches.

The most completely adapted aquatic beetles are members of the family Elmidae. Both larvae, which have caudal gills, and adults, which have a respiratory plastron, can remain submerged indefinitely. Both stages are heavily sclerotized, slow moving, crawling forms which occur on or in the substrate, rooted plants or debris in streams where adults and larvae graze algae or are detritivores (Brown 1972; LeSage & Harper 1976). *Oulimnius latiusculus* occurs in small headwater streams or in sand and gravel at the margin of larger streams (LeSage & Harper 1976). Both *Promoresia tardella* and *Stenelmis crenata* are in larger streams, especially those with stabilized flows and substrates. *P. tardella* is usually associated with aquatic mosses. Elmids are long-lived insects and LeSage & Harper (1976) found that both *O. latiusculus* and *P. tardella* spend two years in the larval and one in the adult stage in Quebec. The three Newfoundland species occur in Quebec (LeSage & Harper 1975). *O. latiusculus* and *P. tardella* are primarily Appalachian, extending north into eastern Canada, while *S. crenata* has a broad range east of the Great Plains (Brown 1972).

The family Helodidae is represented by at least three species of *Cyphon* but their specific identity has not been determined. Larvae of these insects have been reported to occur in small, shallow, detritus-rich pools(Doyen & Ulrich 1978). The adults are terrestrial, frequently found on aerial stems of emergent vegetation as well as on littoral plants. This is the most poorly known of the aquatic beetle families and little is known of their ecology or distribution in Newfoundland.

The family Chrysomelidae constitutes a large group of phytophagus species. Although many species are associated with hydrophytes, only the members of the subfamily Donaciinae can be considered truely aquatic, and this only in the immature stages. For example, *Galerucella nymphaeae* feeds on the leaves of *Nuphar* and *Nymphaea* but all life stages are restricted to the upper surface of the leaves. The larvae of *Donacia* feed on the submerged stems and roots of aquatic vascular plants, principally of the genera *Nuphar, Nymphaea, Potamogeton* and *Sparganium.* Certain species may be restricted to a particular genus of host plants while others may have a wide range (Hoffman 1940; Marx 1957). Adults occur on the aerial portions of the host plant but may also feed on other plants (Schaffer 1925). Larvae have the spiracles of abdominal segment 8 produced as a pair of hollow spines with which they pierce the stem of the host plant and tap into the intracellular air. Pupae, which are submerged in silken cocoons, obtain air in the same way. The length of the life cycle of Newfoundland *Donacia* species is not known, but adults have been recorded as spending up to ten months in the pupal case prior to emerging (Leech & Chandler 1956). Adult occurrence of island species spans the entire growing season and some adults overwinter in terrestrial sites. The wide Newfoundland and continental distributions of the aquatic chrysomelidae reflects the wide distributions of their host plants.

Water beetles demonstrate almost the full range of distribution patterns known for Newfoundland aquatic insects. Most species have wide island distributions as indicated for the Dytiscidae in Fig. 18: at least 70% of the species are likely to be found in all faunal regions. The richest fauna occurs along the west coast, including the Northern Peninsula. The richness in the west is contributed by: species of northern, boreal and subarctic distribution which occur on the island only on the Northern Peninsula (e.g. *Hygrotus canadensis, Agabus arcticus, Gyrinus opacus*); presumed calcophilic species which have been found only in pools overlying limestones (e.g. *Hygrotus suturalis, H. unguicularis*); species associated with turbulent scoured streams (*Oreodytes laevis*); and adventives or marginally established species (*Hygrotus impressopunctatus, Hydroporus criniticoxis*). Admittedly, aqua-

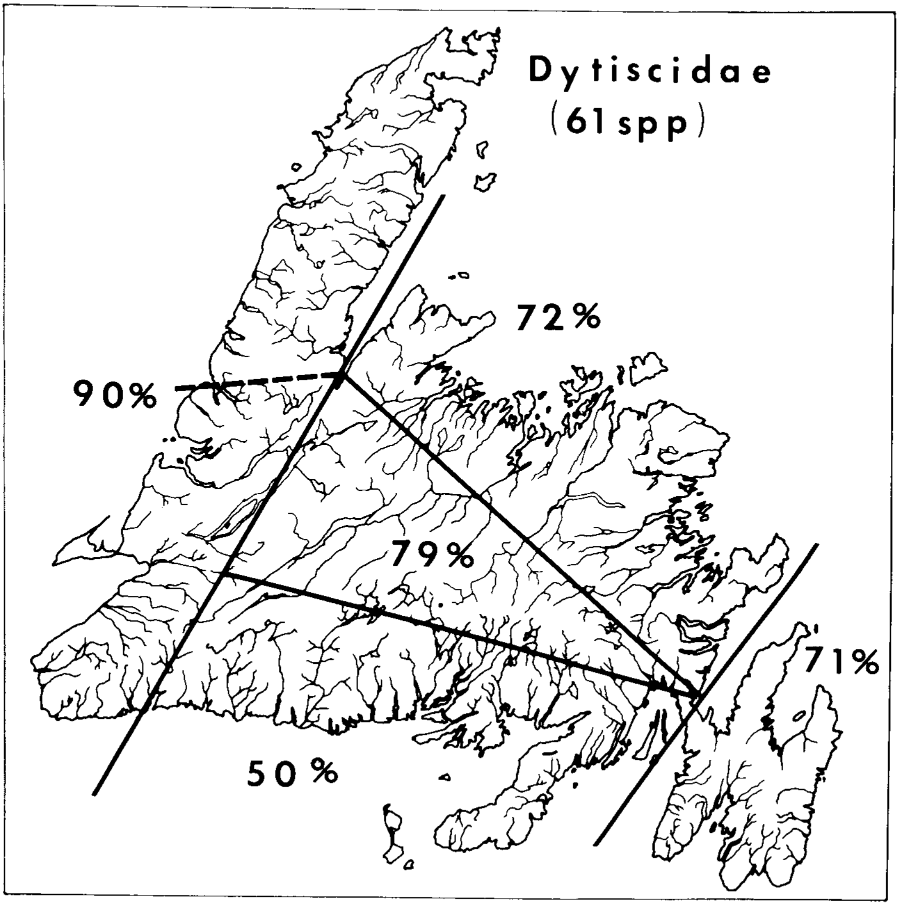


Fig. 18 Percentage representation of the dytiscid beetle fauna in each faunal zone. The low species diversity along the south coast is at least in part due to insufficient collecting.

tic insects, including water beetles, have not been collected as intensively as the island's ground beetles so their distribution is more sketchily known. Nevertheless, it is certain that the progressive faunal reduction from south to north along the Northern Peninsula, as demonstrated by Lindroth (1963) for ground beetles, does not hold for the Dytiscidae nor perhaps for any of the aquatic Coleoptera.

Aside from those species showing the restricted west coast distributions described above, few species show other than general distribution patterns on the island. *Hydroporus acadianus* and *Gyrinus dubius* occur principally on coastal barrens, with most collection records concentrated on exposed peninsular and coastal regions. Several species show Lindroth's (1963) 'continental distribution', that is, occurring principally within the area described by the commercial forests. Such species include *Agabus semipunctatus, A. erichsoni* and *Colymbetes paykulli.*

For the most part, island ranges of ecologically similar species do not suggest geographical partitioning, although there is abundant evidence for this on a microhabitat scale. Perhaps competition between *Hygrotus impressopunctatus* and *H. picatus* is responsible for the restricted range of *H. impressopunctatus*. Interspecific competition between *Ilybius angustior* and *I. biguttulus* can be evoked as the explanation for the apparent disjunction in the island distribution of *I. angustior* (Fig. 19). *I. angustior,* the more northerly distributed of the pair, occurs on the Northern Peninsula and colder coastal or alpine sites while *I. biguttulus* occurs principally in the warmer central portion of the province although there is considerable overlap in ranges in both the west coast and Avalon areas. The wide ecological and geographical range of *I. angustior* on the mainland would suggest that central and eastern Newfoundland possess habitats well within the usual range of conditions occupied by the species (Larson 1975).

The geographical ranges of members of each family are indicated in Table 14. With the exception of the family Elmidae, the majority of the island's species (approximately 70% of the species in each family) have transcontinental distributions. The ranges of these species tend to be centered in the boreal zone with a few entering the low arctic (e.g. *Hydroporus notabilis, Agabus arcticus* and *A. congener*) and others extending into adjacent southern biomes (e.g. *Liodessus affinus, Hygrotus sayi* and *Hydroporus undulatus*). The few species with ranges extending east from the Rocky Mountains are almost exclusively boreal. Species with ranges limited to the continent east of the Great Plains show a variety of distribution patterns, namely: a) boreal in the northeastern United States and adjacent Canada (*Hydroporus aequus, H. brevicornis*); b) boreal and northern deciduous forest biome (*Hydroporus solitarius, Agabus s. seriatus, Ilybius biguttulus, Gyrinus aquiris, G. sayi*); c) generally throughout the forested eastern portion of the continent and entering the southern boreal zone (*Hydroporus pulcher, H. niger*); d) restricted to the Appalachian system and its northern extensions (*Oulimnius latiusculus, Promoresia tardella*); e) or restricted to the Atlantic coast (*Hydroporus carolinus*).

In summary, the island's beetle fauna is derived from species of the eastern boreal region. In fact, it contains almost the full complement of species known from the adjacent regions of Quebec and Labrador (Sherman 1910; Brown 1930, 1932). Some of the species Brown recorded from eastern Quebec

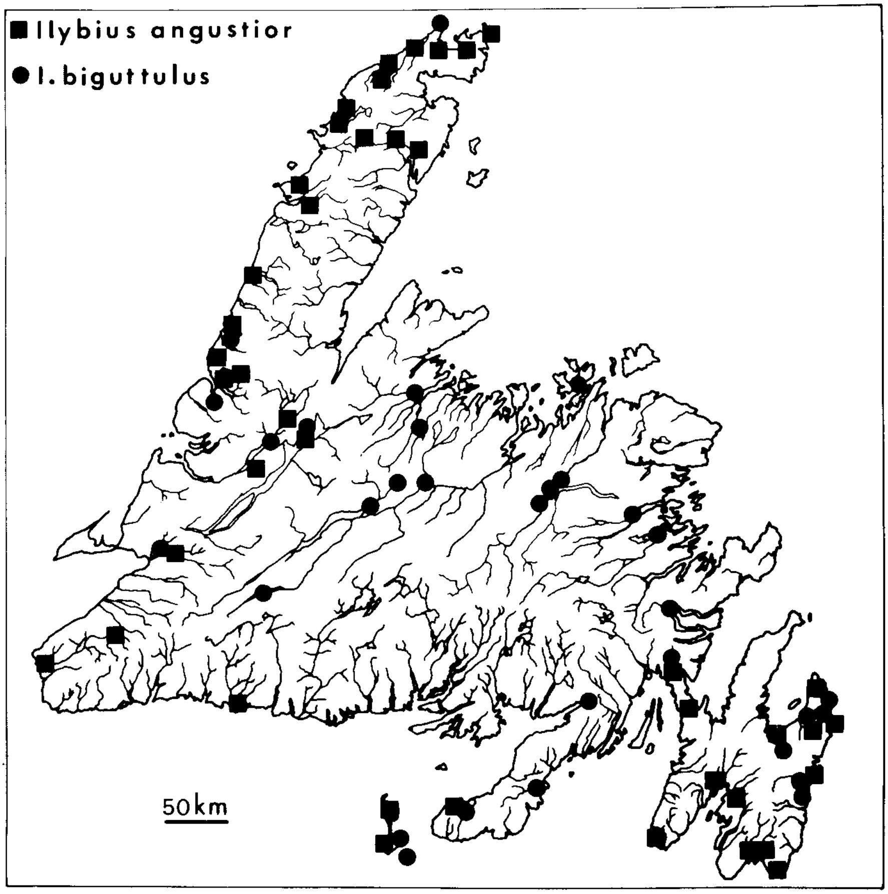


Fig. 19 Collection localities for *Ilybius angustior* and *I. biguttulus*.

Table 14 Summary of the range patterns of Newfoundland species of Coleoptera

Family	Number of species with distribution pattern (%)				
	Transcontinental		East of Rocky Mountains	East of Great Plains	Appalachian and East Coast
	Holarctic	Nearctic			
Haliplidae	–	2 (67)	–	1 (33)	–
Dytiscidae*	15 (25)	29 (49)	4 (9)	6 (10)	4 (7)
Gyrinidae	2 (22)	4 (45)	–	2 (22)	1 (11)
Hydrophilidae*	2 (20)	4 (40)	–	3 (30)	1 (10)
Elmidae	–	–	–	1 (33)	2 (67)
Chrysomelidae	1 (14)	5 (71)	–	–	1 (14)
Total	20	44	4	13	9
Percentage	22	49	4	14	10

* Species totals lower than in checklist as species with poorly known distributions are not included. Family Helodidae omitted for this reason.

but which are absent in Newfoundland, such as *Agabus bifarius*, *A. punctulatus* and *Ilybius subaeneus*, are favoured by warm, eutrophic sites and thus fall into that group of species whose distribution is ecologically limited. It would appear as though the Strait of Belle Isle has had relatively minor influence as a barrier in shaping the island's aquatic beetle fauna.

Wing reduction is uncommon in water beetles and is not known in any Newfoundland species. Adults of the families Chrysomelidae and Helodidae are probably all capable of flight. However, Jackson (1952, 1955) has shown that both genetic and temporal flight muscle reduction occurs frequently in the Dytiscidae. Individuals representing several species of Dytiscidae and Hydrophilidae have been observed flying. Nevertheless, the same factors promoting the development of flightlessness in aquatic Hemiptera would be expected to promote flightlessness in water beetles and it is likely that flight, or the ability of beetles of local populations to fly, will be found to be reduced.

Most Newfoundland species have distributions centered in the boreal zone but a small number are more southerly forms that enter the boreal region in only part of their range. The true boreal fauna contains only a few lotic species, and of these, only *Oreodytes scitulus*, *Deronectes elegans* and *Agabus s. seriatus* can be considered inhabitants of anything other than the slowest flowing, emergent overgrown springs and headwater streams.

On the other hand, the more southerly distributed eastern species have a number of lotic forms. For example *Hydroporus carolinus*, *H. pulcher*, *H. solitarius*, *Oulimnius latiusculus*, *Promoresia tardella* and *Stenelmis crenatus* are all stream species. The lotic Coleoptera fauna is rich in the east but only a few of these species get north into Newfoundland. However, even this small number forms a disproportionately large proportion of the island's lotic fauna.

Order Trichoptera – caddisflies

Caddisflies are an abundant component of the island's aquatic insect fauna. One hundred and sixteen species have been identified to date and it is certain that a significant number of species remain to be discovered. A species list is not presented here as this information is soon to be published elsewhere (Marshall & Larson, in press). However, a general summary of the families present in the fauna, the number of included species and the range of habitats occupied by members of each family are presented in Table 15 and Fig. 20.

The range of habitats occupied by caddisfly larvae is broader than for any other wholly aquatic order of insects and is surpassed only by the Diptera.

Table 15 Distribution patterns of Newfoundland species of caddisflies

Family (n = no. of Newfoundland species)	Transcontinental		East of Rocky Mountains	East of Great Plains	Appalachian and East Coast
	Holarctic	Nearctic			
Rhyacophilidae	–	–	–	3	6
n = 9				33%	67%
Glossosomatidae	1	–	–	–	1
n = 2	50%				50%
Philopotamidae	–	–	–	4	1
n = 5				80%	20%
Polycentropodidae	1	6	–	1	5
n = 13	8%	46%		8%	38%
Hydropsychidae	1	2	2	3	0
n = 8	12%	25%	25%	37%	
Hydroptilidae	–	–	–	3	–
n = 3				100%	
Phryganeidae	–	9	2	2	2
n = 15		60%	13%	13%	13%
Limnephilidae	5	15	3	11	5
n = 39	13%	38%	8%	28%	13%
Odontoceridae	?				
n = 1					
Molannidae	–	–	–	2	–
n = 2				100%	
Leptoceridae	1	3	–	6	1
n = 11	9%	27%		55%	9%
Lepidostomatidae	–	1	1	1	3
n = 6		17%	17%	17%	50%
Brachycentridae	–	–	–	1	–
n = 1				100%	
Helicopsychidae	–	1	–	–	–
n = 1		100%			
Total	9	37	8	37	24
%	7.8	32.2	7.0	32.2	20.9

Larvae occur in both lentic and lotic habitats, permanent as well as temporary, and are among the relatively few insect groups to exist in the deeper waters of ponds and lakes. Aquatic respiration by both larvae and pupae permit these stages to occupy both deep and flowing water habitats. Much of the success of caddisflies has to be attributed to the ability of larvae to spin silk (Wiggins 1977). Silk production is used by many species to produce portable shelters which may be composed of sticks, bark, seeds, pieces cut

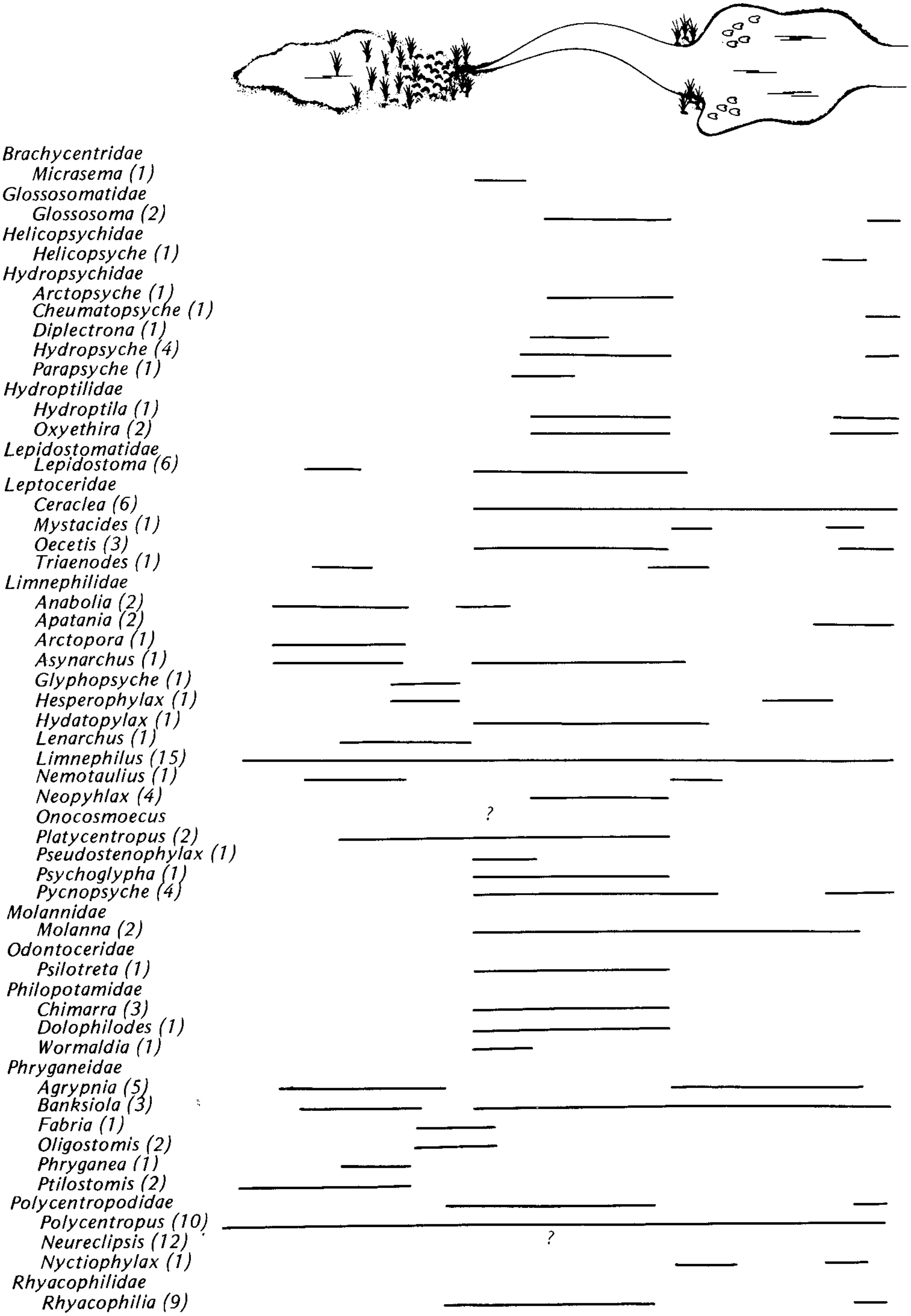


Fig. 20 Ecological distribution of larval Newfoundland Trichoptera.

from living plants, sand and gravel, mollusc shells or even made entirely of silk. Almost any suitable construction material at hand is likely to be used by some caddisfly species. Although each species of caddisfly larva tends to produce a case that is consistent in terms of its architecture and material used, congeners may produce similar cases so that case architecture provides better recognition characteristics at the generic than at the specific level (Wiggins 1977).

Case material, and to a lesser extent form, show parallels with certain habitat types. For example, many stream species construct cases from mineral materials which occur abundantly and in varied sizes in most stream systems and which produce compact high density cases. *Neophylax* and *Glossosoma* larvae, which graze periphyton from exposed rock surfaces in flowing water, construct cases of coarse rock fragments which must provide considerable ballast. Species occurring in protected portions of streams such as pools, eddies and back waters may make cases of less dense material, for example *Hydatophylax* and *Pycnopsyche* larvae (Limnephilidae) use coarse water-logged pieces of wood, bark and twigs arranged longitudinally so that the case has a streamlined aspect. On the other hand, many species found in lentic habitats build bulky cases of leaves or other plant debris (e.g. *Limnephilus* sp., *Platycentropus* sp., Limniphilidae) while others produce thin-walled, light cases (many phryganeid species). The role of such cases may be varied, obviously providing protection, weighting the larvae especially in lotic habitats, and enhancing respiratory efficiency (Wiggins 1977). The variety of case construction and uses of cases are discussed by Wiggins (1977), or in references given by Wiggins.

Another diverse group of Trichoptera larvae uses silk to construct fixed retreats rather than portable cases. These are typically stream species which construct retreats in association with fixed nets which filter food, consisting of water borne particulate material, from the flowing water. Wallace (1975a, b), Wallace & Malas (1976) and Wallace & Merrit (1980) have related the structure and positioning of food capture nets and retreats with the feeding habits of certain net spinning caddisflies. Similar relationships no doubt exist among Newfoundland species. Seasonal occurrence of a species in a stream, position in a drainage basin, position in the substrate and form of retreat and capture net have all been observed to vary between the island's filter feeding species. For example, the spatial distribution of Newfoundland members of the netspinning families Hydropsychidae and Philopotamidae are indicated in Fig. 20.

All major trophic categories are represented among larval caddisflies. Examples of shredders (chewers feeding on living plants or coarse particulate organic material), collectors (filter or suspension feeders and detritivores feeding on fine sediment), grazers (herbivores scraping periphyton from solid substrates) and predators (trophic categories from Cummins 1978) occur in Newfoundland and the diversity of genera in each of these categories in lotic systems is indicated in Table 16. All trophic categories show reduction in diversity in Newfoundland when compared with the fauna of the eastern North American deciduous biome (Wiggins & Mackay 1978) but this reduction is least among the predators. Reduction in other trophic categories is less in cool lotic than in warm lotic habitats as would be expected considering the cool, boreal climate of the island. The major difference however is the impoverishment of grazers relative to shredders (Table 17). Wiggins & Mackay (1978) noted that in the western Cordillera, where coniferous forests predominate, the value of the ratio of shredders to grazers in headwater regions was approximately 1.00 as compared to 1.40 in the east while in downstream sections (warm lotic) the ratio of shredders to grazers was 0.46 in

Table 16 Comparison of numbers of Newfoundland genera of caddisflies (numerator) with the numbers of genera in the Eastern North American deciduous forest biome (denominator). (Based on Wiggins & Mackay 1978, Table 1)

Habitat	Trophic category			
	Shredders	Collectors	Grazers	Predators
Cool lotic	10/21 (48%)	8/12 (67%)	6/15 (40%)	4/5 (80%)
Warm lotic	4/9 (44%)	4/8 (50%)	3/13 (23%)	4/5 (80%)

Table 17 Comparison of relative diversity of Trichoptera genera between trophic categories in Newfoundland and selected continental North American biomes

Habitat	Trophic categories	No. of genera in Nfld	Nfld ratio	E. Deciduous* biome ratio	Cordilleran* ratio
Cool lotic	Shredders Grazers	10:6	1.67	1.40	1.00
(upstream)	Shredders Collectors	10:8	1.25	1.75	2.78
Warm lotic	Shredders Grazers	4:3	1.33	0.67	0.46
(downstream)	Shredders Collectors	4:4	1.00	1.12	1.00

* From Wiggins & Mackay 1978.

the west to 0.67 in the east. Corresponding values for the ratio in Newfoundland are 1.66 in cool lotic habitats and 1.33 in warm lotic sites. Wiggins & Mackay (1978) attributed much of the difference between eastern and western faunas to the effects of streamside vegetation. The coniferous forests of the west provide less shading of the stream promoting plant growth, show less seasonality in input of allochthonous leaves, and their needles have less nutritive value, all factors that would be expected to push the ratio in favor of grazers. Newfoundland, with a boreal vegetation, has conifers as its principal forest and their impact on aquatic systems should be similar to that seen in the west. However, the faunal balance is shifted in the other direction for the percentage of grazers in the fauna is reduced even compared with the eastern deciduous biome. A possible cause for the high shredder to grazer ratio may lie in the low levels of nutrients in Newfoundland water which limit the luxurience of aquatic plant growth and in turn may limit the density and diversity of the grazer fauna. Also, the seasonal pattern of Trichoptera larvae in Newfoundland streams suggests that the island's streams are principally allochthonous input systems. Highest density and diversity of larvae occur in the fall – winter – spring period corresponding to the period of highest allochthonous input from grasses, herbaceous vegetation and deciduous leaves. Over the summer when growth of aquatic vegetation would be expected to be greatest, the fauna of caddisfly larvae is relatively limited and sparse.

The ratio of shredder to collector genera is in turn lower in Newfoundland than in either the deciduous forest biome or the Cordillera. This may also be a reflection on certain peculiarities of Newfoundland streams. Many streams are fed from bogs, areas lacking trees and with low vegetation unlikely to produce the same quantities and quality of allochthonous materials as bankside forest. It might be expected that allochthonous input from such sites would consist of dissolved and fine particulate organic material as opposed to the larger leaves and leaf pieces entering streams in forested areas. Such fine material would be largely unavailable to shredders but could be utilized by collectors. Also, many streams are punctuated by lakes. Lakes provide sites for planktonic development, part of which is swept into the outflow stream to become available to filter feeding populations of insects. It is at such sites that the densest populations of aquatic insects observed on the island exist. Simuliids and net spinning caddisflies may literally produce a continuous carpet on the stream bottom at such sites and several hydropsychid caddisflies have been collected only in these enriched areas.

The larvae of many caddisflies are predaceous, feeding upon a variety of aquatic animals, but mainly other insects. One noteworthy predator is the larva of an unidentified species of *Ceraclea* which feeds on sponges. The larvae burrow in sponge colonies and make cases of silk with sponge spicules incorporated. In the fall, with gemmule formation by the sponges and the disintegration of their superficial tissue, *Ceraclea* larvae pupate and overwinter as pupae. This is one of the very few life histories of an island caddisfly to include overwinter pupation.

Adults of most species can be found from late spring through the summer, particularly late June and July. The short summer season precludes readily distinguishable spring, summer and fall faunae. However, the seasonal occurrence of the adults of a few species deviates from this generalization. Some notable examples are : *Rhyacophila torva* Hagen – an early spring species (Flint 1962), collected only in May; *Apatania niger* Walker has been collected in early June while *A. stigmatella* Zett. flies in September and October; *Limnephilus externus* Hagen, *Glyphopsyche irrorata* Fab. and *Psychoglypha subborealis* Banks are primarily winter species with most collection records in the period September through May; and *Dolophilodes distinctus* Walker adults have been collected almost every month of the year.

With one notable exception, adult caddisflies are active fliers. Winter emerging females of *Dolophilodes distinctus* are wingless while summer females and all males are normally winged (Ross 1944). Three species, *Mystacides sepulchralis* and two brightly colored black and orange or yellow species, *Oligostomis ocelligera* Walker and *O. paradalis* Walker (Phryganeidae) are often found flying during the day but most other species are crepuscular or nocturnal. Many species fly under conditions of low temperatures (*Glyphopsyche irrorata* regularly flies at temperatures near 0°C) and caddisflies comprise a dominant portion of the catch of light traps, especially during periods of cool weather.

Caddisfly distribution on the island is very incompletely known. Most species are generally distributed across the island (Fig. 21) and it is certain that the apparently restricted distributions of many species are collection artifacts. However, the western portion of the island, especially the Long Range Mountains, does have a richer fauna than other regions. Five of the nine *Rhyacophila* species known from the island are restricted to this region. These are species of small, cool, turbulent streams, a habitat more abundantly represented in this region than elsewhere. Several northern boreal or low arctic species, namely *Agrypnia glacialis* Hagen, *Limnephilus minusculus* Banks and *Hesperophylax designatus* Walker, are known only from the Northern Peninsula but this is only a small portion of the total island fauna. For the most part, the lentic and slow or warm water lotic species have general distributions on the island.

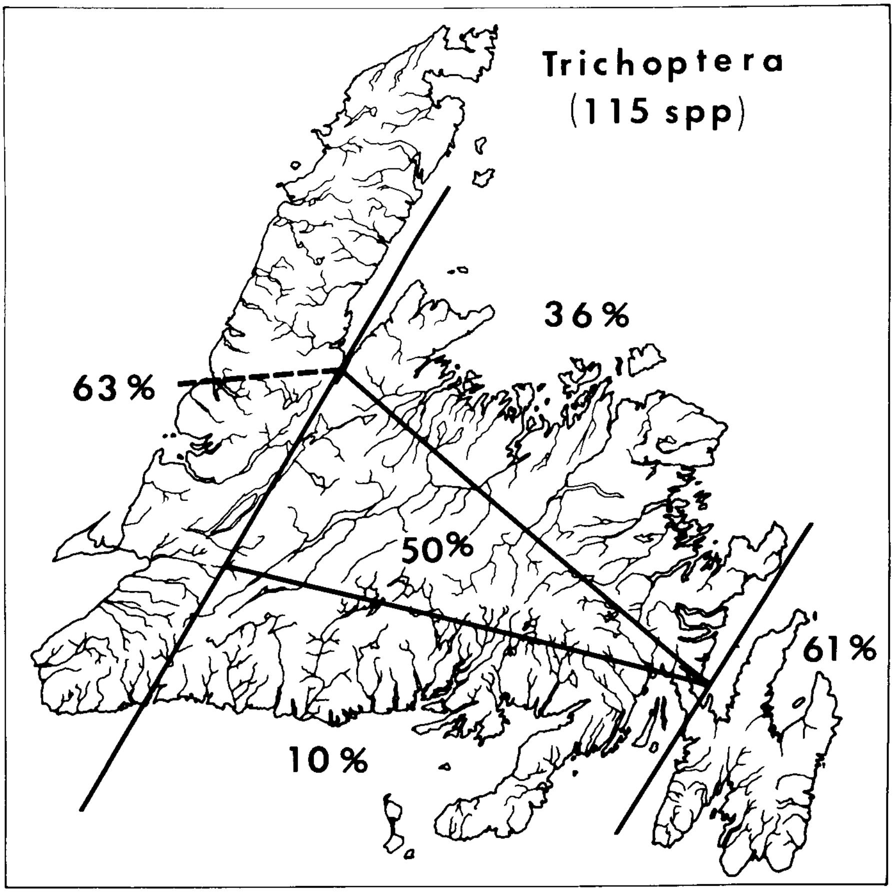


Fig. 21 Percentage representation of the caddisfly fauna in each faunal zone. The low values in both the East and South Coastal areas are at least in part due to insufficient collecting.

Range patterns of the members of the fourteen Newfoundland families of caddisflies are summarized in Table 15. It is apparent that considerable variation exists in the proportion of species showing each distribution pattern between families. For example, of the larger families (containing five or more species) the Limnephilidae, Phyrganeidae and Polycentropodidae each have more than 50 percent of their species transcontinental while the Hydropsychidae, Lepidostomatidae, Philopotamidae and Rhyacophilidae have no, or many fewer, transcontinental members. The proportion of transcontinental species in each family appears to be related to the diversity of habitats

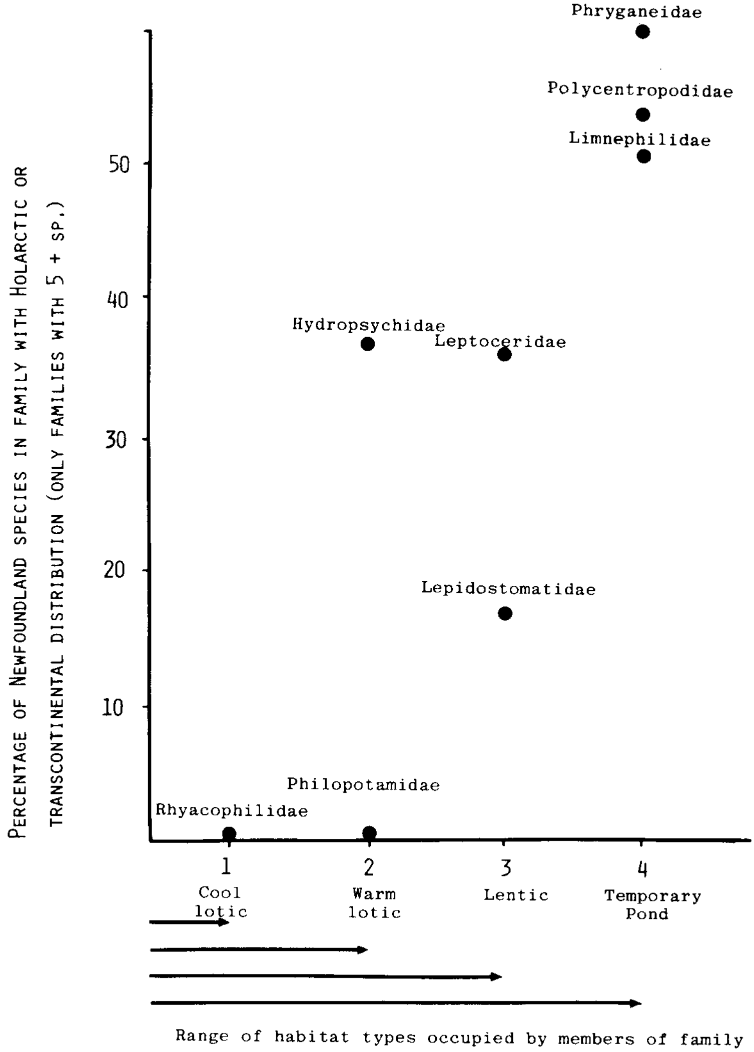


Fig. 22 Relationship between larval habitat and geographical distribution of Newfoundland caddisflies.

occupied by members of the family, and especially by representation of the family in lentic environments (Fig. 22).

Species of cool lotic habitats have the most restricted ranges. For example, of the nine Newfoundland *Rhyacophila*, none are transcontinental and most (67%) are Appalachian. The members of the family Philopotamidae, with greater tolerance for warm water, are more widely distributed in the Carolinian zone while the Hydropsychidae, with species in almost all types of flowing water including both silted and somewhat polluted waters (Ross 1944; Schuster & Etnier 1978), contains species with relatively broad distribution patterns. The family Phryganeidae, which contains mainly lentic or slow flowing water species, has the highest percentage of transcontinental species.

The caddisfly fauna of Quebec is well known (Harper 1979). Most Newfoundland species have been recorded from Quebec but there are a large number of southern Quebec species not known from Newfoundland. In general, most species occuring in Quebec at latitudes and in climatic zones comparable to those of Newfoundland, also occur in Newfoundland. Thus faunal reduction resulting from ocean barriers does not seem important in shaping the island's fauna. Rather the major determinants are probably prevailing ecological conditions consisting of distribution and type of habitats as well as trophic opportunities.

Order Lepidoptera – moths and butterflies

Butterflies and moths do not usually come to mind in the context of aquatic insects. Larvae of many species feed on hydrophilous plants, but lead an entirely aerial existence. The larvae of a relatively few species of moths are aquatic but the degree of adaptation to aquatic life shows considerable variation from one species to the next. Many moth larvae are leaf miners or stem borers in vascular plants and a few species exploit this habitat in hydrophytes, living in the tissue of submerged plants but surrounded by intercellular air. One island species, *Bellura diffusa,* mines in the leaves and petioles of *Nuphar* where it remains in contact with the atmosphere and breathes via modified spiracles. The other two island species of aquatic Lepidoptera are completely adapted aquatic insects. The larvae of both are free-living, case-making forms which feed on the submerged leaves of aquatic plants.

An annotated list of aquatic Lepidoptera known from Newfoundland is presented below (Table 18). The composition and distribution of the island fauna is very incompletely known as there has been no systematic attempt to survey the island's aquatic Lepidoptera fauna. Munroe (1972) records eleven Nymphulinae (Pyralidae) species from Nova Scotia and Prince Edward Island (this includes the two known Newfoundland species) so there is a strong possibility of additional species occurring on the island. The three island species are each known from very few localities but as these are widely spaced, it is likely all three have general island distributions.

Table 18 Annotated list of the aquatic Lepidoptera of Newfoundland

Family NOCTUIDAE

Bellura diffusa (Grote) – Recorded from Newfoundland by Morris 1980. Larvae mine leaves and petioles of *Nuphar*. Wide range east of Great Plains.

Family PYRALIDAE

Munroessa icciusalis avalona Munroe – This subspecies was described by Munroe (1972) from Avalon Peninsula specimens: additional specimens since collected on west coast. Larvae, which lack gills and make biconvex leaf cases, feed on *Potamogeton* and other pond weeds. Transcontinental, with *M. i. avalona* known only from Newfoundland.

Parapoynx maculalis (Clemens) – New record. Larvae possess tufted gills, feed on leaves of *Nuphar* and live in cases made from two irregular *Nuphar* leaf fragments. Wide range east of Great Plains, extending south to Florida (Munroe 1972).

Table 19 Summary of aquatic Diptera fauna of Newfoundland

Family	No. of genera	No. of species	References
Tipulidae	23	115	Alexander 1965a
Ptychopteridae	1	1	Alexander 1965b; Tjeder 1960
Blepharoceridae	1	2	Hogue 1978, pers. comm.
Dixidae	2	2	Colbo & Larson, unpubl.
Chaoboridae	2	3	Borkent 1981, 1979; Mokry, pers. comm.
Culicidae	3	20	Freeman 1952; Pickavance *et al.* 1970; Wood *et al.* 1979; Mokry, pers. comm.
Ceratopogonidae	12	30	Downes & Greiner, pers. comm.
Chironomidae	40		Only generic determinations used as fauna primarily determined from larval identifications. Made by Dr. D. Oliver & Environmental Impact Statements.
Simuliidae	5	22	Shewell 1957; Peterson 1970; Lewis & Bennett 1973; Procunier 1975; Rothfels & Freeman 1977; Colbo, unpubl.
Stratiomyidae	2	2	James 1965; Larson, unpubl.
Tabanidae	4	20	Stone 1938; Freeman 1953; Krogerus *et al.* 1960; Philip 1962; Hudson 1977
Empididae	4	5	Melander 1965; Larson, unpubl.
Dolichopodidae	1	4	Foote *et al.* 1965; Larson, unpubl.
Syrphidae	2	11	Wirth *et al.* 1965; Larson, unpubl.
Coelopidae	1	1	Vockeroth 1965a
Sciomyzidae	4	15	Steyskal 1965
Ephydridae	3	3	Wirth 1965
Sarcophagidae	1	1	Mokry, pers. comm.
Anthomyiidae	1	2	Vockeroth 1965b
Muscidae	3	4	Huckett 1965

Order Diptera – true flies

This is the largest order of aquatic insects on the island. The biting flies are well known due to their importance as pests of man and animals, while on the other hand most groups of the very large family Chironomidae have been identified to genus only. Thus. the taxonomic knowledge of the island's aquatic Diptera is very uneven. In addition, many of the groups of flies contain species which range from fully aquatic to terrestrial. This may occur even within a genus such as *Tipula* and therefore, similarities of ecological distribution may not reflect phyletic relationships. Thus, the combination of limited knowledge of the taxonomy and the scant information on the ecology of many species has made the drawing up of a list of aquatic Diptera difficult and somewhat arbitrary. Nevertheless, it is felt a table of numbers of genera and species with references to literature sources provides a starting point for further investigations. Species have been counted if known to be aquatic or to belong to a genus with aquatic representatives, although if a species of one of the latter genera is known to be terrestrial it has not been included. The number of genera and species in Table 19 is therefore tentative.

Considerable variation exists with respect to the adaptation of immature stages to aquatic environments. For example, immature forms of the families Simuliidae, Chironomidae and Blepharoceridae respire through the cuticle; many species of the family Tupulidae have spiracles variously developed while larvae and pupae of Culicidae are air breathing using a short siphon to reach the atmosphere.

The range of larval feeding types is diverse, including filter feeders, scrapers, collectors, shredders and predators. The degree of trophic specialization in each family may be varied. For example, the Simuliidae are almost exclusive fitlter feeders although some graze: the island's Culicidae are collectors and gatherers while larvae of the closely related family Chaoboridae are predaceous; the family Chironomidae contains species showing the complete spectrum of feeding habits. Larvae of the family Sciomyzidae, with 15 Newfoundland species, are predator-parasites presumably feeding on slugs and snails, thus some may be predators of terrestrial gastropods. It appears that no major trophic group of Diptera has been excluded from the island but it cannot be stated if the diversity within each group is comparable to that of the mainland.

A number of species on the island live in specialized habitats. Larvae of three species of Diptera inhabit the water-filled leaves of pitcher plants (*Sarracenia pupurea*): namely *Wyeomyia smithii* (Culicidae), a filter feeder; *Metriocnemus knabi* (Chironomidae), a detritus feeder; and *Blaesoxipha* *fletcheri* (Sarcophagidae), a scavenger on drowned insects. Larvae of two mosquito species occupy special habitats: *Aedes cantator* in saline rock pools along the coast and *A. atropalpus* in rock pools along rivers. Larvae and pupae of the two Newfoundland species of Blephariceridae are specially modified to adhere to exposed rock surfaces in fast currents. The larvae of the phantom crane fly, *Bittacomorpha clavipes,* lives in plant debris in iron-rich flocculent deposits in depositional areas of small springs and first order streams. Although few detailed studies on Newfoundland aquatic Diptera have been made, it is clear that all freshwater habitats, as well as some salt water splash pools and wrack are colonized by at least one or more dipteran species.

Eight of the island's 20 species of mosquitos are not recorded among the 25 species known from Nova Scotia, while all but *Aedes stimulans* occur in Labrador which has a total of 27 species, including members of the genera *Anopheles* and *Culex* which have no representation on the island. Most species have wide island distributions although four species have been collected only on the tip of the Northern Peninsula. The Newfoundland mosquito fauna is dominated by widespread boreal species. Only one island species, *Aedes stimulans,* is considered by Maire & Aubin (1980) as a species limited to the temperate zone in Quebec. Most Newfoundland mosquitoes are univoltine and only two species, *A. atropalpus* and *A. cantator,* are regularly multivoltine (Wood *et al.* 1979; Mokry, pers. comm.); *Aedes cinereus* can be multivoltine but the number of annual generations in Newfoundland is unknown. All species overwinter in the egg stage except *Culiseta impatiens,* which overwinters as an adult (Wood *et al.* 1979) and *Wyeomyia smithii* which overwinters as a third instar larva.

Egg development in females varies from species which are fully autogenous (*Wyeomyia smithii*), to species autogenous in the first cycle (*Aedes nigripes*), to anautogenous species requiring a blood meal (this probably includes the majority of the island species). Host selection varies between species with some taking avian blood and others mammalian blood with a variable degree of specificity.

Temporal separation of species occurs locally (Mokry, pers. comm.) and has been recorded in the same species in Quebec (Maire & Aubin 1976). Larvae of the various species of mosquito show habitat separation related to vegetation cover and duration of inundation of the habitat (i.e. between temporary pools, muskeg, forest edge and pools within the forest) (Maire & Aubin 1976; Wood *et al.* 1979). Maire (1980) reviewed the ecology and distribution of all arctic species, both in the Palearctic and Nearctic regions, and found that each species occupied a similar habitat throughout its range.

The apparently considerable dispersal power of mosquitoes suggests that the majority of the northern species capable of survival on the island and present in nearby areas of Labrador are probably on the island. The failure to find four species on the Avalon Peninsula known from the Northern Peninsula may indicate some zonation in the island's fauna, but this will require further studies.

The taxonomy of the Simuliidae is such that a detailed analysis of species distribution is not possible. Many of the 22 species known from Newfoundland are known to actually consist of complexes of sibling species (Rothfels 1979). For example, two species, *Simulium venustum* and *S. verecundum,* form a complex with a total of five cytotypes on the island. One of these, the *S. venustum* cytotype CEF/G, is probably the species *S. truncatum* of Europe (Rothfels *et al.* 1978). All simuliid species recorded on the island except *Prosimulium pleurale* are known from the eastern provinces and New England states. *P. pleurale* is found in large northern boreal rivers in the east and mountain rivers in the west. Four species of *Prosimulium,* namely *P. decemarticulatum* (Twinn), *P. fontanum* S. & D., *P. multidentatum* (Twinn) and *P. ursinum* (Edwards) occur in Labrador but not in Newfoundland (Peterson 1970). The fact that only one species of the genus *Cnephia* has been found here indicates there is an impoverishment of the northern members of that genus, which is of interest because *C. ornithophilia,* the species on the island, is southern in distribution (Procunier 1975). On the other hand, there are also species of *Simulium* which occur in the Maritime Provinces, such as *S. jenningsi,* which are not recorded on the island.

Larvae of all species of *Prosimulium, C. ornithophilia* and *Stegopterna mutata* are present from late fall to early spring. One species, *Simulium vittatum,* has larvae present all year round. One of the *S. venustum* cytotypes is univoltine with larvae occurring early in the spring. A member of the *S. verecundum* complex hatches in late spring and is multivoltine. Simuliid species are also separated spatially by differing preferences for stream size, current velocity and lentic outflows (Back & Harper 1979). Three common species are almost exclusively restricted to pond or lake outlets and build up enormous populations there but the species are partially separated by current velocity preference (Colbo 1979).

As with mosquitoes some blackflies are autogenous, such as *P. mixtum, S. vittatum, St. mutata* and *S. decorum.* These develop in winter and summer, at lake outlets and in the mainstream of rivers, thus autogeny is not related to habitat or season in which larval development occurs. On the island all types of simuliid life history patterns are present, colonization of all normal simuliid habitats occurs and both bird and mammalian feeding species are present. It is interesting that only *P. mixtum* of the two closely related species, *P. mixtum* and *P. fuscum* S. & D., occurs on the island, although *P. fuscum* occurs on all the surrounding areas of the mainland (Peterson 1970). *P. mixtum* is autogenous in Newfoundland but not in Ontario, where it co-exists with *P. fuscum* which is autogenous (Rothfels & Freeman 1977; Davis & Syme 1958).

The family Tabanidae with 20 species has a considerably reduced fauna from the 142 for Canada and the 60 recorded from the Maritimes (Lewis & Bennett 1977; Thomas 1978, 1980). Four of the species in Newfoundland have not been recorded from the Maritimes although ranges given by Philip (1962) suggest they occur there. Four Newfoundland species are not recorded from Labrador and appear limited to the northeastern United States and Atlantic Canada. Perhaps they do not occur in Labrador and colonized the island from the south. On the other hand, five species have been recorded in Labrador but not on the island, suggesting the reduced insular tabanid fauna is also lacking in northern taxa.

One hundred and fifteen species of Tipulidae recorded from the island occur in genera known to be aquatic or include aquatic members. However, as little or nothing is known about the immature stages of most species, it is not possible to determine what proportion of these are truly aquatic. The most interesting feature of this family in Newfoundland is the high proportion of the species which are eastern. Also, the vast majority of species are known from more southerly localities with Newfoundland being on the northern end of the range in marked contrast to the family Culicidae. Although a comparatively large number of tipulid species has been recorded from the island, the fauna is still impoverished compared to more southerly regions where considerably more members of this diverse family are found. Although tipulids occur in the majority of Newfoundland aquatic habitats, the habitat, life history and distribution of the majority of the island species are unknown.

Little can be said about other Newfoundland Diptera as they are poorly known and collected. Certainly many more species are present than have been recorded. This is true in families such as Chironomidae, Empididae, Dolichopodidae, Ephydridae, Stratiomyidae and Muscidae. Therefore, it is in this order that the greatest amount of study is required before a good understanding of the island's aquatic insect fauna can be achieved.

Discussion

Reviewing factors shaping local faunas, Eastrop (1978) stated, 'The amount of diversity in a locality is dependent upon the number of opportunities offered and difficulties presented by the environment, the accessibility of the locality to neighbouring populations, the nature of these neighbouring populations and the length of time the locality has been available to them'. Each of these factors, as well as their interactions, has obvious relevance in the development of the Newfoundland fauna, contributing to the faunal composition and patterns of diversity described in the previous section.

All of these faunal determinants are difficult to express quantitatively, especially in a region such as Newfoundland where faunal exploration is still in its infancy. Nevertheless, patterns observed in the distribution and composition of the fauna seem to show several themes which if not adequately defined to produce testable hypotheses, still have heuristic value in the initial stages of organizing biogeographic and ecological observations. These themes, which basically follow Eastrop's conclusions, are developed below.

1. The aquatic insect fauna of the island has an essentially boreal aspect. This is not surprising as the climatic conditions and flora (Rowe 1972) of Newfoundland, as well as those of the most proximate floral and faunal source areas, are characteristically boreal. However, cold maritime influences produce significant climatological deviations from conditions experienced at continental boreal sites: for example, seasonality and climatic extremes are dampened, sunlight decreased and frost-free season lengthened. These climatic effects exert a diverse influence on the biota. Certain northern boreal and subarctic species enter the province on the Northern Peninsula and extend varying distances south along the Long Range Mountain system. On the other hand, certain Carolinian species enter the southwestern and central regions of the province where the climate is warmest (Damman 1976). These form only a small transitional aspect in the fauna for most species are widely distributed giving a high level of faunal homogeneity over the island. Features producing regionality in the insect fauna are principally local topographic, edaphic and climatic effects.

2. The obvious reason for reduction of the island fauna is its isolation from the mainland – the faunal source area. Isolation appears to have had a direct effect on the Plecoptera fauna for the Labrador fauna is richer than that of the island. Isolation effects are not as obvious for other groups. The Odonata fauna of Nova Scotia is much richer than that of Newfoundland so perhaps the broad Cabot Strait is limiting. However, the Odonata fauna of Labrador is impoverished and is comparable to that of Newfoundland suggesting ecological influences are also involved. The orders Hemiptera, Coleoptera and Trichoptera do not show significant reduction due to insularity as the island fauna shows high similarity with Labrador and northern Quebec.

The ability of many recently introduced Maritime species to cross the Cabot Strait in relatively short periods of time (Lindroth 1963; Larson & Jackson 1980) as well as observations on dispersing spruce budworm moths (Greenbank *et al.* 1980) suggest that faunal isolation of Newfoundland from the mainland is more apparent than real, at least for flying insects.

3. Reduction in habitat diversity is a major factor limiting faunal diversity. Precipitation in excess and in a relatively even yearly pattern produces consistency of habitat, reducing opportunities for development of transitory niches. It produces permanently filled basins preventing evaporative enrichment and making prolonged seasonal flooding of terrestrial vegetation uncommon, a process responsible for much of the richness of vernal ponds elsewhere. Bog development homogenizes lentic habitats and results in low nutrient levels, low pH and low productivity which reduce diversity.

4. The aquatic fauna is balanced in terms of the range of major adaptive types present. For example, the only aquatic orders lacking are the Neuroptera and Megaloptera. Within the other orders, the important Nearctic families are represented as well as the dominant temperate genera. What tend to be lacking are narrowly specialized higher taxa. Also, species diversity is reduced in the more generalized groups. As pointed out under the discussion of Ephemeroptera, the fauna is composed of a relatively small number of species (compared to a continental area), each of rather generalized habits and separated from other similar species by distinct ecological, spatial or temporal gaps. This pattern applies principally to phytophagus groups, less to detritivores and least to predators, suggesting that trophic habits influence population features and diversity. It is possible that the low autochthonous production of Newfoundland water is a major factor contributing to lack of species diversity in at least phytophagus forms. This finds some support in the seasonal pattern of ocurrence of the fauna. Among the shredder and collector faunas, most have fall-winter-spring growth periods taking advantage of allochthonous inputs while a much less diverse fauna shows a summer growth pattern. Exceptions exist in the Hemiptera and Coleoptera but these groups have long-lived, feeding adults and do not show the larval-adult trophic specializations shown by most other aquatic insects.

5. Geographical ranges of island species are related to habitat. Lentic species tend to be wide ranging forms that are transcontinental in boreal and north temperate latitudes, occurring through much of the glaciated portion of the continent where abundant habitat exists. Lotic species are more restricted, many with ranges limited in various degrees to the continent east of the Great Plains. Some of the patterns termed southern, Carolinian or Appalachian are shown by species that reach their maximum northern distri-

bution in or near Newfoundland but whose main range is in the forested eastern portion of the continent south of the boreal region. In a very general sense, lentic species have an east-west axis of distribution while lotic species tend to have a north-south axis of distribution.

6. Most of Newfoundland was glaciated in the Wisconsinan glacial period, thus most of the fauna is of relatively recent origin, not exceeding 10,000 years in age (Prest 1970). However, there is some evidence for nunatuk refugial areas in the western Long Range Mountains (Grant 1969) and suggestion of offshore Grand Bank refugia (Lindroth 1963). Although paleontological studies have indicated that insects are evolutionarily conservative and that little evidence of Pleistocene speciation exists (Cooper 1970; Matthews 1980; Morgan and Morgan 1980), the presence of endemic forms in Newfoundland as well as distributionally disjunct natural populations would provide evidence for the existence of refugial areas. No population of Newfoundland aquatic insect is known to be strongly disjunct. However, a few regional endemics have been identified, namely:

Aeshna i. interrupta – Newfoundland and Magdalen Island populations are recognizable but only weakly differentiated by unstable characteristics (Walker 1958). It is probably best not to put much weight on this population for the species is notably variable across its range.

Hydroporus acadianus – known only from Newfoundland and Cape Breton Island. The species belongs to a taxonomically difficult and confused group and until the taxonomy is understood, this apparently limited distribution should be regarded with caution.

Gyrinus dubius – a distinctive gyrinid species known only from Newfoundland, Labrador and adjacent Quebec.

Munroesa icciusalis avalona – a weakly differentiated subspecies based on pale ground color of wings. The subspecies was described from the Avalon Peninsula but specimens from S. W. Newfoundland approach the Nova Scotian form in color.

The lack of evidently disjunct populations and the small list of regional endemics does not provide much evidence for the existence of glacial refugial areas. However, both *H. acadianus* and *G. dubius* are species typical of the coastal barrens and thus are ecologically good candidates for survival in coastal periglacial habitats. The distribution and ecology of these species warrants careful study.

7. Man has had a significant impact on the composition of Newfoundland's terrestrial insect fauna through introductions, inadvertant or purposeful (Lindroth 1963; Commonwealth Agricultural Bureau 1971; Morris 1982). This influence has not extended into the aquatic environment. No island

species of aquatic insect (with the possible exception of certain Diptera, e.g. *Eristalis arbustorum* and *E. tenax*) is likely to have had an anthropogenic origin. The fauna is derived entirely from the fauna of eastern continental North America. Aquatic species in common with the Palaearctic region are transcontinental in North America (this does not include the marine littoral species, e.g. *Cercyon litoralis* Gyll.), thus transatlantic dispersal mechanisms need not be invoked.

8. Human impacts have probably had only minor and localized effects on the island's insect fauna. Pollution, ranging from slight eutrophication to gross contamination with industrial wastes, to widespread application of forest insecticides, affects large areas of the province. Alteration of drainage systems and patterns for log transporation, hydroelectric generation or domestic consumption have also affected many drainage basins. However, the impacts of such activities on the fauna have probably been only minor or localized to date. The lack of regionality in the fauna and the wide habitat and distributional ranges of most species makes the fauna as whole resilient to such impacts.

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References

Alexander, C. P., 1965a. Family Tipulidae, pp 16–90. In: A catalog of the Diptera of America north of Mexico (ed. A. Stone *et al.*). U.S. Dept. Agric., Agric. Handb. 276 pp.

Alexander, C. P., 1965b. Family Ptychopteridae, pp 97–98. In: A catalog of the Diptera of America north of Mexico (ed. A. Stone *et al.*). U.S. Dept. Agric., Agric. Handb. 276 pp.

Allen, H. L., 1971. Primary productivity, chemo-organotrophy, and nutritional interactions of epiphytic algae and bacteria on macrophytes in the littoral of a lake. Ecol. Monogr. 41: 97–127.

Allen, R. K., 1980. Geographic distribution and reclassification of the subfamily Ephemerellinae (Ephemeroptera: Ephemerellidae), pp 71–81. In: Advances in Ephemeroptera biology (ed. J. F. Flannagan & K. E. Marshall). New York: Plenum.

Allen, R. K. & Edmunds, G. F., Jr., 1962. A revision of the genus *Ephemerella* (Ephemeroptera, Ephemerellidae) V. The subgenus *Drunella* in North America. Misc. Publ. Entomol. Soc. Am. 3(5): 146–179.

Allen, R. K. & Edmunds, G. F., Jr., 1963. A revision of the genus *Ephemerella* (Ephemeroptera: Ephemerellidae) VII. The subgenus *Eurylophella*. Can. Entomol. 95: 597–623.

Allen, R. K. & Edmunds, G. F., Jr., 1965. A revision of the genus *Ephemerella* (Ephemeroptera, Ephemerellidae) VIII. The subgenus *Ephemerella* in North America. Misc. Publ. Entomol. Soc. Am. 4(6): 243–282.

Anderson, R. D., 1971. A revision of the Nearctic representatives of *Hygrotus* (Coleoptera: Dytiscidae). Ann. Entomol. Soc. Am. 64: 503–512.

Arnett, R. H., 1963. The beetles of the United States. Washington: Catholic Univ. of Am. Press. 1112 pp.

Bach, C. & Harper, P. P., 1979. Succession saisonière émergence, voltinisme et répartition de mouches noires des Laurentides (Diptera: Simuliidae). Can. J. Zool. 57: 627–639.

Balfour-Browne, J., 1948. The aquatic Coleoptera of Newfoundland and Nova Scotia. Can. Entomol. 80: 156–165.

Bednarik, A. F. & McCafferty, W. P., 1979. Biosystematic revision of the genus *Stenonema* (Ephemeroptera: Heptageniidae). Can. Bull. Fish. Aquat. Sci. 201: 73 pp.

Benke, A. C., 1976. Dragonfly production and prey turnover. Ecology 57: 915–927.

Berner, L., 1959. Newfoundland Mayflies (Ephemeroptera). Opusc. Entomol. 24: 212–214.

Biström, O., 1978. Dytiscidae from Newfoundland and adjacent areas (Coleoptera). Ann. Entomol. Fenn. 44: 65–71.

Borkent, A., 1979. Systematics and bionomics of the species of the subgenus *Schadonophasma* Dwyar and Shannon (*Chaoborus*: Chaoboridae). Quaest. Entomol. 15: 122–255.

Borkent, A., 1981. The distribution and habitat preferences of the Chaoboridae (Culicomorpha: Diptera) of the Holarctic Region. Can. J. Zool. 59: 122–123.

Bowers, W., 1980. Observation and collection of *Agrion aequabile* (Say) from Badger Newfoundland. Osprey 11(5): 70–74.

Brinck, P., 1958. On a collection of stoneflies (Plecoptera) from Newfoundland and Labrador. Opusc. Entomol. 23: 47–58.

Brinck, P., 1960. On a collection of Gyrinidae (Coleoptera) from Newfoundland and Labrador. Opusc. Entomol. 25: 76–81.

Brittain, J. E., 1980. Mayfly strategies in a Norwegian subalpine lake, pp 179–186. In: Advances in Ephemeroptera biology (ed. J. F. Flannagen & K. E. Marshall). New York: Plenum.

Brooks, A. R. & Kelton, L. A., 1967. Aquatic and semiaquatic Heteroptera of Alberta, Saskatchewan, and Manitoba (Hemiptera). Mem. Entomol. Soc. Can. 51: 92 pp.

Brown, H. P., 1972. Aquatic dryopoid beetles (Coleoptera) of the United States. U. S. Environ. Prot. Agency, Biota of Freshwater Ecosystems, Identification Manual No. 6. 82 pp.

Brown, W. J., 1930. Coleoptera of the north shore of the Gulf of the St. Lawrence. Can. Entomol. 62: 231–237; 239–246.

Brown, W. J., 1932. Additional notes on the Coleoptera of the north shore of the Gulf of the St. Lawrence. Can. Entomol. 64: 198–205.

Bruce, W., 1976. Age, growth, maturity and food habits of landlocked salmon (*Salmo salar*) in Soldiers Pond, a Newfoundland lake. Can. Fish. Mar. Serv. Tech. Rep. No. 668. 16 pp.

Burks, B. D., 1953. The mayflies or Ephemeroptera of Illinois. Bull. Illinois Nat. Hist. Survey 26: 216 pp.

Calabrese, D. M., 1977. The habitats of *Gerris* F. (Hemiptera: Heteroptera: Gerridae) in Connecticut. Ann. Entomol. Soc. Am. 70: 979–983.

Campbell, J. M., 1979. Coleoptera, pp 357–387. In: Canada and its insect fauna (ed. H. V. Danks). Mem. Entomol. Soc. Can. 108.

Cannings, R. A. & Stuart, K. M., 1977. The dragonflies of British Columbia. B. C. Prov. Mus. Handb. 35. 254 pp.

Clifford, H. F., 1969. Limnological features of a northern brown-water stream, with special reference to the life histories of the aquatic insects. Amer. Midl. Nat. 82: 578–597.

Cobb, D. G. & Flannagan, J. F., 1980. The distribution of Ephemeroptera in northern Canada, pp 155–166. In: Advances in Ephemeroptera biology (ed. J. F. Flannagan & K. E. Marshall). New York: Plenum.

Colbo, M. H., 1979. Distribution of winter-developing Simuliidae (Diptera), in Eastern Newfoundland. Can. J. Zool. 57: 2143–2152.

Commonwealth Agricultural Bureau, 1971. Biological control programmes against insects and weeds in Canada. Commonw. Inst. Biol. Control, Technical Communication No. 4. 266 pp.

Cooper, E. R., 1970. Interpretation of Quaternary insect fossils. Annu. Rev. Entomol. 15: 97–120.

Corbet, P. S., 1962. A biology of dragonflies. London: Witherby. 247 pp.

Corbet, P. S., 1974. Entomological reflections. Bull. Entomol. Soc. Can. 6: 70–75.

Corbet, P. S., 1980. Biology of Odonata. Annu. Rev. Entomol. 25: 189–217.

Cummins, K. W., 1978. Ecology and distribution of aquatic insects, pp 29–31. In: An introduction to the aquatic insects of North America (ed. R. W. Merritt & K. W. Cummins). Dubuque, Iowa: Kendall/Hunt.

Damman, A. W. H., 1976. Plant distribution in Newfoundland especially in relation to summer temperatures measured with the sucrose inversion method. Can. J. Bot. 54: 1561–1585.

Dance, K. W., 1979. Stream insects of western Newfoundland. Osprey 10(4): 64–75.

Davies, D. M., & Syme, P., 1958. Three new Ontario blackflies of the genus *Prosimulium* (Diptera: Simuliidae). II. Ecological observations and experiments. Can. Entomol. 90: 744–759.

Davis, C. C., 1972. Plankton dynamics in a Newfoundland lake. Verh. Int. Ver. Limnol. 18: 278–283.

Davis, C. C., 1976. Simultaneous quantitative comparison of planktonic Crustacea in two Newfoundland boreal lakes. Int. Rev. Gesamten Hydrobiol. 61: 807–823.

Dosdall, L. M. & Lehmkuhl, D. M., 1979. Stoneflies (Plecoptera) of Saskatchewan. Quaest. Entomol. 15: 3–116.

Doyen, J. T. & Ulrich, G., 1978. Aquatic Coleoptera, pp 203–231. In: An introduction to the aquatic insects of North America (ed. R. W. Merritt & K. W. Cummins). Dubuque, Iowa: Kendall/Hunt.

Drake, C. J. & Harris, H. N., 1934. The Gerrinae of the Western Hemisphere (Hemiptera). Ann. Carnegie Mus. 23: 179–240.

Eastop, V. F., 1978. Diversity of the Sternorrhyncha within major climatic zones, pp 71–88. In: Diversity of insect faunas (ed. L. A. Mound & N. Waloff). Symposium of the Royal Entomological Society of London, 5. Oxford: Blackwell.

Edmunds, G. F., Jr., Jensen, S. L. & Berner, L., 1976. The mayflies of North and Central America. U. of Minnesota Press. 330 pp.

Fall, H. P., 1922a. A review of the North American species of *Agabus*. Mount Vernon, N.Y. 36 pp.

Fall, H. P., 1922b. The North American species of *Gyrinus*. Trans. Am. Entomol. Soc. 47: 269–306.

Fall, H. P., 1923. A revision of the North American species of *Hydroporus* and *Agaporus*. Mount Vernon, N. Y. 129 pp.

Fall, H. P., 1927. The North American species of *Ilybius*. Entomol. News 38: 281–285.

Flint, O. S., 1962. Larvae of the caddisfly genus *Rhyacophila* in eastern North America (Trichoptera: Rhyacophilidae). Proc. U.S. Nat. Mus. 113: 465–493.

Foote, R. H., Coulson, J. R. & Robinson, H., 1965. Family Dolichopodidae, pp 482–530. In: A catalog of Diptera of America north of Mexico (ed. A. Stone *et al.*). U.S. Dept. Agric., Agric. Handb. 276.

Forsberg, C., 1967. Dissolved organic carbon in some lakes in Uppland, Sweden. Oikos 18: 210–216.

Freeman, T. N., 1952. Interim report of the distribution of the mosquitoes obtained by the Northern Insect Survey. Can. Def. Res. Board Environ. Protection Tech. Rep. 1: 1–2. 43 maps.

Freeman, T. N., 1953. Interim report of the distribution of the tabanids obtained by the Northern Insect Survey. Can. Def. Res. Board, Environ. Protection Tech. Rep. 4: 1–3. 35 maps.

Galewski, K., 1971. A study on morphobiotic adaptations of European species of Dytiscidae (Coleoptera). Pol. Pismo Entomol. 41: 488–702.

Grant, D. R., 1969. Surficial deposits, geomorphic features and late Quaternary history of the terminus of the Northern Peninsula of Newfoundland and adjacent Quebec–Labrador. Marit. Sediments 5: 123–125.

Greenbank, D. O., Schaefer, G. W. & Rainey, R. C., 1980. Spruce budworm (Lepidoptera: Tortricidae) moth flight and dispersal: new understanding from canopy observations, radar and aircraft. Mem. Entomol. Soc. Can. 110. 49 pp.

Gyselman, E. C., 1980. The mechanisms that maintain population stability of selected species of Ephemeroptera in a temperate stream, pp 309–319. In: Advances in Ephemeroptera biology (ed. J. F. Flannagan & K. E. Marshall), New York: Plenum.

Harper, P. P., 1973. Life histories of Nemouridae and Leuctridae in Southern Ontario (Plecoptera). Hydrobiologia 41: 309–356.

Harper, P. P., 1978. Plecoptera, pp 105–118. In: An introduction to the aquatic insects of North America (ed. R. W. Merritt & K. W. Cummins), Dubuque, Iowa: Kendall/Hunt.

Harper, P. P., 1979. Liste préliminaire des Trichoptères (insects) du Quebec. Ann. Soc. Entomol. Que. 24(3): 148–172.

Hitchcock, S. W., 1974. The Plecoptera or stoneflies of Connecticut. Conn. Geol. Nat. Hist. Surv. Bull. 107: 262 pp.

Hoffman, C. E., 1940. Morphology of the immature stages of some northern Michigan Donaciini (Chrysomelidae, Coleoptera). Pap. Mich. Acad. Arts Sci. 25: 243–290.

Hogue, L. C., 1978. The net-winged midges of Eastern North America with notes on new taxonomic characters in the family Blephariceridae (Diptera). Los. Ang. Cty. Mus. Contrib. Sci. 291: 1–41.

Huckett, H. C., 1965. Family Muscidae, pp 869–915. In: A catalog of the Diptera of America north of Mexico (ed. A. Stone *et al.*). U.S. Dept. Agric., Agric. Handb. 276.

Hudson, A., 1977 Additional records of Newfoundland Tabanidae. Can. Entomol. 109: 639–640.

Hungerford, H. B., 1948. The Corixidae of the Western Hemisphere (Hemiptera). Univ. Kans. Sci. Bull. 23: 827 pp.

Hynes, H. B. N., 1976. The biology of Plecoptera. Annu. Rev. Entomol. 21: 135–153.

Jackson, D. J., 1952. Observations on the capacity for flight of water beetles. Proc. R. Entomol. Soc. Lond. (A) 27: 57–70.

Jackson, D. J., 1955. Observations on flying and flightless water beetles. J. Linn. Soc. Lond. Zool. 43: 18–42.

James, H. G., 1970. Immature stages of five diving beetles (Coleoptera: Dytiscidae), notes on their habits and life history, and a key to aquatic beetles of vernal woodland pools in southern Ontario. Proc. Entomol. Soc. Ont. 100: 52–97.

James, M. T., 1965. Family Stratiomyidae, pp 299–319. In: A catalog of the Diptera of America north of Mexico (ed. A. Stone *et al.*). U.S. Dept. Agric., Agric. Handb. 276.

Jamieson, A., 1974a. Results of water analysis on selected streams and lakes of Newfoundland and Labrador, 1972–1973. Can. Fish. Mar. Serv. Data Record Series No. NEW/D-74-3. 32 pp.

Jamieson, A., 1974b. A water quality atlas for streams and lakes of insular Newfoundland. Can. Fish. Mar. Serv. Data Record Series No. NEW/D-74-4. 22 pp.

Jamieson, G. S. & Scudder, G. G. E., 1979. Predation in *Gerris* (Hemiptera): reactive distance and locomotion rates. Oecologia 44: 13–20.

Jansson, A. & Scudder, G. G. E., 1974. The life cycle and sexual development of *Cenocorixa* species (Hemiptera, Corixidae) in the Pacific Northwest of North America. Freshw. Biol. 4: 73–92.

Kerekes, J., 1973. The influence of water renewal on the nutrient supply in small, oligotrophic (Newfoundland) and highly eutrophic (Alberta) lakes, pp 383–400. In: Proceedings, Lakes of Western Canada Symposium. University of Alberta, Edmonton.

Kerekes, J., 1974. Limnological conditions in five small oligotrophic lakes in Terra Nova National Park, Newfoundland. J. Fish. Res. Board Can. 31: 555–583.

Kerekes, J., 1977. Factors relating to annual planktonic primary production in five small oligotrophic lakes in Terra Nova National Park, Newfoundland. Int. Rev. Gesamten Hydrobiol. 62: 345–370.

Kerekes, J., 1978. Aquatic Resources Inventory, Gros Morne National Park, Newfoundland, Part 5. Limnological conditions. Canadian Wildlife Service, Atlantic Region, Halifax. 155 pp.

Krogerus, H., Lindroth, C. H., Palmen, E. & Tuomikoski, R., 1960. Zoological results of two expeditions to Newfoundland and adjacent areas. Ann. Entomol. Fenn. 26: 58–59.

Larson, D. J., 1975. The predaceous water beetles (Coleoptera: Dytiscidae) of Alberta: systematics, natural history and distribution. Quaest. Entomol. 11: 245–498.

Larson, D. J. & Jackson, B. S., 1980. First record of a Cinnabar Moth, *Tyria jacobaeae*, in Newfoundland. Can. Field-Nat. 94: 343–344.

Lawton, J. H., 1970. Feeding and food energy assimilation in larvae of the damselfly *Pyrrhosoma nymphula* (Sulzer). J. Anim. Ecol. 39: 669–689.

Leech, H. B., 1970. *Copelatus glyphicus* (Say) and *Suphisellus bicolor* (Say), water beetles new to California and presumably introduced (Coleoptera: Dytiscidae and Noteridae). Proc. Calif. Acad. Sci. 37: 237–248.

Leech, H. B. & Chandler, H. P., 1956. Aquatic Coleoptera, pp 293–371. In: Aquatic insects of California (ed. R. L. Usinger). Berkeley: U. of Calif. Press.

Lehmkuhl, D. M., 1979. Ephemeroptera, pp 305–308. In: Canada and its insect fauna (ed. H. V. Danks). Mem. Entomol. Soc. Can. No. 108.

LeSage, L. & Harper, P. P., 1975. Les Dryopoides aquatiques du Québec (Coléoptères). Ann. Soc. Entomol. Que. 20: 157–168.

LeSage, L. & Harper, P. P., 1976. Cycles biologiques d'Elmidae (Coléoptères) du ruisseaux des Laurentides, Québec. Ann. Limnol. 12: 139–174.

Lewis, D. J. & Bennett, G. F., 1973. The blackflies (Diptera: Simuliidae) of insular Newfoundland. I. Distribution and bionomics. Can. J. Zool. 51: 1181–1187.

Lewis, D. J. & Bennett, G. F., 1977. Biting flies of the eastern Maritime Provinces of Canada. I. Tabanidae. Can. J. Zool. 58: 1582–1600.

Lindberg, H., 1958. Hemiptera Heteroptera from Newfoundland, collected by the Swedish–Finnish Expedition of 1949 and 1951. Acta Zool. Fenn. 96: 1–25.

Lindroth, C. H., 1955. The Carabid beetles of Newfoundland. Opusc. Entomol. Suppl. 12. 160 pp.

Lindroth, C. H., 1963. The fauna history of Newfoundland. Illustrated by Carabid beetles. Opusc. Entomol. Suppl. 23. 112 pp.

Maire, A., 1980. Ecologie comparée des espèces de Moustiques holarctiques (Diptera: Culicidae). Can. J. Zool. 58: 1582–1600.

Maire, A. & Aubin, A., 1976. Inventaire et classification écologique des biotopes à larves de Moustiques (Culicidae) de la région de Radisson (Territaine de la Baine de James Quebec). Can. J. Zool. 54: 1979–1991.

Maire, A. & Aubin, A., 1980. Les Moustiques de Québec (Diptera: Culicidae) essai de synthèse écologique. Mem. Soc. Entomol. Que. 6: 1–107.

Marshall, J. S. & Larson, D. J. (in press). The adult caddisflies (Trichoptera: Insecta) of Newfoundland. Memorial Univ. Nfld. Occas. Pap. Biol.

Marx, E. J. F., 1957. A review of the subgenus *Donacia* in the western hemisphere (Coleoptera, Donaciidae). Bull. Am. Mus. Nat. Hist. 112: 195–278.

Matthews, J. V., 1980. Tertiary land bridges and their climate: backdrop for development of the present Canadian insect fauna. Can. Entomol. 112: 1089–1103.

McDunnough, J., 1930. The Ephemeroptera of the north shore of the Gulf of St. Lawrence. Can. Entomol. 62: 54–62.

McDunnough, J., 1931. The *bicolor* group of the genus *Ephemerella* with particular reference to the nymphal stages (Ephemeroptera). Can. Entomol. 63: 30–42.

McDunnough, J., 1932. Further notes on the Ephemeroptera of the north shore of the Gulf of St. Lawrence. Can. Entomol. 64: 78–91.

Melander, A. L., 1965. Family Empididae, pp 446–481. In: A catalogue of the Diptera of America north of Mexico (ed. A. Stone *et al.*) U.S. Dept. Agric., Agric. Handb. 276.

Merritt, R. W. & Cummins, K. W., 1978. An introduction to the aquatic insects of North America. Dubuque, Iowa: Kendall/Hunt. 441 pp.

Morgan, A. V. & Morgan, A., 1980. Faunal assemblages and distributional shifts of Coleoptera during the late Pleistocene in Canada and the northern United States. Can. Entomol. 112: 1105–1128.

Morihara, D. K. & McCafferty, W. P., 1979. The *Baetis* larvae of North America (Ephemeroptera: Baetidae). Trans. Am. Entomol. Soc. 105: 139–221.

Morris, R. F., 1969. Occurrence of the damselfly, *Agrion aequabile*, in Newfoundland. Can. Entomol. 101: 163.

Morris, R. F., 1980. Butterflies and moths of Newfoundland and Labrador. The Macrolepidoptera. Agric. Can. Publ. 1691. 407 pp.

Morris, R. F., 1982. Introduced terrestrial insects. In: Biogeography and ecology of the Island of Newfoundland (ed. G. R. South) The Hague: Dr. W. Junk.

Munroe, E., 1972. The moths of America north of Mexico. Fascicle 13.1A. Pyraloidea, Pyralidae (Part). London: Classey. 134 pp.

Murray, A. R. & Harmon, T. J., 1969. A preliminary consideration of the factors affecting the productivity of Newfoundland streams. Fish. Res. Board Can. Tech. Rep. 130. 312 pp.

Neave, F., 1930. Migratory habits of the mayfly, *Blasturus cupidus* Say. Ecology 11: 568–576.

Newman, E., 1839. On the synonymy of Perlites, together with brief characters of the old, and a few new species. Ann. Mag. Nat. Hist. 3: 32–37, 84–90.

Pajunun, V. I., 1977. Population structure in rock-pool Corixidae (Hemiptera, Corixidae) during the reproductive season. Ann. Zool. Fenn. 14: 26–47.

Peterson, B. V., 1970. The *Prosimulium* of Canada and Alaska (Diptera: Simuliidae). Mem. Entomol. Soc. Can. 69: 216 pp.

Philip, D. B., 1962. Records of Tabanidae from Labrador and Newfoundland. Opusc. Entomol. 28: 230–236.

Pickavance, J. R., Bennett, G. F. & Phipps, J., 1970. Some mosquitoes and blackflies from Newfoundland. Can. J. Zool. 48: 621–624.

Popham, E. J., 1964. The migration of aquatic bugs with special references to the Corixidae (Hemiptera, Heteroptera). Arch. Hydrobiol. 60: 450–496.

Porter, T. R., Riche, L. G. & Traverse, G. E., 1974. Catalogue of rivers in insular Newfoundland. Vols. A, B, C, D. Can. Fish. Mar. Serv. Data Record Series No. NEW/D-74-9.

Prest, V. K., 1970. Quaternary geology of Canada, pp 676–764. In: Geology and economic minerals of Canada (ed. R. J. W. Douglas). Dept. E. M. R. & Info. Can., Ottawa.

Pritchard, G., 1964. The prey of adult dragonflies in northern Alberta. Can. Entomol. 96: 821–825.

Procunier, W. S., 1975. A cytological study of two closely related blackfly species *Cnephia doctensis* and *Cnephia ornithophilia*. Can. J. Zool. 53: 1627–1637.

Reynolds, J. D., 1975. Feeding in corixids (Heteroptera) of small alkaline lakes in central B. C. Verh. Int. Ver. Limnol. 19: 3073–3078.

Ricker, W., 1944. Some Plecoptera from the far North. Can. Entomol. 76: 174–185.

Ricker, W., 1947. Stoneflies of the Maritime Provinces and Newfoundland. Trans. R. Can. Inst. 26: 401–414.

Ricker, W., 1952. Systematic studies in Plecoptera. Indiana Univ. Publ. Ser. 18: 1–200.

Ricker, W., 1964. Distribution of Canadian stoneflies. Gewasser u. Abwasser 34/35: 50–71.

Ricker, W., Malouin, R., Harper, P. & Ross, H. H., 1968. Distribution of Quebec stoneflies. Nat. Can. (Que.) 95: 1085–1123.

Ricker, W. & Ross, H. H., 1968. North American species of *Taeniopteryx* (Plecoptera, Insecta). J. Fish. Res. Board Can. 25: 1423–1439.

Ross, H. H., 1944. The caddisflies, or Trichoptera, of Illinois. Ill. Nat. Hist. Surv. Bull. 23(1): 326 pp.

Rothfels, K. H., 1979. Cytotaxonomy of blackflies (Simuliidae). Annu. Rev. Entomol. 24: 507–539.

Rothfels, K. H., Fereday, R. & Kaneps, A., 1978. A cytological description of sibling species of *Simulium venustum* and *S. verecundum* with standard maps for the subgenus *Simulium* Davies. Can. J. Zool. 56: 1110–1128.

Rothfels, K. H. & Freeman, D. M., 1977. The salivary gland chromosomes of seven species of *Prosimulium* in the *mixtum* (III1-1) group. Can. J. Zool. 55: 482–507.

Rowe, J. S., 1972. Forest regions of Canada. Can. For. Serv. Publ. 1300. 172 pp.

Sailer, R. I., 1948. The genus *Trichocorixa* (Corixidae, Hemiptera), pp. 289–407. In: The Corixidae of the Western Hemisphere (Hemiptera) (ed. H. B. Hungerford). Univ. Kans. Sci. Bull. 32: 827 pp.

Schaeffer, C., 1925. Revision of the new world species of the tribe Donaciini of the coleopterus family Chrysomelidae. Brooklyn Mus. Sci. Bull. 3: 45–165.

Schuh, T., 1967. The shore bugs (Hemiptera: Saldidae) of the Great Lakes Region. Contrib. Am. Entomol. Inst. 2: 1–35.

Schuster, G. A. & Etnier, D. A., 1978. A manual for the identification of the larvae of the caddisfly genera *Hydropsyche* Pictet and *Symphitopsyche* Ulmer in eastern and central North America (Trichoptera: Hydropsychidae). U.S. Environ. Prot. Agency Report EPA-600/4-78-060. 128 pp.

Scudder, G. G. E., 1975. Field studies on the flight muscle polymorphism of *Cenocorixa* (Hemiptera: Corixidae). Verh. Int. Ver. Limnol. 19:3064–3072.

Scudder, G. G. E., 1976. Water-boatmen of saline waters (Hemiptera: Corixidae), pp 263–289. In: Marine insects (ed. L. Cheng). Amsterdam: North Holland.

Scudder, G. G. E., 1977. An annotated checklist of the aquatic and semi-aquatic Hemiptera (Insecta) of British Columbia. Syesis 10: 31–38.

Scudder, G. G. E., 1979. Hemiptera, pp 329–348. In: Canada and its insect fauna. (ed. H. V. Danks). Mem. Entomol. Soc. Can. 108.

Scudder, G. G. E. & Meredith, J., 1972. Temperature induced development in the indirect flight muscle of adult *Cenocorixa* (Hemiptera: Corixidae). Dev. Biol. 29: 330–336.

Sherman, J. D., 1910. List of Coleoptera of Labrador. J. N. Y. Entomol. Soc. 18: 173–197.

Shewell, G. E., 1957. Interim report on distributions of black flies (Simuliidae) obtained in the Northern Insect Survey. Can. Def. Res. Board Environ. Protection Tech. Rep. 7: 1–3, 47 maps.

Smetana, A., 1974. Revision of the genus *Cymbiodyta* Bed. (Coleoptera: Hydrophilidae). Mem. Entomol. Soc. Can. 93. 113 pp.

Southwood, T. R. E., 1978. The components of diversity, pp 19–40. In: Diversity of insect fauna (eds. L. A. Mound & N. Waloff) London: Blackwell.

Spence, J. R. & Scudder, G. G. E., 1980. Habitats, life cycles, and guild structure among water striders (Heteroptera: Gerridae) on the Fraser Plateau of British Columbia. Can. Entomol. 112: 779–792.

Spence, J. R., Spence, D. H. & Scudder, G. G. E., 1980. Submergence behaviour in *Gerris*: Underwater basking. Am. Midl. Nat. 103: 385–391.

Steyskal, G. C., 1965. Family Sciomyzidae, pp 685–695. In: A Catalog of the Diptera of America north of Mexico (ed. A. Stone *et al.*) U.S. Dept. Agric., Agric. Handb. 276.

Stone, A., 1938. The horseflies of the subfamily Tabaninae of the Nearctic region. U.S. Dept. Agric. Misc. Publ. 305: 171 pp.

Thomas, A. W., 1978. Records of horseflies and deerflies (Diptera: Tabanidae) in New Brunswick. Can. J. Zool. 56: 1546–1549.

Thomas, A. W., 1980. New records for some Canadian horseflies and deerflies (Diptera: Tabanidae). Entomol. News 91: 59–60.

Tjeder, B., 1960. The 'phantome cranefly' in Newfoundland (Diptera, Ptychopteridae). Opusc. Entomol. 25: 145.

Tones, P. I., 1975. The life cycle of *Trichocorixa verticalis interiores* Sailer (Hemiptera, Corixidae) with special reference to diapause. Freshw. Biol. 7: 31–36.

Usinger, R. L., 1963. Aquatic Hemiptera, pp 182–228. In: Aquatic insects of California (ed. R. L. Usinger). U. of Calif. Press.

Valle, K. J., 1955. Odonata from Newfoundland. Ann. Entomol. Fenn. 21: 57–60.

Vannote, R. L., Minshall, G. W., Cummins, K. W., Sedell, J. S. & Cushing, C. E., 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. 37: 130–137.

Vepsälänen, K., 1974. The life cycles and wing lengths of Finnish *Gerris* Fabr. species (Heteroptera, Gerridae). Acta Zool. Fenn. 141. 73 pp.

Vockeroth, J. R., 1965a. Family Coelopidae, pp 679–680. In: A catalog of the Diptera of America north of Mexico (ed. A. Stone *et al.*) U.S. Dept. Agric., Agric. Handb. 276.

Vockeroth, J. R., 1965b. Subfamily Scatophaginae, pp 826–843. In: A catalog of the Diptera of America north of Mexico (ed. A. Stone *et al.*) U.S. Dept. Agric., Agric. handb. 276.

Vollenweider, R. A., 1968. The scientific basis of lake and stream eutrophication, with particular reference to phosphorus and nitrogen as eutrophication factors. Techn. Rep. Organ. Econ. Coop. Dev. Paris. DAS/CSI/68, 27. 182 pp.

Walker, E. M., 1953. The Odonata of Canada and Alaska. Vol. I. Univ. of Toronto Press. 292 pp.

Walker, E. M., 1958. The Odonata of Canada and Alaska. Vol. II. Univ. of Toronto Press. 318 pp.

Walker, E. M. & Corbet, P. S., 1975. The Odonata of Canada and Alaska. Vol. III. Univ. of Toronto Press. 307 pp.

Walker, F., 1853. Catalogue of the specimens of Neuropterous insects in the collection of the British Museum 3: 477–585.

Walley, G. S., 1930. Heteroptera from the North Shore of the Gulf of St. Lawrence. Can. Entomol. 62: 75–81.

Walley, G. S., 1932. A second report on Hemiptera from the North shore of the Gulf of St. Lawrence. Can. Entomol. 64: 152–153.

Wallace, J. B., 1975a. The larval retreat and food of *Arctopsyche*, with phylogenetic notes on feeding adaptations in Hydropsychidae larvae (Trichoptera). Ann. Entomol. Soc. Am. 68(1): 167–173.

Wallace, J. B., 1975b. Food partitioning in net-spinning Trichoptera larvae: *Hydropsyche venularis, Cheumatopsyche etrona*, and *Macronema zebratum* (Hydropsychidae). Ann. Entomol. Soc. Am. 68(3): 463–472.

Wallace, J. B. & Malas, D., 1976. The fine structure of capture nets of larval Philopotamidae (Trichoptera), with special emphasis on *Dolophilodes distinctus*. Can. J. Zool. 54(10): 1788–1802.

Wallace, J. B. & Merritt, R. W., 1980. Filter-feeding ecology of aquatic insects. Annu. Rev. Entomol. 25: 103–122.

Wallis, J. B., 1926. Some new Coleoptera. Can. Entomol. 58: 89–95.

Wallis, J. B., 1933. Revision of the North American species, (north of Mexico), of the genus *Haliplus*, Latreille. Trans. R. Can. Inst. 19: 1–76.

Waters, T. F., 1961. Standing crop and drift of stream bottom organisms. Ecology 42: 532–537.

Whitehouse, F. C., 1948. Catalogue of the Odonata of Canada, Newfoundland and Alaska. Trans. R. Can. Inst. 27: 3–56.

Wiggins, G. B., 1977. Larvae of the North American caddisfly genera (Trichoptera). Univ. of Toronto Press. 401 pp.

Wiggins, G. B. & Mackay, R. J., 1978. Some relationships between systematics and trophic ecology in Nearctic aquatic insects, with special reference to Trichoptera. Ecology 59(6): 1211–1220.

Wilcox, R. S., 1980. Ripple communication. Oceanus. 23: 61–68.

Williams, D. D., 1979. Aquatic habitats of Canada and their insects, pp 211–234. In: Canada and its insect fauna (ed. H. V. Danks). Mem. Entomol. Soc. Can. No. 108.

Williamson, E. B., 1906. Dragonflies (Odonata) collected by Dr. D. A. Atkinson in Newfoundland, with notes on some species of *Somatochlora*. Entomol. News 17: 133–139.

Wirth, W. W., 1965. Family Ephydridae, pp 734–759. In: A catalog of the Diptera of America north of Mexico (ed. A. Stone *et al.*). U.S. Dept. Agric., Agric. Handb. 276.

Wirth, W. W., Sedman, Y. S. & Weems, H. V., Jr., 1965. Family Syrphidae, pp 557–625. In: A catalog of the Diptera of America north of Mexico (ed. A. Stone *et al.*). U.S. Dept. Agric., Agric. Handb. 276.

Wiseman, R., 1973. The limnology and sport fish populations of selected Avalon Peninsula lakes. Can. Fish. Mar. Serv., Progress Report. No. 100. 167 pp.

Wiseman, R. & Whelan, W. G., 1974. The limnology and sport fish populations of ten Avalon Peninsula lakes. Can. Fish. Mar. Serv. Data Report. No. NEW/D-74-7. 107 pp.

Wood, D. M., Dang, P. T. & Ellis, R. A., 1979. The mosquitoes of Canada (Diptera: Culicidae). The insects and arachnids of Canada. Part 6. Agric. Can. Pub. 1696. 390 pp.

Young, E. G., 1965a. The incidence of flight polymorphism in British Corixidae and description of the morphs. J. Zool. (Lond.) 146: 567–576.

Young, E. G., 1965b. Flight muscle polymorphism in British Corixidae: ecological observations. J. Anim. Ecol. 34: 353–390.

Yoxall, W. H., 1980. The water balance in Newfoundland. Water Resour. Bull. 16: 1030–1033.

Zimmerman, J. R., 1980. Use of multivariant procedures in studies of species problems in the *sculptilis* group of North American *Colymbetes* (Coleoptera: Dytiscidae). Coleopt. Bull. 34: 213–226.

Zimmerman, J. R. & Smith, R. L., 1975. The genus *Rhantus* (Coleoptera: Dytiscidae) in North America. Part I. General account of the species. Trans. Am. Entomol. Soc. 101: 33–123.