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LONG-TERM CHANGE IN RIVER INVERTEBRATE COMMUNITIES

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ABSTRACT

Finding rules that govern species distribution and coexistence is a fundamental aim of ecological research. The rapidly expanding and increasingly mobile human race is challenging our understanding of some these rules. Using long-term macroinvertebrate data collected from two river systems with contrasting legacies from human activity, this thesis investigates drivers of change in community structure and function, mechanisms underpinning these changes and how these changes affect the accurate assessment of the ecological condition of river systems.

The reformation of the river invertebrate communities within the River Clyde system was not predicted by the simple improving measures of water physico-chemistry or life history characteristics of the re-colonising community. This has serious implications for the accurate assessment of river health which is at present largely reliant on the physio-chemical tolerance of macroinvertebrates to indicate prevailing environmental conditions. It is argued that reference condition predictions, like those obtained from the RIVPACS programme, may not be suitable when assessing the ecological health of a river subjected to long-term modification from human activity, like the River Clyde.

Significant differences in the stable isotope signatures of resident and colonising populations of *Rhyacophila dorsalis* (a predatory Trichopteran) provided insight into some mechanisms underlying differences between reforming communities. Trophic position estimates for some colonising populations of *R. dorsalis* were shown to be lower than expected considering their predatory status and, colonisation patterns were significant in predicting changes in occupied trophic position.

The River Endrick is recognised internationally in terms of biodiversity. Over the last 50 years, the diversity of macroinvertebrate fauna of the river has significantly reduced, five species have become locally extinct and there has been a significant change in the distribution of 29 other species. The macroinvertebrate community in the headwater of the river has undergone a dramatic change in structure and function. The contrasting changes to the headwater community and changes in the structure and function of the macroinvertebrate community in the river system require further investigation.

This thesis demonstrates the importance of investigating long-term change.

TOP 100 WORDS

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AUTHORS DECLARATION

I hereby declare that the work on this thesis has not been submitted as part of any other degree and is based on individual research carried out by myself. Any published or unpublished material not of my own has been acknowledged in the text.

Jennifer Ann Dodd

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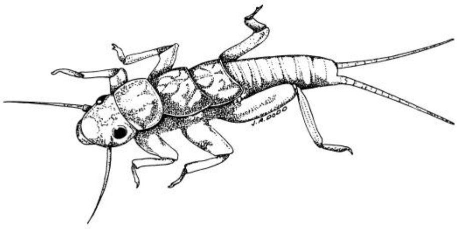

Founded on observations made by the angling fraternity of the River Clyde, the work contained within this thesis has only been made possible through the support of numerous individuals.

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Etheridge, E. C. 2009 Aspects of the conservation biology of *Coregonus lavaretus* in Britain. PhD thesis, University of Glasgow

CHAPTER 1 General Introduction

Freshwater systems are losing diversity faster than terrestrial and marine systems (Dudgeon, et; al., 2006) and rivers particularly, have been highlighted recently as being under the greatest threat from pervasive human activity (Vörösmarty, et al., 2010).

River systems cover only 0.006% of the surface of the earth, yet freshwater ecosystems contain 6% of all described species (Dudgeon, et al., 2006). Their importance as the largest source of renewable fresh water has, at least in part, driven global efforts to restore river systems impacted by human activity (Vörösmarty, et al., 2010), although effort is highly skewed towards developed regions (e.g. USA and Western Europe) (Vörösmarty, et al., 2010). Despite their importance in economic and species diversity terms, there is still only a poor understanding of the processes by which animal communities in these systems respond to change. This is partly due to a shortage of long-term studies detailing change over appropriate time scales (Jackson & Füreder, 2006).

1.1 Community ecology in a contemporary setting

Finding rules that govern species distribution and coexistence is a fundamental aim of ecological research. Through empirical studies (Odum, 1953, Huston, 1994) and theoretical modelling (May, 1973; Drake, 1990) we now have a better understanding of some of the fundamental rules that govern species distribution and how ‘natural’ communities are assembled (Chesson, 2000), but there are still significant gaps in our understanding (Bell, 2000; Tilman, 2004; Adler, et al., 2007).

Eutrophication, pollution, non-native species introductions, habitat destruction and water abstraction are all well documented threats to the riverine biota (Carpenter, el. al., 1992). Each of these stressors are common globally but usually occur in relative isolation (Malmqvist & Rundle, 2002). Contrasting this, global climate change has the potential to effect unprecedented changes over the coming century on a global scale (Parmesan & Yohe, 2002; Parmesan, 2006), through a combination of temperature changes, alterations to atmospheric and hydrological conditions and species invasions (IPCC, 2007). The complicated interactions of these myriad stressors influencing freshwater systems means disentangling relative influence and uncovering mechanisms which are driving change in species distribution and community structure and function is at best, challenging.

To assess ecological change accurately, target restoration effort appropriately and forecast the effects of human activity on ecosystem structure and function, an understanding of how communities are modified as a result of local and global environmental change is required.

1.2 Restoration ecology

Restoration of disturbed systems is a complex process influenced by multiple deterministic and stochastic factors. Physical disturbance can alter the availability of suitable habitat (e.g. the physical removal of habitat during a catastrophic flood (Snyder & Johnson, 2006)), changes to available resources will affect species assemblage and abundance (e.g. fire affecting the nutrients available in soil (Coetsee, et al., 2010)), the dispersal abilities and proximity of colonising populations will influence colonisation patterns (Sutherland, 1974; Palmer, 1996; Urban & De Meester, 2009), and changes to species range as a result of changes to global climate (e.g. Hickling et al., 2005) and the increased rate of colonisation and establishment of non-native species (Cohen & Carlton, 1998; Lockwood, et al., 2009) will also affect the structure and function of a community (Suding et al., 2004; Olsson et al., 2009; Paillex, et al., 2009).

The ability to accurately measure the success of restoration is essential. Accurate assessment of communities undergoing restoration or those deemed to have been restored is dependent on the predictability of restored community structure. If the order in which species colonise a community is deterministic, given certain environmental conditions, then the results of colonisation (i.e. community structure) is predictable. However, if the assembly of a community is sensitive to the arrival order of colonists, community structure is much less predictable.

Recently, through empirical investigation, the effect of historic changes to community structure and function has been highlighted as significant in influencing contemporary community structure and function (Fukami & Morin, 2003; Ledger, et al., 2006; Svensson, et al., 2009). Influences of early colonists can affect the successful establishment of additional species, for example, through direct competition for resources where one competitor consumes more resources and prevents another from establishing (Tillman, 1980); through intraguild predation, where one competitor predates upon another (Price & Morin, 2004); or through interference competition, where one species directly interferes with another by killing or hindering feeding (Chao & Levin, 1981; Amarasekare, 2002). These priority or, founder effects have been shown to significantly affect the structure of reassembled communities (Ledger, et al., 2006; Gerla, et al., 2009).

Much research in this area has either focussed on the effects of invasive species on community structure and function (Suding et al., 2004; Erlandsson, et al., 2006; Ehrenfeld, 2010), or has been confined to plant communities (Baer et al,. 2004; MacDougall & Turkington, 2005). To further our understanding of community formation and the resultant effects on community function, investigation of drivers and mechanisms that underpin community formation in a 'natural' setting is necessary.

Currently, many assessments of riverine community recovery adopt the 'reference condition approach' (Stoddard, et al., 2006), where communities that have been impacted by human activities are compared to a perceived ideal, often taking the form of either an analogous community deemed to be free of impact or to a historic reference community. If consideration is made of the many influences affecting river communities and the effects from founder members, is the 'reference condition approach' still appropriate or even feasible?

1.3 Measuring ecological change

Currently, the most commonly cited indicator of ecological change is 'biodiversity'. The etymology of this word reveals its modern origin from the late 1960s and it is frequently used in place of more clearly defined, long established terms, such as species richness and species diversity (Purvis & Hector, 2000).

Species richness is a measurement of the number of species within a given area. It is usually acutely determined from samples of the whole community and, when combined with a measurement of relative abundance, a measure of species diversity is produced. These measurements are two of the most common ecological indicators used to detect change within ecosystems as they can be applied to the entire species range within an area, from soil microbes to top predators, or it can be used to focus on an organism subset (eg. woodland fungi) (Huston, 1994).

Species richness and diversity vary naturally. Gradients of species richness and diversity have been studied widely in ecology and many of the drivers underlying species distributions have been well described. For example, diversity gradients associated with latitude show opposing relationships with terrestrial and aquatic systems. The diversity of terrestrial systems increases with increasing latitude, while aquatic diversity decreases with increasing latitude. These gradients have been linked with temperature and precipitation differences (Huston, 1994).

1.4 Bioindicators

Some specific species or groups of species have provided a mechanism through which to monitor the health and integrity of specific environments or ecosystems. These organisms are commonly referred to as bioindicators and are used to monitor and detect changes to the ecosystem arising from the influence of human activity. One advantage bioindicators have is the ability to detect cumulative changes within an ecosystem which can be difficult or impossible to detect using physical and chemical measurements only.

Species used as bioindicators have been drawn from across the animal and plant kingdoms. Lichens and mosses are often used to indicate local air quality as increased pollutant level has been shown to reduce species diversity in both these groups. In the aquatic environment, sea birds have been used to monitor heavy metals entering the marine food chain (e.g. Burger & Gochfeld, 2000) and the bioaccumulation of human derived chemical components in fish tissue is used to monitor both freshwater and marine environments (e.g. Winter et al., 2005). One group of bioindicators that have been used worldwide to assess the health of running water are macroinvertebrates (invertebrates that can be seen with the naked eye).

1.5 Macroinvertebrates as bioindicators in running water

River systems are highly varied in terms of flow, habitat and productivity (Vannote et al., 1980). Consequently, macroinvertebrate communities inhabiting these systems are generally heterogeneous, containing representatives from many phyla, with a wide range of abilities to tolerate a broad range of physical, chemical and biotic environmental conditions. Thus, river systems contain species which are variable in their sensitivities to pollution (water physico-chemistry), and combined with both their relatively sedentary nature and moderately long life spans, means macroinvertebrate communities are shaped by the prevailing environmental conditions within an area.

Using macroinvertebrate to monitor the biological health of running water was initially formalised in the early 1900's by Kolkwitz and Marsson (1909) through their development of the saprobic system for assessing organic pollution. Kolkwitz and Marsson postulated that when a river received a heavy load of organic material, through the process of ‘natural’ purification, the macroinvertebrate community would change downstream of the pollution influence through a series of zones of decreasing severity of impact (Kolkwitz, 1950). It was only in the latter half of the 1900’s that these methods received serious consideration for use in U. K. river system assessment (Hynes, 1966; Hawkes, 1997).

To render the biological data collected for river bioassessment more accessible to non-biologists, it became necessary to develop and present results in the form of an index or score. The first widely accepted index used by river biologists in the U. K. was the Trent Biotic Index (Trent River Board, 1960; Woodiwiss, 1964). This was then followed by the development of the Biological Monitoring Working Party (B. M. W. P.) scoring system (Biological Monitoring Working Party, 1978). The final version of this scoring system assigns a score of 1 (organic pollution tolerant) to 10 (organic pollution sensitive) to common macroinvertebrate families found in flowing water within the U. K. The B. M. W. P. score is the sum of the values of the B. M. W. P. families recorded in a sample.

As, like many other ecological indices, the B. M. W. P. scoring system is influenced by the number of taxa in the sample, which is affected in turn by the sample size and, sampling and sample processing proficiency. To overcome this inherent weakness, the calculated B. M. W. P. score is divided by the number of contributing taxa, thus providing an average score, or Average Score per Taxon (A. S. P. T.). It is this monitoring index system that is currently in use throughout the U. K. and has lead to the development of similar indices worldwide (AUSRIVS (Australia), Davies 2000; BEAST (North America), Reynoldson el al., 2000; $\text{SEPAC}_{\text{SRI}}$ (Sweden), Davy-Bowker et al., 2006; PERLA (Czech Republic), Kokeš et al., 2006).

1.6 The importance of assessing long-term change

Biological communities are flexible entities. Natural variations in the biotic and abiotic environment shape community structure. Natural change in community structure can be seasonal as the community responds to the changes in the availability of food resources and the associated life history cycles (Anderson & Cummins, 1979). Other variations in community structure are episodic and are often associated with dramatic effects to community structure (e.g. destruction and re-growth following a forest fire (Coetsee, et al., 2010), or the response of macroinvertebrate communities following a severe flood (Snyder & Johnson, 2006)).

To quantify change which is a result of long-term human influence, community information needs to be collected over long enough time periods to differentiate accurately long-term trend signals superimposed on all other sources of variation in community structure (i.e. seasonal and episodic). This is problematic. Most scientific studies are restricted by the availability of resources to maintain data collection over long time periods, with the majority conducted over time periods of less than 5 years (Jackson & Füreder, 2006) and study periods of this length are unlikely to be long enough to allow detection of long-term trends (Bêche & Resh, 2007). Only relatively few studies from freshwaters have been conducted which are significantly longer.

Established in 1988 to provide chemical and biological data on the extent and degree of acidification of surface waters in the UK, the Acid Waters Monitoring Network has provided information about the long-term response of freshwaters to reductions in air pollution. Following international efforts to reduce air pollution, atmospheric levels of sulphur and nitrogen oxides (associated with acid rain) have reduced (Davies, et al., 2005; Fowler et al., 2005) and water physico-chemistry of acid-sensitive sites have improved followed this reduction (Davies, et al., 2005). While there have been some small improvements in the biotic structure of these acid-sensitive sites (Monteith, et al., 2005) the response of the biota to improvements in water quality has not followed a similar recovery trajectory as water physico-chemistry and communities are still impoverished of acid-sensitive species (Monteith, et al., 2005; Layer, et al., 2010). Compared with the recovery of the water physico-chemistry, the differential response of the biota has been attributed to multiple mechanisms. For example, the water physico-chemistry may still not be sufficient to support acid-sensitive taxa, there may be time lags associated with the dispersal capabilities of acid-sensitive species, or possibly a hysteresis in recovery as a result of ecological interactions closing off communities to acid-sensitive colonisation (Monteith, et al., 2005; Layer, et al., 2010).

Data collected over a 25 year period from an acid affected stream (Broadstone Stream, UK) have provided valuable insights into patterns of change in food web structure (Hildrew & Townsend, 1976; Hildrew et al., 1985, Lancaster & Robertson, 1995, Woodward & Hildrew 2001). Following acidification the predatory component of the food web has gone through distinct stages, initially aquatic predators dominating this system were *Plectrocenemia conspersa* (Trichoptera: Polycentropodidae), *Sialis fuliginosa* (Megaloptera: Sialidae) and predatory Chirnonomidae (Hildrew & Townsend, 1976; Hildrew et al., 1985, Lancaster & Robertson, 1995), in 1995 a new predator, *Cordulegaster boltonii* (Anisoptera: Cordulegasteridae), invaded the system (Woodward & Hildrew, 2001) and since then brown trout (*Salmo trutta*) have invaded. The information gathered during the studies conducted in this stream has provided detailed descriptions of trajectories through which the recovery of the riverine community is progressing.

Using macroinvertebrate data collected over 5 years (1985 to 1989) from a Welsh river system, Weatherly & Ormerod (1990) established that persistence (constancy) in macroinvertebrate communities changed in concert across catchments, but their data encompassed too few years to attribute causal factors. Through an extension of this study and the collection of data spanning a 25 year period (1985 to 2005), Durance & Ormerod (2007) were able to attributed these large scale temporal changes in community persistence to local climate cycles associated with the North Atlantic Oscillation (NAO) (Durance & Ormerod, 2007).

Research focusing on the effects invasive species have on ecosystems have highlighted the need to assess change over long time frames (Strayer, et al., 2006). For example, in the US the imported species of fire ant, *Solenopsis invicta*, becomes invasive as the species spreads to new areas and reduces the abundance of native ant species (Porter & Savignano, 1990). However, 12 years following initial invasion of this species to an area, local populations of native ant species and other arthropods had increased to pre-invasion levels (Morrison (2002), highlighting the importance of conduction research over periods that are biological meaningful.

The results from the studies detailed above have provided insight and targeted research direction to aid in the understanding of the how biological communities respond to long-term changes. These studies also highlight that, despite collecting information for decades, the continuation of these datasets is required to resolve the long-term recovery dynamics of systems affected by human influences.

1.7 Quantifying long-term change

In this thesis, two long-term biological data sets of macroinvertebrate community data, spanning 32 (the River Clyde) and 50 years (the River Endrick), are used to look for long-term community change.

1.7.1 River Clyde history

The River Clyde (located in west central Scotland) has supported and continues to support a large percentage (~ 30%; General Register Office for Scotland Report, 2007) of Scotland’s population. As a result the river has been subjected to large, often continuous inputs of pollutants from numerous sources of a varied nature and, has in the past been described as one of the worst polluted river basins in the U. K. (Hammerton, 1986).

The Rivers (Pollution Prevention) (Scotland) Acts of 1951 and 1965 were the first of the river pollution Acts in Scotland to initiate major improvements to polluting discharges to river systems (Hammerton, 1986). More recently, the European Commission enacted the Water Framework Directive (OJL, 2000) which “aims to improve fresh and salt water resources within the member states of the European Commission”. This European environmental legislation resulted in the enactment of the Water Environment and Water

Services (Scotland) Act 2003. These legislation have shifted the regulation of freshwater sources from local, site monitoring methods to an integrated approach at the scale of the river basin level.

Water quality within Scotland is currently monitored by the Scottish Environment Protection Agency (S. E. P. A.) and was monitored previously by its predecessor organisation, the Clyde River Purification Board (C. R. P. B.), using water physico-chemistry (e.g. dissolved oxygen, pH, alkalinity) since 1965 and macroinvertebrates since 1975. Macroinvertebrate data have been collected by both organisations using the same standard techniques (Doughty, R. C., *pers. comms.*, 21/08/2007). Using the water physico-chemical information collected by both the S. E. P. A. and the C. R. P. B., changes to elements of water physico-chemistry within the River Clyde have been assessed since the mid 1970's through the Harmonised Monitoring Scheme (Anderson et al., 2010), a UK government organisation. Within the River Clyde the physico-chemistry of the water has shown decreasing levels of nitrogen, orthophosphate, suspended solids, and biochemical oxygen demand, and increasing levels of saturated oxygen (Anderson et al., 2010). These changes suggest that the physico-chemistry of the water is improving and is likely to be now supporting a more diverse macroinvertebrate community. The situation is however complex. There is strong seasonality in some of the trends and overall concentrations of some of the measured physico-chemical components remain relatively high. For example, in the River Clyde, orthophosphate is found at high concentrations relative to the other river systems in Scotland, and although there is no overall annual change in orthophosphate concentration, the spring and summer months have shown a decreasing trend in orthophosphate (Anderson, et al., 2010).

Generally the biological (macroinvertebrates) and chemical (water physico-chemistry) quality of the River Clyde has improved (Milne & Best, 1986, S. E. P. A., 2008). Using biotic indices (B. M. W. P. score) and water physico-chemistry measurements the S. E. P. A. have classified the collected samples in a standard way since 1996 (S. E. P. A., 2008, Doughty, R. C., *pers. comms.*, 21/08/2007). Using data available from the S. E. P. A. website (S. E. P. A., 2006) the proportion of samples collected from the River Clyde that were attributed to "seriously polluted" water quality class (i.e. category D) has reduced from 0.07 in 1996 to 0.03 in 2006, while the proportion of samples that were attributed to "excellent" water quality (i.e. category A1) has increased from 0.01 in 1996 to 0.1 in 2006 (Figure 1.1).

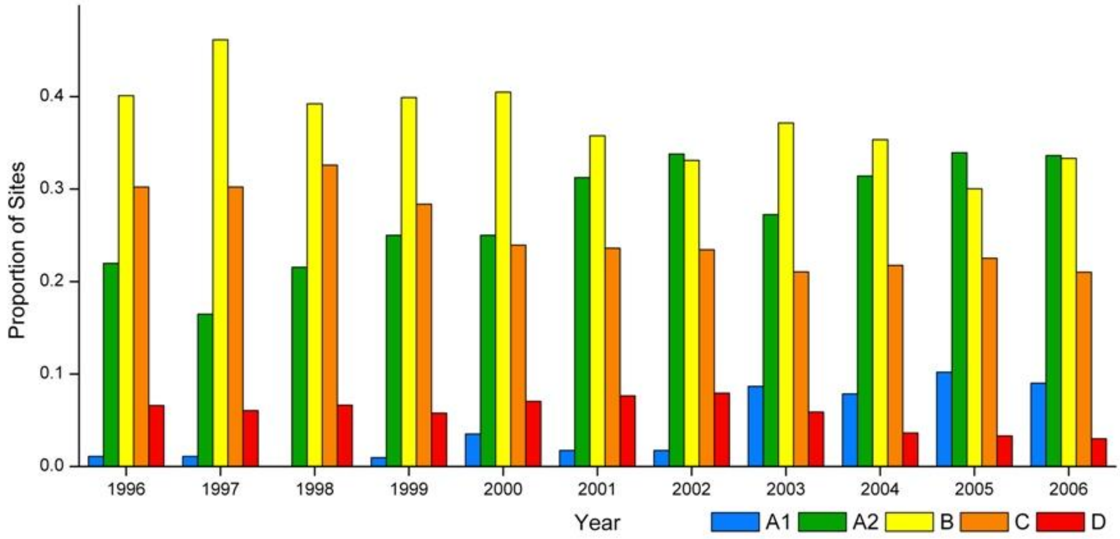


Figure 1.1: Proportion of sites within the River Clyde catchment, between 1996 and 2006, belonging to the water quality classes A1, "excellent", A2 "good", B, "fair", C, "poor" and D, "seriously polluted" (S. E. P. A., 2006)

While the general water quality within the catchment has improved there are still some problems which may be affecting the macroinvertebrate biota. Due to the presence of large coal measures that fall within the catchment of the River Clyde watercourse (Appendix A), there has been and continues to be some influence from mine water (S. E. P. A., 2008). Although most mines within the catchment are now disused, there has been an increase in mining activity in the relatively small patch of coal measures located in the south west of the catchment (see Appendix A), resulting in mine water discharging to the local river, the Douglas Water. Continuous monitoring of macroinvertebrate data in the Douglas Water commenced in 1990 and as such data collected from this watercourse is not included in the analysis.

The Douglas Water is a large tributary which joins the main channel of the River Clyde approximately 76 km from the main channel source. The effects of the open cast mine working are associated with an increase in electrical conductivity of the water due to an increase in dissolved ions entering the water arising from the disturbed geology (Hynes, 1966). Using available water chemistry data collected at a site approximately 2 km downstream of the confluence of the Douglas Water with the main channel of the River Clyde, an assessment of temporal change in the electrical conductivity of river water, between 1978 and 2003, has not shown any simple linear change (linear regression of electrical conductivity ($\mu S\ cm^{-1}$) on sampling date; $F_{(1,112)}=0.022$, $p=0.884$; Figure 1.2). It is therefore assumed that any negative influences from open cast mining operations affecting the Douglas Water have been diluted and are thus unlikely to cause acute effects on the main river channel.

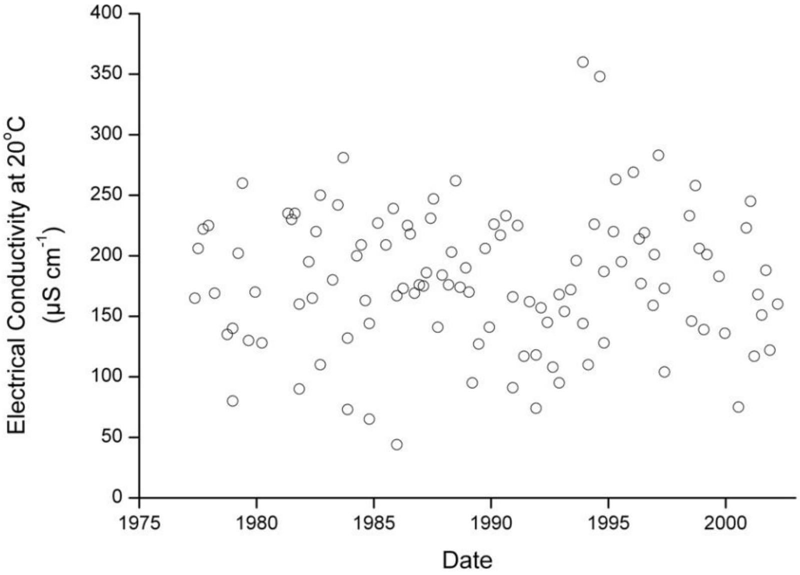


Figure 1.2: No significant linear change in electrical conductivity (measured as µS cm^{-1} at 20 ^{o}C) of the River Clyde at the site approximately 2km downstream of the confluence of the Douglas Water with the River Clyde main channel.

The general synopsis of water quality change in the River Clyde is one of improvement, but complex patterns of change are likely given the degree of urbanisation within the catchment and the complex interaction between changes in water chemistry and the resultant effects on the macroinvertebrate community.

1.7.2 River Clyde data set

The comprehensive monitoring of water physico-chemistry and macroinvertebrate fauna from the River Clyde by the S. E. P. A. and the C. R. P. B. forms the basis of the River Clyde dataset. The sampling programme was initiated in 1975 by the C. R. P. B and has continued since and from 1990 onwards has been under the control of the S. E. P. A.

Available only as hard copies, the 6,188 field sheets were input to a database created in Microsoft Excel version 2003. Due to the risk of data input error, checking mechanisms were put in place for each sample (i.e. field sheet) input. Following the completion of data entry, the entire database was checked for any inconsistency by simple comparisons of input data and calculated metrics, and a random 1% of the data was re-input and comparisons made with the original database. The error rate of data entry was remarkably low and most errors were associated with the entry of duplicates of a single sample which were easily removed.

To investigate changing community structure in the River Clyde, only samples collected from sites that were monitored annually between 1975 and 2006 were analysed. The inclusion of sites was based on a compromise between temporal consistency and spatial spread within the catchment (Appendix A). To mitigate the direct effects of changes to specific bankside operations (e.g. sewage treatment works) any samples that were collected to monitor specific discharges or were collected in response to a pollution event were removed from the database. Data from all sites from 1991 to 1994 were lost by the S. E. P. A. in storage and thus not available for analysis. The final dataset for the River Clyde comprised 3,446 samples collected from 65 sites between 1975 and 2006.

1.7.3 River Endrick history

The River Endrick is also located in west central Scotland and is the largest river draining into Loch Lomond (by surface area, the largest lake in the U.K.). Despite a shared watershed and close proximity (Appendix A), the River Endrick has escaped the same level of human influence to the water course as that experienced by the River Clyde as a result of the very low population density within the catchment (<0.1% of Scotland’s population, General Register Office for Scotland Report, 2001). No significant changes in water physico-chemistry have been detected through the Harmonised Monitoring Scheme (Anderson et al., 2010), although suspended solids within the Loch Lomond catchment area are decreasing (Anderson et al., 2010). Evidence from recent monitoring of the Endrick watercourse by the S. E. P. A. has not recorded any sites of “seriously polluted” or “bad” water quality and in very recent years only sites of “excellent” or “good” water quality have been recorded (S. E. P. A., 2006) (Figure 1.3). Generally water quality within the River Endrick catchment has been and remains of good ecological quality.

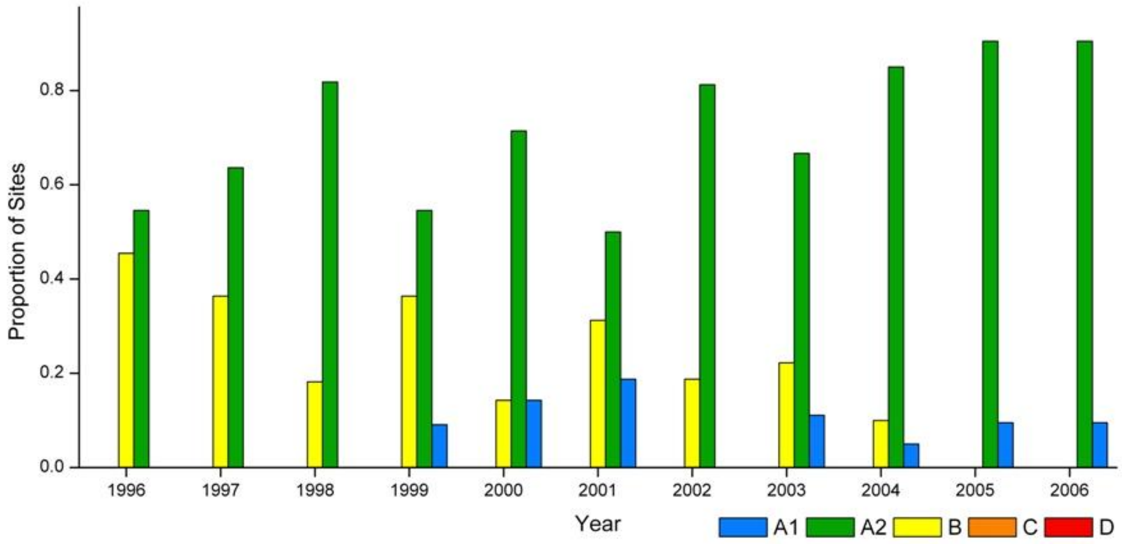


Figure 1.3: Proportion of sites within the River Endrick catchment, between 1996 and 2006, belonging to the water quality classes A1, "excellent" A2 "good", B, "fair", C, "poor" and D, "seriously polluted" (S. E. P. A., 2006)

1.7.4 River Endrick data set

An ecological study of the invertebrate and vertebrate fauna of River Endrick between 1959 and 1963 was undertaken by P.S. Maitland as PhD research through the University of Glasgow (Maitland, 1963). One component of this work was to establish a reliable check-list of the species of invertebrates found in the River Endrick. Twelve sampling sites were chosen along the main river channel from the river source (defined here as the "start of the highest rising tributary" (Maitland, 1966a)) to the mouth (the point at which the river enters Loch Lomond (Figure 6.1). "The twelve stations [sites] were selected more or less at random along the length of the river, though care was taken not to site any where fauna might be influenced by unnatural factors – e.g. near a sewage works or a ford" (Maitland, 1966a). Samples were collected at these 12 sites in October 1959, February 1960 and June 1961. These samples are referred to as the 1960 study period. To investigate community structure change in the River Endrick, 7 of the original 12 sites were re-sampled in 2010 using exactly the using the same timing and method employed in the 1960 study (Appendix A).

1.8 Overall aims and thesis structure

The main focus of this thesis is to investigate how long-term change is manifest in macroinvertebrate river communities using two river systems with contrasting legacies from human activity. Although there is a good general understanding of the short term response of macroinvertebrate communities to changes in their local environment (e.g. Hynes, 1966; Clarke, et al., 2005), the long-term response to change is less well understood (Jackson & Füreder, 2006). Work in this thesis aims to improve our general understanding of long-term change in river systems based on the findings from six studies, presented as six chapters. The general aims of each are:

1. In a river recovering from environmental degradation, are the response trajectories (i.e. colonisation rates) of macroinvertebrate Families significantly related to dispersal ability or physiological tolerance of water chemistry?

The general aim of chapter 2 is to test the hypothesis that colonisation rate of macroinvertebrate Families is linked with either dispersal ability or physiological tolerance of water physico-chemistry, or both. Dispersal ability was measured as a simple measure of flight capability associated with the winged adult stage in the insect groups and physiological tolerance was measured as the pollution tolerance of the macroinvertebrate family.

2. What are the environmental drivers of community richness in a river recovering from water quality degradation?

The general aim of chapter 3 is to define and quantify the effects of some of the common measurements of local and landscape environmental change (e.g. land use, water physico-chemistry and natural site characteristics) have in controlling macroinvertebrate community richness.

3. Can communities recovering from long-term environmental degradation achieve ‘pristine’ condition?

The general aim of chapter 4 is to test the hypothesis that communities re-forming following a period of degradation can achieve a composition similar to that expected in the absence of human influence. This assumption forms the basic underlying principle of ecological monitoring.

4. Do colonisation patterns affect resource use within a re-forming community?

The general aim of chapter 5 is to test the effects differing colonisation trajectories have on the resource use of a colonising predator. The resource use of a coloniser affects the individual directly but also affects the other members of the community that is being colonised. Both these affects can have implications for the future functionality of the community.

5. Changes in the species composition and distribution in the River Endrick after 50 years.

The general aim of chapter 6 was to assess changes in the species composition of the River Endrick by comparing contemporary empirical data with historical data collected in 1960.

6. Have the changes in species composition in the River Endrick affected community structure and/or function?

The general aim of chapter 7 was to investigate changes to the macroinvertebrate community structure and function over a period of 50 years. As this river has had minimal influence from human activity, changes here may have arisen as a result of larger scale environmental patterns.

CHAPTER 2 Spatial and temporal changes in aquatic macroinvertebrate families in the River Clyde

2.1 Introduction

A fundamental question in ecology is; what determines species occurrence through time and space? The contemporary answer to this question is particularly important as pervasive human activity is now challenging traditional, long held, views of species distributions. Non-native species introductions, climate change and the modification and destruction of habitat are occurring at rapidly increasing rates (Cohan & Carlton, 1998; Lockwood et al., 2009), and are changing species distributions at local and regional levels (e.g. the expansion of the northern limit of many Odonate species within the UK as a result of climate change (Hickling et al.,2005)), to species distribution changes on a global scale (e.g. the introduction and establishment of the American signal crayfish (*Pacifastacus leniusculus*) (Gladman et al., 2009) and Chinese mitten crab (*Eriocheir sinensis*) within UK waterways).

Fluctuations in species occurrence may arise over short time frames as a result of changing community dynamics in response to shifting local environmental conditions. To quantify changes in species distributions which are not a result of short term fluctuations, data must be collected over long enough time periods to reflect fundamental changes to species distributions and not temporary modification, which can be misleading.

Freshwater systems, particularly rivers are now recognised as the most endangered ecosystems in the world (Dudgeon et al., 2006; Vörösmarty et al., 2010). Their importance as the largest source of renewable fresh water has at least in part driven global efforts to restore river systems impacted by human activity (Vörösmarty et al., 2010), although effort is highly skewed towards developed regions (e.g. USA and Western Europe) (Vörösmarty, et, al., 2010). Despite this there is still only a poor understanding of the process by which animal communities respond to restoration efforts. This is, at least in part, due to a shortage of long-term studies detailing change over biologically meaningful time scales (Jackson & Füreder, 2006).

My analysis of long-term changes in spatio-temporal distributions, made use of 32 years of macroinvertebrate monitoring data collected from 65 sites within a large river system recovering from a period of water quality degradation. Using this data, I attempted to quantify changes in temporal occurrence and spatial distribution of aquatic macroinvertebrate families in the River Clyde.

2.2 Methods

To determine temporal and spatial relationships of macroinvertebrate families I used data on freshwater invertebrate community structure collected from a large river system between 1975 and 2006.

2.2.1 Study area

The River Clyde is located in West Central Scotland (between Lat: 56^o N & 55^o 30’ N and Long: 004^o 73’ W & 003^o 55’ W). The catchment covers an area of 3,125 km^2 with a total river length of 4,165 km and 26 km^2 of freshwater lochs and reservoirs. Landuse in the catchment is dominated by agriculture (45%) and natural and semi-natural habitats (37%) with urban landuse comprising 18%, the remaining 1% being lochs and reservoirs. Although urban landuse does not dominate, in 2006, 31% (1.6M) of the total population of Scotland lived within the catchment (General Register Office for Scotland Report, 2007). With a history of heavy industry, the River Clyde has been described in the past as one of the worst polluted river basins in Britain (Hammerton, 1986).

2.2.2 Invertebrate community composition

Family occurrence within the River Clyde was determined from existing datasets. Invertebrate community samples were collected from 65 sites (n=3446; mean annual number collected per site = 2 ± 0.02 S.E.), using a standard kick-sampling method, during routine water quality monitoring by the Scottish Environment Protection Agency (SEPA) and its predecessor organisations. The family groups recorded (detection or non-detection) were those from the current BMWP taxon list (not including Aphelocheridae, Brachycentridae, Goeridae, Lepidostomatidae, Odontoceridae, Psychimyiidae and Valvatidae, due to taxonomic and recording issues at the start of the study period) which are routinely recorded as part of the BMWP system (Armitage et al., 1983) used to assess running water quality in Great Britain.

2.2.3 Common macroinvertebrate families in the River Clyde

To determine which families typified the community structure of the River Clyde catchment and to avoid including those families which appeared in collected samples only sporadically, the number of sites at which each family had been recorded in the River Clyde was determined. Only those families which had been recorded at a minimum of 15 of the 65 sites were determined as suitable representatives of the River Clyde macroinvertebrate community, and only these families were used in any further analysis.

2.2.4 Site characteristics

For each site, a number of characteristics were measured; distance from the river source (km), altitude (m), slope (m km^{-1}) were all derived from 1:50,000 scale Ordnance Survey maps using the methods detailed by Murray-Bligh et al. (1997) and; discharge category (Murray-Bligh et al., 1997), which provides a site specific measure of average annual discharge in cubic metres per second (m^3 s^{-1}), was provided by the SEPA hydrology unit. Due to the highly correlated nature of these variables (e.g. a site located at high altitude will likely be located in a smaller, steeper stream with a lower annual discharge, than a site located further downstream), principle components analysis (PCA) was used to produce a simplified specific index of relative position of each site within the catchment (i.e. the extracted first principle component score).

2.2.5 Spatial occurrence and temporal change

To determine spatial distribution and temporal changes for each of the common macroinvertebrate families, a binary logistic regression was used. For each common family separately, the detection/non-detection of the family was first regressed on site position (first principle component score), sample year and a simple interaction between year and site position (year*site position). If the interaction term did not contribute significantly to the regression, it was removed and the detection/non-detection of the family was regressed on year and site position. If either year or site position did not contribute significantly, that variable (i.e. year or site position) was removed, and the regression of the detection/non-detection of the family was then undertaken using only the variable that did contribute significantly to the regression (i.e. only year or site position).

The results from the logistic regression would therefore indicate three things: (1) if the family showed a significant spatial distribution pattern (site position) within the catchment, (2) if there had been a significant temporal change (year) in the occurrence of a family within the catchment and, (3) if the temporal change in family occurrence was significantly different at specific positions within the catchment (site position and year interaction).

2.2.6. Temporal change associated with simple life characteristics

The regression coefficient of year (not including an interaction) regressed on family detection/non-detection in a logistic regression provides an indication of the relationship each family has with temporal change (year coefficient). A relatively large regression coefficient associated with year will indicate a relatively rapid change in the occurrence of a family within the catchment (i.e. relatively rapid colonisation), while a small coefficient would indicate relatively slower colonisation. To determine whether significant changes in the temporal occurrence of a family (i.e. colonisation rate) were related to simple measures of life history characteristics, the regression coefficient associated with year was first regressed on the revised BMWP score (Walley & Hawkes, 1997) of the family and secondly ANOVA was used to test the effect of flight capability (0 = no flight capability, 1 = capable of flight dispersal). Families which included aerial dispersal during their life cycle (i.e. those for which the adult stages had ability for flight, e.g. Beatidae) were defined as having flight capability (i.e. 1). The remaining families were defined as having no flight capability (i.e. 0). This is only one mechanism through which freshwater macroinvertebrates disperse, many of the families in this study disperse through other mechanisms, for example, drifting in the water current (e.g. Gammaridae (Elliot, 2002)) or through upstream movements within the watercourse (e.g. Rhyacophilidae (Elliot, 1971).

To conform with the assumptions of normality, the measurements for the site characteristics were log transformed ($x' = \log_{10}(x + 1)$) before all analysis. To account for any pseudo-replication associated with repeat site sampling, all regressions included sampling site as a random variable. All statistical analyses were performed using R version 2.11.1 (R Development Core Team, 2010).

2.3 Results

2.3.1 Common macroinvertebrate families from River Clyde

Of the families comprising the BMWP list, 64 were recorded from the River Clyde catchment and 42 of these were recorded from a minimum of 15 sites and thus deemed common families (Table 2.1).

2.3.2 Site characteristics PCA

The first principle component from the PCA of natural site variables (PC1) explained 69.6% of total variance in site characteristics. Slope and altitude were negatively loaded (−0.492 and −0.393 respectively) while distance from source and discharge category were positively loaded (0.549 and 0.549 respectively), thus the first principle component provided a good index for site location within the catchment. Sites with low scores were generally smaller sized, located at a higher altitude (small upland), while sites with large scores were large rivers located at a lower altitude (large lowland).

2.3.3 Spatial occurrence and temporal change

Using sample year and site position (PC1), individual logistic regressions of the 42 common macroinvertebrate families produced 34 significant models (Table 2.1). The individual regressions fell into six general categories; (1) a significant temporal change in occurrence which differs significantly depending on location within the catchment (i.e.

regressions with a significant interaction between sample year and site position); (2) a significant increase in occurrence over the study period and significantly higher probability of occurrence at large lowland sites (i.e. regressions with both year (positive coefficient) and site position (positive coefficient) contributing significantly); (3) a significant increase in occurrence over the study period and significantly higher probability of occurrence at small upland sites (i.e. regressions with both year (positive coefficient) and site position (negative coefficient) contributing significantly); (4) a significant increase in occurrence over the study period but no simple spatial distribution (i.e. year only contributing to the regression); (5) no significant change in occurrence over the study period, but a significant spatial distribution (i.e. site position only contributing to the model); and (6) no significant temporal change over the study period and no significant spatial distribution.

Four families had significantly changed their probability of occurrence over the study period, and the rate of these changes in occurrence were significantly related to the position of the family within the catchment (i.e. situation 1 above; Table 2.1). Two families (Haliplidae and Polycentropodidae), had a significant decrease in their probability of occurrence over the study period, and these decreases were significantly higher at larger more lowland sites. Two families (Erpobdellidae and Simuliidae) had significantly increased their probability of occurrence over the study period. Erpobdellidae had a higher rate of increase in occurrence in smaller more upland sites and Simuliidae had a higher rate of increase in occurrence in larger more lowland sites.

Six families had a significant increase in probability of occurrence over the study period and had a higher probability of occurrence in large lowland sites (i.e. situation 2 above; Table 2.1).

Thirteen families had a significant increase in probability of occurrence over the study period and had a higher probability of occurrence in small upland sites (i.e. situation 3 above; Table 2.1).

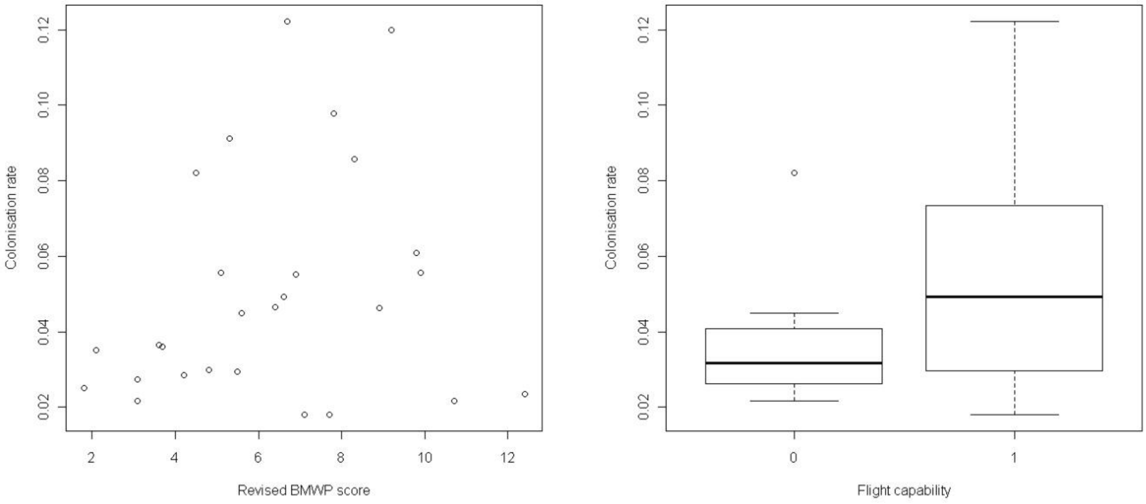
Eight families had a significant increase in probability of occurrence over the study period but had no simple spatial relationship (i.e. situation 4; Table 2.1). The lack of spatial relationship is either due to ubiquity throughout sampling sites throughout the catchment (e.g. Baetidae, Rhyacophilidae, Tipulidae and Chironomidae are recorded from all sites) or a more complex distribution pattern that does not following the simple description derived from the PC1 score.

Three families (Lynmaeidae, Planorbidae and Gyrinidae) showed a significantly higher probability of occurrence at large lowland sites but did not show any significant change in occurrence over the study period (i.e. situation 5; Table 2.1)

The remaining eight families had no significant simple relationship with spatial occurrence (site position) and had not changed the probability of their occurrence over the study period (i.e. situation 6 above; Table 2.1)

2.3.4 Temporal change associated with simple life characteristics

The regression coefficient associated with the year variable (i.e. colonisation rate) showed no significant relationship with pollution tolerance (i.e. revised BMWP score) (linear regression; p=0.275; Figure 2.1) or flight capability (ANOVA; p=0.158; Figure 2.1).



(a) (b)

Figure 2.1: Relationship between colonisation rate (regression coefficient from temporal logistic regression) and (a) pollution tolerance and (b) flight capability (0 = no capability of flight dispersal; 1 = capable of flight dispersal).

Table 2.1: Recorded site frequency (65 sites in total) for the 42 common families, revised BMWP scores and coefficients and significance values from the associated logistic regressions. Spatial distribution is site position (i.e. extracted PC1 scores); temporal change is year; spatio-temporal interaction is the interaction term, site position*year. Significance levels corrected for multiple tests (Bonferroni method, $\beta = \alpha/N$); $p<0.05$=*, $p<0.01$=**, $p<0.001$=***.

Family	**Recorded Site Frequency**	**Revised BMWP Score**	**Regression Intercept**	**Spatial Distribution (Sig.)**		**Temporal Change (Sig.)**		**Spatio-Temporal Interaction (Sig.)**	
Families showing significant temporal change in their occurrence which differs significantly across the catchment									
Haliplidae	52	4.0	73.067	31.303	***	-0.038	***	-0.016	**
Polycentropodidae	51	8.6	20.075	28.642	***	*-0.011*	*NS*	-0.014	***
Erpobdellidae	65	5.8	-124.500	-20.210	**	0.063	***	0.010	**
Simuliidae	63	2.8	-47.206	21.352	**	0.024	***	-0.010	**

Table 2.1: Continued.

Family	**Recorded Site Frequency**	**Revised BMWP Score**	**Regression Intercept**	**Spatial Distribution (Sig.)**	**Temporal Change (Sig.)**	**Spatio-Temporal Interaction (Sig.)**
Families showing significant increase in temporal occurrence and show increased probability at larger more lowland sites						
Planariidae	59	4.2	-56.753	0.192 ***	0.028 ***	
Dendrocoelidae	32	3.1	-56.911	0.735 ***	0.027 ***	
Ancylidae	64	5.6	-88.921	0.227 ***	0.045 ***	
Sphaeriidae	65	3.6	-72.501	0.291 ***	0.037 ***	
Physidae	40	1.8	-52.230	0.562 ***	0.025 ***	
Glossiphoniidae	65	3.1	-43.538	0.492 ***	0.022 ***	
Asellidae	64	2.1	-69.134	0.525 ***	0.035 ***	
Heptageniidae	65	9.8	-120.500	0.189 ***	0.061 ***	
Ephemerellidae	64	7.7	-36.892	0.115 **	0.018 ***	
Caenidae	57	7.1	-37.236	0.336 ***	0.018 ***	
Elmidae	65	6.4	-91.788	0.164 ***	0.046 ***	
Hydropsychidae	65	6.6	-97.655	0.125 ***	0.049 ***	
Leptoceridae	56	7.8	-196.800	0.406 ***	0.098 ***	

Table 2.1: Continued.

Family	**Recorded Site Frequency**	**Revised BMWP Score**	**Regression Intercept**	**Spatial Distribution (Sig.)**		**Temporal Change (Sig.)**		**Spatio-Temporal Interaction (Sig.)**
Families showing significant increase in temporal occurrence and show increased probability at smaller more upland sites								
Gammaridae	65	4.5	-162.100	-0.184	***	0.082	***	
Leptophlebiidae	56	8.9	-94.333	-0.385	***	0.046	***	
Perlodidae	54	10.7	-44.268	-0.141	***	0.022	***	
Dytiscidae	65	4.8	-60.869	-0.181	***	0.030	***	
Hydrophilidae	61	5.1	-112.800	-0.132	*	0.056	***	
Limnephilidae	64	6.9	-110.600	-0.248	***	0.055	***	
Families showing a significant increase in occurrence over the study period but show no significant simple spatial distribution								
Baetidae	65	5.3	-177.955			0.091	***	
Leuctridae	58	9.9	-111.555			0.056	***	
Chloroperlidae	42	12.4	-49.171			0.024	**	
Rhyacophilidae	65	8.3	-170.357			0.086	***	
Hydroptilidae	53	6.7	-246.600			0.122	***	
Sericostomatidae	58	9.2	-240.800			0.120	***	
Tipulidae	65	5.5	-58.143			0.029	***	
Chironomidae	65	3.7	-68.693			0.036	**	

Table 2.1: Continued.

Family	**Recorded Site Frequency**	**Revised BMWP Score**	**Regression Intercept**	**Spatial Distribution (Sig.)**	**Temporal Change (Sig.)**	**Spatio-Temporal Interaction (Sig.)**
Families showing no significant change in occurrence over the study period but have a significant spatial distribution						
Lymnaeidae	65	3.0	0.056	0.351 ***		
Planorbidae	57	2.9	-2.606	0.438 *		
Gyrinidae	28	7.8	-5.015	0.821 *		
Families showing no significant change in occurrence over the study and no simple spatial distribution						
Hydrobiidae	65	3.9				
Oligochaeta	65	3.5				
Taeniopterygidae	53	10.8				
Nemouridae	63	9.1				
Capniidae	28	10.0				
Perlidae	18	12.5				
Corixidae	20	3.7				
Sialidae	36	4.5				

2.4 Discussion

Significant relationships in both spatial distribution and temporal change in 31 macroinvertebrate families have been highlighted from this study conducted over a 32 year period in the River Clyde. All of these families, except Haliplidae and Polycentropodidae, have shown a significant increase in their probability of occurrence over the 32 year period, which is a likely result of the improvements made to the chemical water quality within the river system over this period.

The majority (27) of families showed increase in occurrence throughout the catchment which was generally similar at all sites (i.e. there was no significant effect of the interaction of site position and year). Two families, Erpobdellidae and Simuliidae, did show significant differences in the rates at which their occurrence increased as a result of their location within the catchment. Erpobdellidae and Simuliidae both showed more rapid increases in occurrence at smaller more upland sites when compared with larger more lowland sites. The reasons for these site-dependent temporal changes are not clear.

Erpobdellidae are predatory Hirudinea (Moog, 2002) with an ability to withstand poor water quality (revised BMWP score is 2.8 (Walley & Hawkes, 1997)). Against the background of general improving water quality within the River Clyde, it is counter intuitive that this group are colonising water which is of generally very good quality (pers. obs.), where supposition suggests that this group would be out competed for niche space by other predatory species better adapted for these cleaner conditions. A PhD thesis undertaken in 1969 (MacPhee, 1969) detailed the limit of Erpobdellidae on the main stem of the River Clyde approximately 40km downstream of its detection in 2006 indicating that Erpobdellidae have expanded their range on the main stem of the river by 40km over a 37 year period. Historically, the factor limiting Erpobdellidae distribution to the lower reaches of the river system has changed, allowing invasion of the upper reaches of the watercourse where it is now common. Erpobdellidae within the River Clyde are most commonly represented by *Erpobdella octoculata* and it is this species which is invading these cleaner waters (pers. obs.). *E. octoculata* is an actively foraging predator (Kreuter et al., 2008) which shows some preference for the isopod *Asellus aquaticus* (Kreuter et al., 2008). *A. aquaticus* have also undergone a range expansion within the River Clyde, and have expanded their limit upstream on the main stem (MacPhee, 1969). It is possible that change within the river system allowing *A. aquaticus* to expand its range has in turn facilitated the range expansion of *E. octoculata*.

Simuliidae within the River Clyde system are more common in the upper reaches where they have shown a significantly higher rate of increase in occurrence compared with larger more lowland sites. Simuliidae are passive filter feeders (Jensen, 1996; Moog, 2002). Possible changes to the land management in the upper reaches of the river system may have increased the amount of particulate organic matter entering the watercourse, thus increasing the available food resource from this family.

Against this background of general water quality improvement, two families, Haliplidae and Polycentropodidae, both decreased in occurrence within the River Clyde over the study period. For both families, these decreases were significantly higher at large lowland sites. Mature Haliplid larvae perform season migrations to terrestrial overwintering and/or pupation sites close to the water’s edge (Nilsson, 1996). The reduction of the detection of this family has been significantly higher in larger more lowland parts of the catchment, where there has been increased development of the riverine corridor as part of urban expansion and flood prevention schemes. It may be likely that the loss of this family has arisen as a result of the loss of suitable overwintering and pupation habitats.

Polycentropodidae are predatory net-spinning case less Trichoptera (Edington & Hildrew, 1995) and the reasons for the reduction in their occurrence within the River Clyde are not clear. Toxic chemicals have been shown to influence the structure of nets spun by another Trichopteran, *Hydropsyche angustipennis* (Petersen & Petersen, 1984) and may be influencing nets spun by Polycentropodidae, reducing fitness and contributing to their decline. However, it must be noted that the other net spinning Trichopteran families in this study have not shown this decline, including the family Hydropsychidae.

Twenty two families had shown a significant simple spatial relationship within the River Clyde. Six families had a significantly higher probability of occurrence at small upland sites and 16 had a significantly higher probability of occurrence at large lowland sites. There were some very general patterns within the two groups of families. The only Plecopteran with a significant spatial distribution, Perlodidae, was associated with a higher probability of occurrence in small upland sites. Perlodidae are generally large predators requiring clean well oxygenated water (Moog, 2002) which are more commonly found in the upper parts of river catchments. All Molluscan, Tricladian or Hirudinean groups showed a significantly higher probability of occurrence at large lowland sites. These groups are generally associated with slower flows (Moog, 2002) found in lower sections of river systems.

Colonisation rate (i.e. the regression coefficient associate with year) showed no significant simple relationship with either pollution tolerance or flight capability. Following the improvements to the physico-chemical quality of the water within the river, those families with increased dispersal (i.e. capable of flight) should have been able to colonise sites at a faster rate. However, there is considerable variability in flight ability between the families in this study (Verberk et el., 2008), so the simple measure of flight capability used here may be dampening more subtle effects of dispersal ability. Furthermore, in this study no account has been taken of the contribution of invertebrate drift to the colonisation of sites within this study. Colonisation rate was also not significantly related to the pollution tolerance measurement of a family used here. The pollution tolerance of a family could be viewed as its physiological response to prevailing water physico-chemistry, and following the changes to water physico-chemistry it is expected that the number of families with low tolerance of poor water physico-chemistry will increase. It is this relationship that forms the bedrock of water quality monitoring.

The results from this study have shown that there is no simple relationship between the rate at which a family colonises a site and, the dispersal ability and the tolerance of that family to changes in water physico-chemistry. This implies firstly, that a simple colonisation trajectory cannot be attributed to dispersal capability (in terms of flight) and water physico-chemical tolerance and secondly, that the colonisation and establishment of families within the community is affected to a greater degree by intrinsic factors.

The reversion of communities impacted by human activity to a more natural state is clearly complex. Classical views of river community recovery from a polluting influence have most often followed community development downstream as the polluting influence wanes (e.g. Hynes, 1966). More recently, some studies have attempted to account for temporal change but are often conducted over relatively short time frames (Jackson & Füreder, 2006). The results from this study have shown that changes in the spatio-temporal distribution of macroinvertebrate families following restoration in a river recovering from water quality degradation are complicated. While the majority of families detailed in this study have increased their occurrence over the 32 year period, two families have shown significant declines and another has shown counter intuitive spatial changes. In addition to these changes, colonisation rates were shown to be unrelated to both flight capability and pollution tolerance. It is likely therefore, that interactions within the existing community are contributing to the successful/unsuccessful colonisation and establishment of additional community members.

CHAPTER 3 Drivers of community diversity

3.1 Introduction

Freshwater systems, particularly rivers, are now recognised as the most endangered ecosystems in the world (Dudgeon et al., 2006; Vörösmarty et al., 2010). Their importance as the largest source of renewable fresh water has, at least in part, driven global efforts to restore river systems impacted by human activity (Vörösmarty et al., 2010), although effort is highly skewed towards developed regions (e.g. USA and Western Europe) (Vörösmarty et al., 2010). Despite this, there is still only a poor understanding of the processes by which animal communities revert to a more natural state, most commonly due to a shortage of long-term studies detailing change over biologically meaningful time scales (Jackson & Füreder, 2006).

Ecosystem recovery is a response to the removal or modification of a negative influence resulting in a positive change towards a more natural state within an ecosystem. Understanding the processes by which aquatic ecosystems recover and to what extent human induced disturbance and natural drivers influence change is crucial for a targeted approach to the rehabilitation of river systems.

There is a good understanding of the natural drivers that influence macroinvertebrate community structure. A simple suite of map derived (e.g. altitude, slope, geographical location) and site derived (e.g. substrate composition, river width) measurements have been shown to have strong associations with macroinvertebrate community structure. The strengths of these associations provides the basis for modelling which aims to predict 'natural' community structure at a sampling site (e.g. RIVPACS (UK), Wright et al., 1984; PERLA (Czech Republic), Kokeš et al., 2006; AUSRIVS (Australia), Simpson & Norris, 2000).

Human induced modifications to rivers are less well understood and are most commonly associated with negative influences (e.g. land use changes, modifications to the physical structure of the river, pollutant inputs and changes to hydrology (Paul & Meyer, 2001; Allan, 2004)). The interconnectivity of human induced modifications; coupled with complicated remedial action needed to rectify their negative influence has been highlighted by rehabilitation studies from urban (Nienhaus et al., 2002; Suren & McMurtie, 2005) and agricultural landscapes (Lorenz et al., 2009). While there have been some inroads made to set standards for successful river rehabilitation projects (Ward et al., 2001; Palmer et al., 2005), an understanding of the long term relative importance of landscape and local influences affecting river communities is key to understanding the recovery process and has the ability to inform a targeted approach to stream rehabilitation.

In this study I analysed long-term data (32 years) of freshwater invertebrate communities from a large river system recovering from a period of water quality degradation. I specifically attempted to identify local and landscape scale drivers of change in structuring the richness of the macroinvertebrate community and quantify the magnitude of the effects.

3.2 Methods

3.2.1 Study area

The River Clyde is located in west central Scotland (between Lat: 56^o N & 55^o 30' N and Long: 004^o 73' W & 003^o 55' W). The catchment covers an area of 3,125 km^2 with a total river length of 4,165 km and 26 km^2 of freshwater lochs and reservoirs. Land use in the catchment is dominated by agriculture (45%) and natural and semi-natural habitats (37%) with urban land use comprising 18%, the remaining 1% being lochs and reservoirs. Although urban land use does not dominate, in 2006, 31% (1.6M) of the total population of Scotland lived within the catchment (General Register Office for Scotland Report, 2007). With a history of heavy industry, the River Clyde has been described in the past as one of the worst polluted river basins in Britain (Hammerton, 1986).

3.2.2 Invertebrate community composition

Invertebrate community samples were collected from 59 sites (N = 2971; mean annual number of samples per site = 2 ± 0.02 S.E.), providing a broad spatial coverage within the catchment (Figure 3.1), using a standard kick-sampling method, during routine water quality monitoring by the Scottish Environment Protection Agency (SEPA) and its predecessor organisations between 1975 and 2006 (years 1991-1994 data were missing due to loss of records). Community richness was determined from the list of 82 macroinvertebrate families (not including Aphelocheridae, Brachycentridae, Goeridae, Lepidostomatidae, Odontoceridae, Psychimyiidae and Valvatidae, due to taxonomic and recording issues at the start of the study period) which are recorded as part of the BMWP system (Armitage et al., 1983) used to assess running water quality in Great Britain. Using data at the taxonomic resolution provided by family from the constrained BMWP taxon list to determine community richness has been proven as a highly significant ($r = 0.854$, $p < 0.0001$) representation of species richness found at running water sites in Great Britain (Wright et al., 1998).

3.2.3 Site characteristics

For each site a number of characteristics were measured (Table 3.1).

3.2.3.1 Natural site characteristics

Natural site characteristics (i.e. those which have shown strong associations with the prediction of macroinvertebrate fauna in models like RIVPACS (Wright et al., 1984)); distance from the river source (km), altitude (m), slope (m km^{-1}) were all derived from 1:50,000 scale Ordnance Survey maps using the methods detailed by Murray-Bligh et al. (1997) and; discharge category (Murray-Bligh et al., 1997), which provides a site specific measure of average annual discharge in cubic metres per second (m^3 s^{-1}), was provided by the SEPA hydrology unit (Table 3.2).

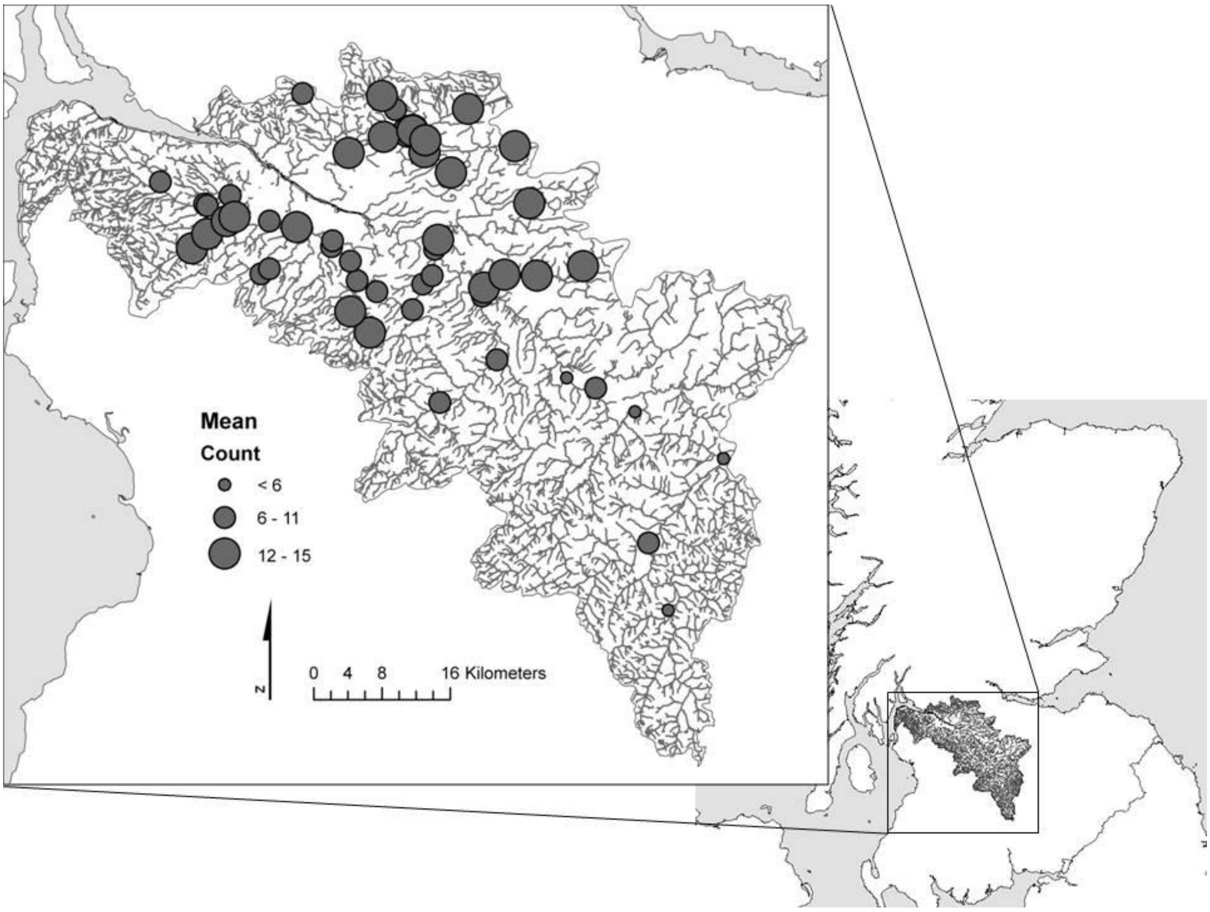


Figure 3.1: Location of the 59 sites at which invertebrate data were collected (2971 samples). The size of the dot is relative to the mean number of samples collected at the associated water chemistry site in the year preceding the invertebrate sample collection.

3.2.3.2 Land use characteristics

Land use characteristics for the watershed catchment upstream of the sampling site, were extracted from the CORINE Land Cover 1990 (CLC1990) dataset (EEA, 1990) using ArcGIS 9.2 (ESRI, 2007).

3.2.3.3 Physico-chemistry characteristics

Water physico-chemistry at the invertebrate sampling sites was derived from existing data collected by SEPA throughout the River Clyde since 1961. Routinely, 10 components of water chemistry were analysed and recorded (Table 3.1). As physico-chemistry samples were rarely collected at the same location as the biotic sample, sites were paired based upon their proximity along the water course. Each invertebrate sampling site was paired with a chemistry sampling site located within a mean distance of 1km (± 2km standard deviation) up- or downstream and with no ingress of a major tributary between paired sites.

The frequency of samples collected at water chemistry sampling sites showed some spatial differences (Figure 3.1), with many of the sampling sites in the upper part of the catchment having a lower mean sampling effort. Each of the 60 water chemistry sampling records was inspected for systematic monthly and/or annual bias in the sampling time series. For each site, an x-y plot of month on year was created and the date (month & year) of each sampling occasion plotted (Figure 3.2). A visual inspection of the x-y plot for each of the water chemistry sites showed no systematic trend in the sample collection time series.

Generally the water physico-chemistry within the River Clyde has improved over the study period (Figure 3.2) however, the highly correlated nature of these measured results in complex relationships which are difficult to disentangle (Figure 3.3).

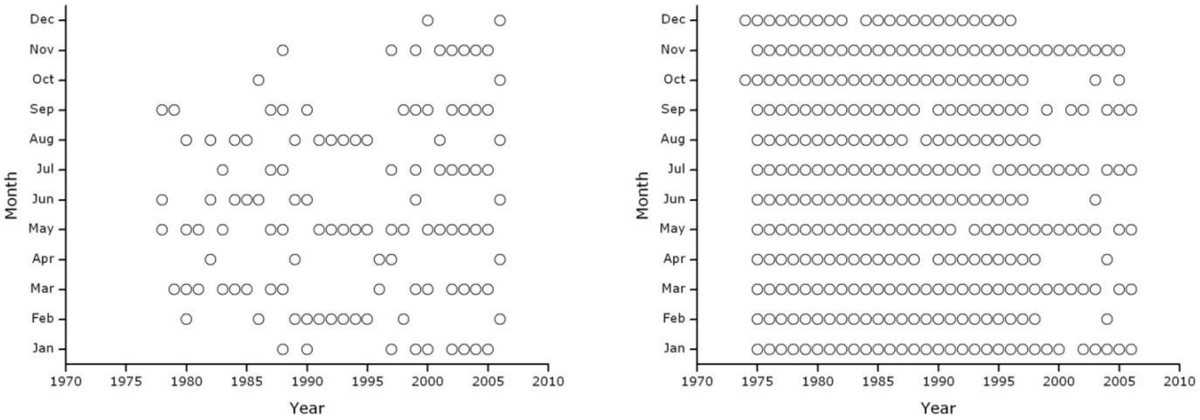
As most of the freshwater invertebrate families here analysed have an annual life cycle and, are therefore likely to be influenced by historic changes in water physico-chemistry, a mean for each of the 10 chemical measures was calculated for the year preceding the collection of each invertebrate sample. This provided a measure of the average value for water physico-chemistry in the year prior to a specific invertebrate community sample. While this measure may not encapsulate the entire influence changing water physico-chemistry has on community structure, an annual average measurement is likely to provide a better indication of water chemistry change than a point measurement.

3.2.4 Statistical methods

To identify and quantify the underlying determinants driving spatio-temporal variation in community taxon richness, a combination of principal components analysis (PCA) and linear regression was used.

3.2.4.1 Environmental drivers of community richness

Explanatory spatial variables were grouped according to the environmental element to which they were related; natural site characteristics, upstream land use or water physico-chemistry (Table 3.1). Due to the highly correlated nature of the spatial explanatory variables (e.g. a site located at high altitude will likely be located in a smaller, steeper stream with a lower annual discharge, than a site located further downstream), PCA was used to produce an index which best described variation within these three environmental elements. For each of the three environmental elements separately, a PCA was undertaken and the values of the first principal component score (i.e. the one explaining the most amount of variation) were extracted, thus each sample had a unique measurement of natural site characteristic, upstream land use and water physico-chemistry. To determine the unique relationship change community richness had, sample community richness was then regressed on these scores in three separate linear regressions.

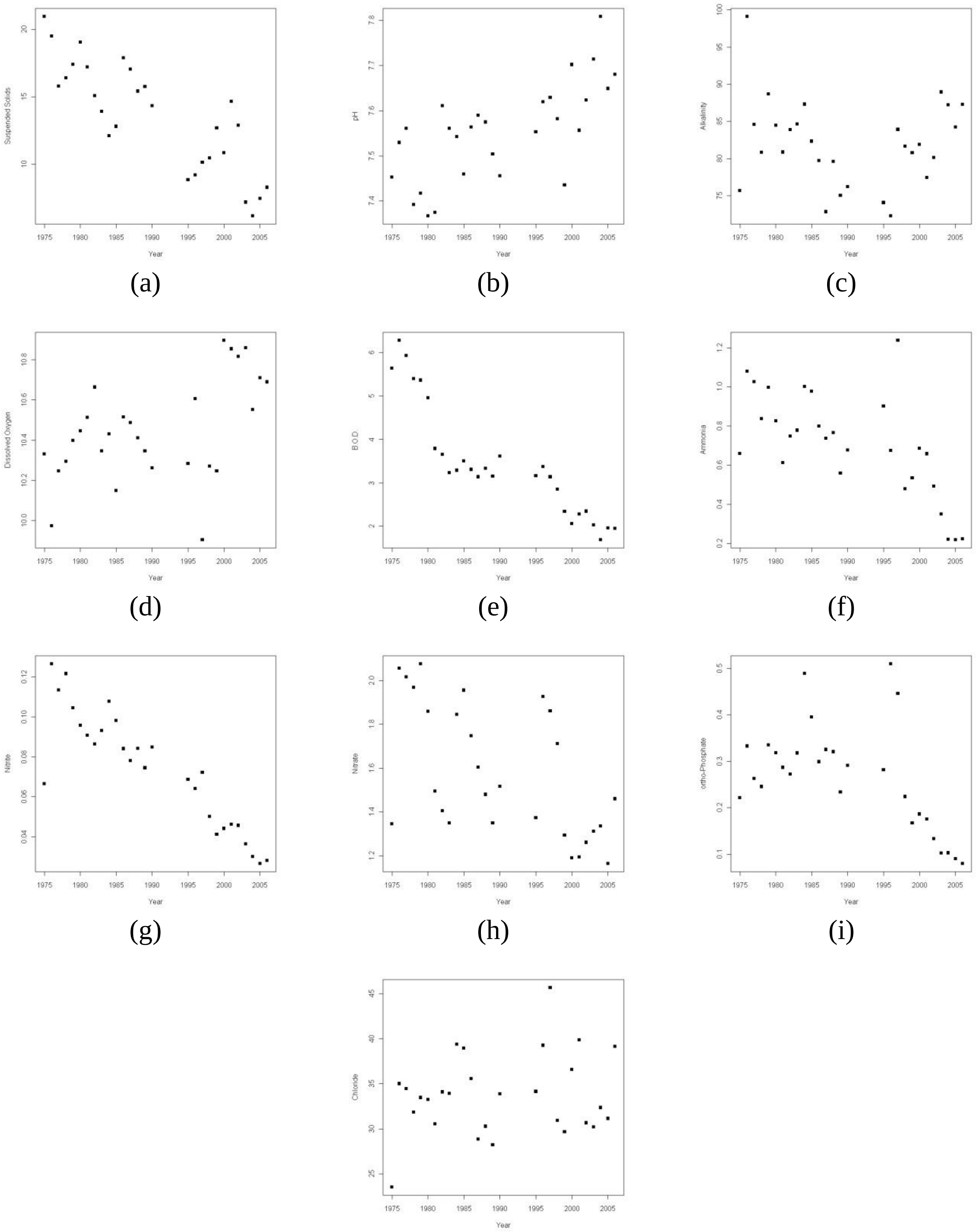


(a) (b)

Figure 3.2: Example of typical temporal sampling patterns at two water chemistry sites; (a) mean annual sampling frequency = 5, (b) mean annual sampling frequency = 11.

3.2.4.2 Temporal change

To account for temporal change in the macroinvertebrate community within the River Clyde, community richness (sample richness), sample BMWP score, and sample ASPT score were separately regressed on sample year. To account for temporal change in water physico-chemistry, the first principal component from the PCA was regressed on year.



(a) (b) (c)

(d) (e) (f)

(g) (h) (i)

(j)

Figure 3.3: Temporal change in mean physico-chemical metrics measured from the River Clyde (1975 to 2006); (a) suspended solids (mg L^{-1}); (b) pH; (c) alkalinity (mg L^{-1}); (d) dissolved oxygen (mg L^{-1}); (e) biochemical oxygen demand (mg L^{-1}); (f) ammonia (mg L^{-1}); (g) nitrite (mg L^{-1}); (h) nitrate (mg L^{-1}); (i) ortho-phosphate (mg L^{-1}); (j) chloride (mg L^{-1}). All metrics are significantly ($p<0.001$) correlated (Spearman method) with year, except alkalinity and chloride.

3.2.4.3 Univariate relationship with community richness

To determine the unique relationship each variable and community richness had, each of the 19 explanatory variables were regressed on community richness separately.

3.2.4.4 Community richness change within the River Clyde

For each of the 19 environmental variables which had a significant relationship with community richness, the regression equation explaining the relationship was used to calculate community richness change over the range of variables (minimum to maximum) for that environmental variable recorded from the River Clyde (Table 3.1). For example, dissolved oxygen values over the 32 year period within the River Clyde varied from 6.23 to 21.7 mg L^{-1}. This range was then used to calculate the change in community richness associated with this change in dissolved oxygen. Thus, for the range of each environmental variable the resultant relative change in community richness could be quantified.

To conform with the assumptions of normality, where appropriate, data were transformed (see Table 3.1 for details) before all analysis. To account for any pseudo-replication associated with repeat site sampling, all linear regressions included sampling site as a random variable. All statistical analyses were performed using R version 2.11.1 (R Development Core Team, 2010).

3.3 Results

3.3.1 Environmental elements defined by PCA

3.3.1.1 Natural site variables PCA

The first principal component from the PCA of natural site variables explained 71.2% of total variance in natural site characteristics. Slope and altitude were negatively loaded while distance from source and discharge category were positively loaded (Table 3.1). Thus the first principal component provided a good index of where a site was located within the catchment. Sites with large negative PC1 scores were low discharge, close to the source of the river, at high altitude with high slope, while sites with large positive loadings were large rivers, with low slope, located at lower altitude far from the river source.

3.3.1.2 Upstream land use variables PCA

The first principal component from the PCA of upstream land use variables explained 51.6% of total variance in upstream land use. Urban and agricultural land use had negative loadings while semi-natural, natural and open water land use had positive loadings (Table 3.1), thus the first principal component provided a good index of the degree to which land upstream of a sampling site retained natural characteristics. Sites associated with large negative loadings had more developed land use (i.e. increased urban and agricultural land), while sites with large positive loadings had more naturalised land use (i.e. semi- natural and natural land types).

3.3.1.2 Water physico-chemistry variables PCA

The first principal component from the PCA of water chemistry variables explained 51.9% of total variance in site associated water physico-chemistry. All variables, except dissolved oxygen, had negative loadings (dissolved oxygen was positively loaded) (Table 3.1). The first principal component thus provided a good general index of water physico-chemistry, with a large negative value associated with poorer water quality (e.g. high nitrates, high suspended solids, high BOD (biochemical oxygen demand), low dissolved oxygen) and a large positive value associated with better water quality (e.g. higher dissolved oxygen, lower suspended solids).

3.3.2 Environmental elements relationship with community richness

All three separate regressions of the environmental elements on community richness were significant (Table 3.2). Water physico-chemistry had a highly significant ($p < 0.001$) positive relationship with community richness, indicating that with increasing water quality the macroinvertebrate community became richer. Upstream land use had a significant positive relationship with community richness, indicating that increasing amounts of semi-natural and natural land use upstream increased community richness. Natural site characteristics had a significant negative relationship with community richness, indicating that community richness was significantly higher at large lowland sites compared to small upland sites.

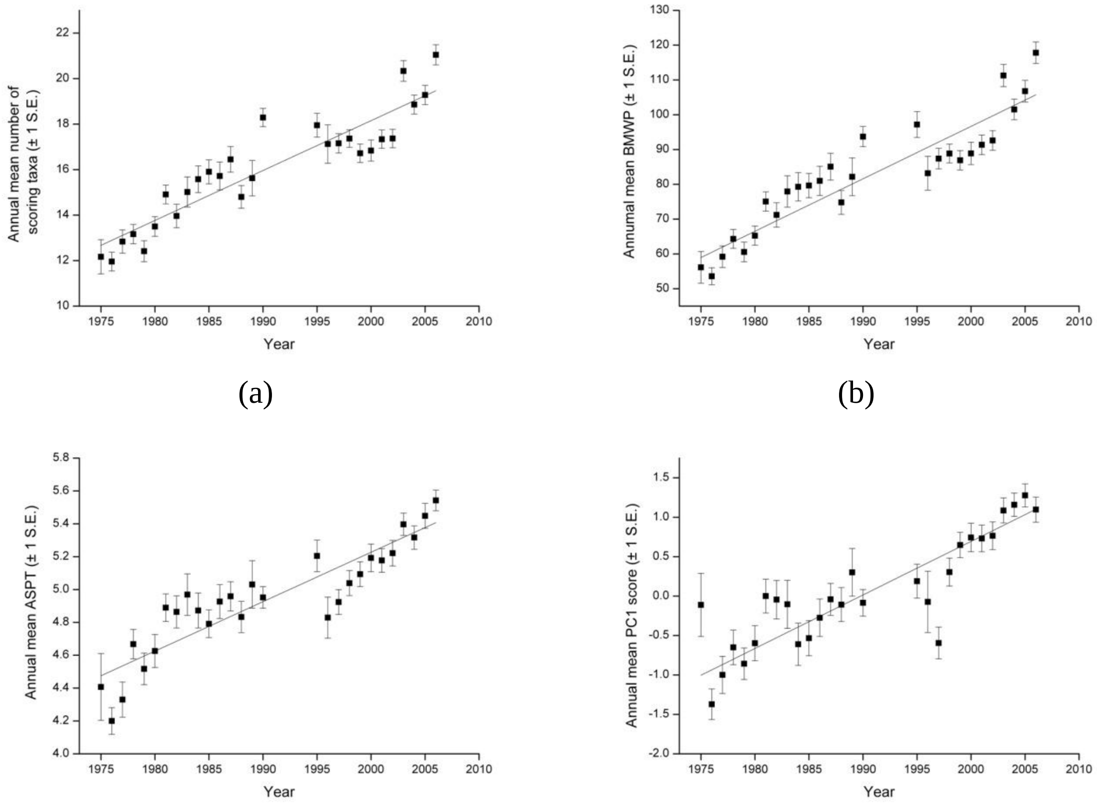
3.3.3 Temporal change in the macroinvertebrate community and environmental elements

The linear regression of community richness on year produced a highly significant ($F_{(1,2969)} = 487$; $p < 0.001$) linear relationship (community richness = 0.19 (± 0.01) * Year – 365.35 (± 13.53) (± 1 S.E.)), which equated to a gain of 6 families to the River Clyde macroinvertebrate community over the 32 year study period (Figure 3.4). The linear regression of BMWP score and ASPT on year were both highly significant positive relationships (BMWP, $F_{(1,2969)} = 583.8$, $p < 0.001$; ASPT, $F_{(1,2969)} = 313.1$, $p<0.001$; Figure 3.3). The linear regression of water physico-chemistry on year was a highly significant ($F_{(1,2969)} = 260$, $p < 0.001$) positive relationship indicating that, using my index of water physico-chemistry, water quality within the River Clyde has improved significantly over the 32 year period (Figure 3.4).

3.3.4 Univariate community richness relationships

3.3.4.1 Natural site characteristics

Slope, distance from source and discharge category were significant in predicting community richness within the River Clyde catchment. Slope showed a significant negative relationship, while distance from source and discharge category had significant positive relationships with community richness (Table 3.1). Altitude did not have a significant linear relationship with community richness.



(a) (b)

(c) (d)

Figure 3.4: Temporal relationship and significant linear regression of (a) community richness; (b) BMWP score; (c) ASPT; and (d) principal component index (PC1) of water physico-chemistry, in the River Clyde between 1975 and 2006 (1991 to 1994 data missing).

3.3.4.2 Upstream land use

All land use types, except agricultural land use, had a significant univariate relationship with community richness (Table 3.1). The area of upstream semi-natural, natural and open water land use had significant positive relationship with community richness while the area of upstream urban land use had a significant negative relationship (Table 3.1).

3.3.4.3 Water physico-chemistry

Eight water physico-chemistry variables had a significant relationship with community richness (Table 3.1). Six (BOD, ammonia, suspended solids, ortho-phosphate, nitrite and nitrate) had a significant negative relationship with community richness, and two (pH and dissolved oxygen) had a positive relationship (Table 3.1).

Table 3.1: Variables used in this study grouped by environmental elements. Range is the minimum and maximum value of the variable recorded from the River Clyde within the 32 year study period; transformation refers to the data transformation used (log = $\log_{10}(x+1)$ and arcsin = $\arcsin(\sqrt{x})$); PC1 loading are the variable loadings from the first principal component from each environmental element PCA; regression results are the regression coefficients and significance from the linear regression of community richness on the explanatory variable (only significant regressions are detailed). Community change is the loss (negative) or gain (positive) in community richness associated with the explanatory variable range recorded from the River Clyde (e.g. increasing BOD from 0.58 to 20.42 mg L^{-1} results in the loss of 15.6 families from the macroinvertebrate community).

Model Variables	**Units**	**Range (min-max)**	**Trans.**	**PC1 Loading**	**Regression Results**			**Community Change**
					Beta	**Intercept**	**Sig.**	
Natural site characteristics								
Discharge Category *	(units)	1-9	log	0.550	6.100	11.812	0.0129	4.3
Distance from Source	(km)	4.9-123.4	log	0.540	3.143	11.812	0.0341	4.2
Slope	(m km^{-1})	0.6-26.3	log	-0.506	-3.402	18.129	0.0163	-4.2
Altitude	(m)	2-169	log	-0.388				

* Discharge category ranges (m^3s^{-1}): Category 1<0.31; 2=0.31-0.62; 3=0.62-1.25; 4=1.25-2.5; 5=2.5-5.0; 6=5-10; 7=10-20; 8=20-40; 9=40-80

Table 3.1: Continued.

Model Variables	Units	Range (min-max)	Trans.	PC1 Loading	Regression Results			Community Change
					Beta	Intercept	Sig.	
Upstream land use								
Semi-Natural	(% cover)	0-87	arcsin	0.502	4.952	14.091	0.0070	6.0
Natural	(% cover)	0-50	arcsin	0.488	5.227	13.886	0.0328	4.1
Urban	(% cover)	0-92	arcsin	-0.472	-7.266	18.448	<0.0001	-9.3
Agricultural	(% cover)	3-87	arcsin	-0.413				
Open Water	(% cover)	0-9	arcsin	0.341	16.471	14.753	0.0073	0.6
Physico-chemistry								
Ammonia	(mg L^{-1})	0.01-12.37	log	-0.375	-12.873	18.113	<0.0001	-14.4
BOD	(mg L^{-1})	0.58-20.42	log	-0.325	-13.818	24.337	<0.0001	-15.6
Nitrite	(mg L^{-1})	0.002-0.933	log	-0.370	-45.743	17.280	<0.0001	-13.1
ortho-Phosphate	(mg L^{-1})	0.002-5.350	log	-0.346	-17.489	17.415	<0.0001	-14.0
Suspended Solids	(mg L^{-1})	1.04-146.5	log	-0.260	-5.601	21.924	<0.0001	-10.4
Nitrate	(mg L^{-1})	0.083-9.65	log	-0.328	-11.089	20.207	<0.0001	-11.0
pH	(units)	6.64-9.08	log	-0.147	134.041	-108.895	<0.0001	16.1
Dissolved Oxygen	(mg L^{-1})	6.23-21.7	log	0.279	32.665	-18.545	<0.0001	16.2
Chloride	(mg L^{-1})	6.8-285.87	log	-0.352				
Alkalinity	(mg L^{-1})	13.83-318.33	log	-0.315				

Table 3.2: Results from the individual regressions of community richness on the three environmental elements.

Environmental Element	Beta	Intercept	t-statistic	Sig.
Water physico-chemistry	1.529	15.827	24.364	<0.0001
Upstream land use	0.899	15.929	3.693	0.0005
Natural site characteristics	-0.666	15.974	-2.578	0.0125

3.3.5 Community richness change within the River Clyde

In total, 15 of the original 19 explanatory variables were significant in predicting variation in community richness within the River Clyde. The change in community richness associated with these 15 relationships was calculated for the range of associated recorded values from the River Clyde using the regression equation (Table 3.1). The largest gain to the macroinvertebrate community was 16.2 families associated with increasing dissolved oxygen from 6.23 to 21.7 mgL^{-1} and the largest loss was 15.6 families associated with increasing BOD from 0.58 to 20.42 mgL^{-1}.

3.4 Discussion

Clear and distinct drivers of community richness have been shown from the River Clyde over the 32 year study period. The effects of water physico-chemistry, land use and natural site characteristics all show significant relationships with macroinvertebrate community richness. The correlation of these variables makes quantifying their differential effects a complicated process. Most of the variables used in this study are common metrics measured as part of the process to assess the ecological state of running water. By using a combination of principal components analysis and linear regression I have attempted to quantify the influence of each variable in structuring macroinvertebrate community richness. My results highlight the relative importance of these drivers in structuring community richness in the River Clyde system over a 32 year period, but individual results must not be viewed in isolation.

The drivers detailed in this study show variation in their spatial and temporal scale, which reflected their relative influence in determining community richness variation. Water physico-chemistry was the strongest driver, compared with upstream land use and natural site characteristics. Water physico-chemistry varies spatially and over short time frames (this is particularly pronounced in a river recovering from a period of water quality degradation). Conversely, upstream land use and natural site characteristics show less temporal variation. Characteristics like slope and altitude remain constant over millennia, and upstream land use can remain relatively constant for years.

3.4.1 Water physico-chemistry

Principal components analysis of the 10 water chemistry measurements, taken in the year preceding the macroinvertebrate sample, highlighted the correlation between variables commonly used to define physico-chemical water quality. Principal component one provided a biologically relevant index for water quality (i.e. negative loadings associated with BOD, ammonia nitrate etc and positive loading associated with dissolved oxygen) with increasingly negative PC1 scores indicative of poorer water quality. The relationship between this index for water quality and macroinvertebrate community richness was highly significant and, although no direct comparison can be made between this relationship and the other two environmental elements (i.e. upstream land use and natural site characteristics), the strength of the relationship (i.e. $p < 0.0001$) suggests that, of the environmental elements analysed here, water quality is likely to be more important in explaining variation and driving change in macroinvertebrate community richness.

Reductions in the amount of ammonia, nitrite and nitrate within the River Clyde accounted for individual gains of 14.4, 13.1 and 11 families to the macroinvertebrate community. Increasing concentrations of nitrogen based compounds, like ammonia, have been shown to reduce macroinvertebrate abundance (Versteeg et al., 1999) and affect macroinvertebrate community structure, with higher concentrations of ammonia and nitrate leading to dominance by a few species (Maul et al., 2004; Hichman & Lotfi, 2007). Decreasing BOD within the river system also showed a significant negative relationship with community richness. Within the River Clyde a decrease in BOD from 20.42 mgL^{-1} to 0.58 mgL^{-1} accounted for an increase of 15.6 families to the macroinvertebrate community. Ortho-phosphate, suspended solids, pH (of the range measured here) and dissolved oxygen also showed significant relationships in structuring community richness.

3.4.2 Upstream land use

The first principal components score of the PCA of the five upstream land use types provided an intuitive index for upstream land use type. Negative values of PC score 1 were associated with upstream land use dominated by increasingly developed land (i.e. agricultural and urbanised land), while positive values were associated with more naturalised land use (i.e. semi-natural, natural and open water). Macroinvertebrate community richness was significantly higher at sites which were dominated by more naturalised upstream land use compared to those sites with increased upstream modification.

This relationship was reflected in the univariate analysis of the upstream land use types, with urban land use showing a highly significant negative relationship with community richness and, semi-natural, natural and open water each having a significant positive relationship with community richness. Although only accounting for 18% of the total landuse type within the catchment, upstream urban land use had the strongest relationship ($p<0.0001$) with community richness change. The overarching influence of this land use type was calculated to account for the loss of 9.3 families from the macroinvertebrate community if upstream urbanised land increased from 0 to 92%, roughly equating to a loss of one family for every 10% increased in urbanised land. Urban land-use affects macroinvertebrate communities, through modifications to almost all conceivable aspects of the surrounding landscape and watercourse. Alteration of the riparian zone in urban environments can result in more erratic hydrology caused by runoff over impervious substrates, modifications to the instream habitat through sediment inputs and channelisation, and restricted interactions at aquatic and terrestrial margins (Paul & Meyer, 2001; Allan, 2004).

Increased upstream semi-natural land use significantly increased macroinvertebrate community richness. Semi-natural land use within the River Clyde catchment is dominated by natural grasslands (79% of semi-natural land use) and coniferous forest (18%). Generally, semi-natural grasslands within the catchment are used as rough grazing for sheep, which may result in slight nutrient enrichment increasing productivity. The positive relationship between coniferous forest and stream macroinvertebrate richness does not follow usual trend where this type of forestry has been reported to have a negative impact on richness (e.g. Ormerod et al., 1993). However, in the areas of the River Clyde where there is managed forestry, generally plantations have followed Forestry Commission guidelines (Forests & Water Guidelines, 2003) by employing a buffer zone of planted native deciduous trees. It is likely that these buffer zones have increased the coarse particulate organic matter through leaf litter which has been shown to have a positive effect on community richness through resource provision in terms of food (Wallace et al., 1997) and case building materials (Eggert & Wallace, 2003). . Natural land use within the catchment is dominated by moors and heath (95% of total natural land use) which soil type in most commonly peat in the River Clyde catchment which has shown here to have a significant positive relationship with community richness.

3.4.3 Natural site characteristics

The first PC score from the PCA of natural site characteristics provided an index for the location of a site within the catchment. Negative scores were associated with small sites located at higher altitude (small upland), while positive scores were associated with larger sites at lower altitude (large lowland). PC1 showed a positive relationship with community richness, with large lowland sites having significantly higher community richness than those sites located in small upland parts of the catchment. Of the natural site characteristics discharge category, distance from the river source and slope were significant drivers in the prediction of community richness change. Increasing discharge category and distance from the river source significantly increased community richness. Both of these characteristics are a good surrogate for river size, with increasing discharge category and distance from source corresponding to increasing width and depth, which have been shown to have a positive correlation with family richness (Wright et al., 1998). With increasing river size it is likely that there is an increase in the number of micro- and macro-habitats available, thus allowing a greater number of species to be supported. Other studies have shown that discharge category is important in structuring macroinvertebrate communities (Wright et al., 1984; Murphy & Davy-Bowker, 2005). Increasing slope significantly reduced community richness which has been highlighted before (Wright et al., 1998).

3.4.4 Temporal change in community richness

Over the 32 year study period community richness in the River Clyde has increased on average by the addition of 6 families (0.18 families yr^{-1}) to the macroinvertebrate community. Other documented recovery times vary from less than a few months in response to flood disturbance, to recovery times in excess of 52 years as a result of channelisation (Niemi et al., 1990), however direct comparison here with published recovery times is difficult due to variations in sampling methods, biotic metrics quantified and the endpoints of recovery selected.

Within the River Clyde there has been a significant improvement in the water quality, as revealed from the regression of water physico-chemistry PC1 score on year. As, of the three environmental elements, water quality had the strongest relationship with community richness change, it is therefore likely that the significant temporal change in macroinvertebrate community richness is dominated by improvements made to water quality within the catchment.

By using a spatially and temporally extensive dataset, I have been able to quantify the effects of various environmental drivers in changing macroinvertebrate community richness. The highly complex interacting nature of these variables results in the reporting of only general patterns. I recognise that the relationships detailed here are River Clyde specific; however the provision of results from a long-term study of a recovering river system is rare and providing results which can be interpreted for other study areas is key to further our understanding of restoration ecology, a relatively new area of scientific study.

CHAPTER 4 Do shifting dynamics of disturbed riverine invertebrate communities prevent them achieving a ‘pristine’ condition?

4.1 Introduction

Freshwater systems, particularly rivers are now recognised as the most endangered ecosystems in the world (Dudgeon et al., 2006; Vörösmarty et al., 2010). Their importance as the largest source of renewable fresh water has at least in part driven global efforts to restore river systems impacted by human activity (Vörösmarty et al., 2010), although effort is highly skewed towards developed regions (e.g. USA and Western Europe) (Vörösmarty et al., 2010).

The restoration and recovery of disturbed systems is a complex process influenced by multiple deterministic and stochastic factors. The dispersal abilities and proximity of colonising populations will influence colonisation patterns (Palmer, 1996; Sutherland, 1974; Urban & De Meester, 2009). The type of disturbance can influence habitat and resource availability through changes to the habitat as a direct result of the disturbance (e.g. catastrophic flood event) or change the resource availability (e.g. fire affecting soil nutrients). These and many other factors constitute the ecological history of a community which has been shown to influence the endpoint structure of reassembled communities (Fukami & Morin, 2003; Ledger et al., 2006).

Currently, the assessment of the degree to which a system has been disturbed often involves a comparison of current community composition to either a historic reference or a perceived ideal (Salagdo et al., 2010; Szkokan-Emilson et al., 2010). Given recent insights into the role that ecological history plays in shaping contemporary community composition, it is likely to be over-simplistic to use historic or perceived reference points as a bench mark against which to measure community recovery.

One widely used model of impact assessment is the reference condition approach used to assess the biological quality of running waters. Pioneered by Wright et al. (1984), the RIVPACS (River InVertebrate Prediction and Classification System) software approach has provided a template for water quality assessment which is now used worldwide (AUSRIVAS (Australia), Davies 2000; BEAST (North America), Reynoldson el al., 2000; $\text{SEPAC}_{\text{SRI}}$ (Sweden), Davy-Bowker et al., 2006; PERLA (Czech Republic), Kokeš et al., 2006). RIVPACS software generates a list of ‘target’ fauna based on a small suite of environmental characteristics (e.g. site distance from the source of the river, altitude, slope) which have been shown to be highly significant in predicting with good accuracy the macroinvertebrate community composition at a site free from human mediated impact (Wright et al., 1984). The target fauna are listed as probabilities of capture at a site and these probabilities are used to generate biotic indices. These predicted biotic indices are then compared to those calculated from the collected sample and, deviations from unity are frequently reported as a measure of the current biological state of a stretch of river. Deviation from predicted community composition does provide a suitable assessment of the degree to which the community at a site has been impacted, but is this deviation suitable to assess the degree of recovery of a community following disturbance?

In this study I tested the validity of RIVPACS v.III+ (Clarke et al., 2005) predictions in a large river system recovering from a period of water quality degradation. Using long-term data, I tested whether recovering communities are likely to attain a composition similar to the ‘target’ composition predicted by RIVPACS.

4.2 Methods

To test the likelihood that recovering communities attain a composition similar to the ‘target’ composition predicted by RIVPACS we used data on freshwater invertebrate community composition collected from a large river (catchment area = 3,125 km^2), the River Clyde (Lat: 56^o N & 55^o 30 N and Long: 004^o 73W & 003^o 55W) between 1975 and 2006. The River Clyde is recovering from a period of water quality degradation and its invertebrate communities show a general increase in diversity. However, significant differences occur between sites in the rate of change in community diversity.

Invertebrate community samples were collected from 65 sites (N = 3446; mean annual number collected per site = 2 ± 0.02 S.E.), using a standard kick-sampling method, during routine water quality monitoring by the Scottish Environment Protection Agency (SEPA) and its predecessor organisations. Community richness was determined from the list of 82 macroinvertebrate families (not including Aphelocheridae, Brachycentridae, Goeridae, Lepidostomatidae, Odontoceridae, Psychimyiidae and Valvatidae, due to taxonomic and recording issues at the start of the study period) that are recorded as part of the BMWP system (Armitage et al., 1983) which is used to assess running water quality in Great Britain. Using data at the taxonomic resolution provided by families from the constrained BMWP taxon list to determine community richness has been proven as a highly significant ($r = 0.854$, $p < 0.0001$) representation of species richness found at running water sites in Great Britain (Wright et al., 1998).

4.2.1 Common macroinvertebrate families in the River Clyde

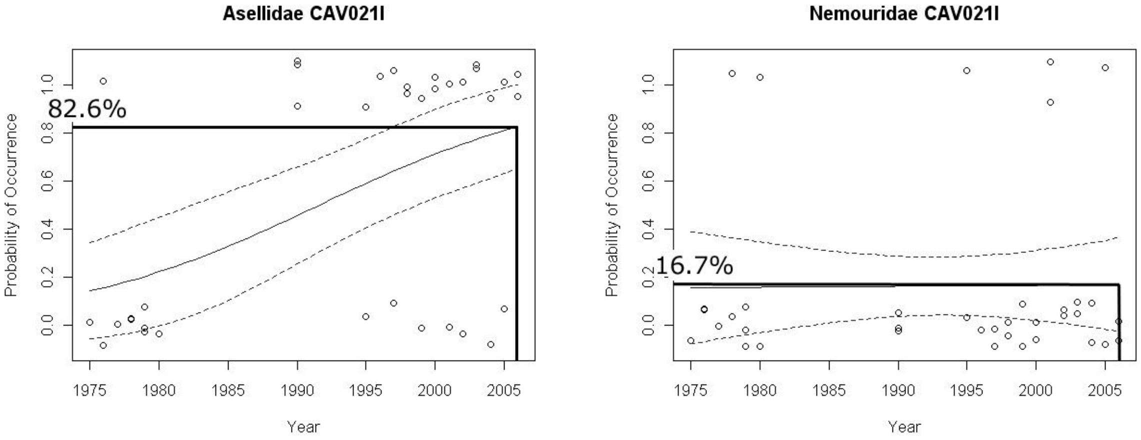
To determine which families typified the community composition of the River Clyde catchment and to avoid including those families which appeared in collected samples only sporadically, the number of sites at which each family had been recorded in the River Clyde was determined. Only those families which had been recorded at a minimum of 15 of the 65 sites were determined as suitable representatives of the River Clyde macroinvertebrate community.

4.2.2 Definition of site recovery

To determine which sites were recovering, the annual rate of change in family richness was calculated using linear regression. Number of families recorded in a sample was regressed on sampleyear for each site separately providing a site specific measurement of annual rate of change in family richness. Those sites showing a significant (Bonferroni corrected) increase in family richness were determined to be recovering.

4.2.3 Site community composition in 2006

Each family's presence or absence was recorded for each of the 65 sites throughout the 32 year period. The start date of monitoring varied between sites with the majority (50 sites) starting in 1975 and 1976, and the latest starting in 1979 (8 sites). Monitoring then continued until 2006 (years 1991-1994 data were missing due to loss of records), for all sites except two where monitoring ceased in 2003 and 2005. To determine the probability of occurrence of the common macroinvertebrate families at a site in 2006 and to reduce the stochastic effect of variation in the detection of a family at a site, the presence/absence of a family was regressed on year in a logistic regression (Figure 4.1). This provided a measurement of the probability of occurrence for each of the common families in the River Clyde for each of the 65 sites.



Asellidae CAV021I

Nemouridae CAV021I

Figure 4.1: Probability of occurrence of families Asellidae and Nemouridae from one of the sites on the River Clyde. Using the logistic regression, the probability of occurrence of the families is 82.6% and 16.7% respectively in 2006.

4.2.4. 'Target' community composition

For all sites showing a significant change in family richness (i.e. undergoing recovery) the 'target' community was predicted using RIVPACS III+ software (Clarke et al., 2005). Measurements of the environmental variables taken in 2006 in two sampling seasons defined as spring (February-May) and autumn (September-January) were used to predict the probability of capture of each family at a site in the absence of stress. At each site separately, the probability of capture of each family was averaged for the two seasons to provide a site specific measurement of the probability of capture for each of the most common families (those recorded at a minimum of 15 of the 65 sites) found in the River Clyde in 2006.

4.2.5. Comparison of community composition

To determine the likelihood of RIVPACS predicting a suitable ‘target’ macroinvertebrate composition for the River Clyde, for each of the common families individually, the probability of capture at a site (as determined from RIVPACS software) was paired with the probability of occurrence at a site (as determined from the logistic regression). Paired t-tests were used to test the statistical difference between the predicted probability of capture (RIVPACS predictions) and the observed probability of occurrence (logistic regression results) for each of the common families separately. To conform to the assumptions of normality, data were arcsine transformed ($x' = \text{arcsine}\sqrt{x}$) before statistical testing.

All statistical analysis was performed using R version 2.11.1 (R Development Core Team, 2010).

4.3 Results

4.3.1 Common macroinvertebrate families from River Clyde

Of the families comprising the BMWP list, 64 were recorded from the River Clyde catchment and 42 of these were recorded from a minimum of 15 sites and thus deemed common families (Table 4.1).

4.3.2 Definition of site recovery

Linear regressions of number of families recorded on year for each of the 65 sites in this study indicated 37 sites which had shown a significant (Bonferroni corrected) change in the number of macroinvertebrate families recorded over the 32 year period. The rate of change in number of families ranged from an increase of 0.143 families per year to 0.545 families per year.

Table 4.1: Mean of all sites (± 1 standard error), minimum and maximum, probability of occurrence (site logistic regression results) and probability of capture (RIVPACS predictions) for the 42 common macroinvertebrate families in the River Clyde between 1975 and 2006.

Family	**Probability of occurrence (Site)**			**Probability of capture (RIVPACS)**		
	Mean (± S.E.)	**Min.**	**Max.**	**Mean (± S.E.)**	**Min.**	**Max.**
Ancylidae	80.6 (3.3)	0.0	100.0	67.5 (1.4)	46.9	80.0
Asellidae	69.2 (5.8)	0.0	100.0	26.8 (2.5)	4.3	52.0
Baetidae	99.3 (0.5)	83.3	100.0	97.8 (0.2)	94.6	99.4
Caenidae	32.6 (5.1)	0.0	98.7	55.9 (3.6)	20.3	83.4
Capniidae	4.1 (1.1)	0.0	27.8	4.0 (0.3)	0.0	7.5
Chironomidae	94.0 (1.4)	62.7	100.0	96.3 (0.3)	93.8	98.9
Chloroperlidae	21.9 (3.9)	0.0	76.4	30.0 (2.4)	8.8	59.6
Corixidae	1.8 (0.8)	0.0	17.1	3.9 (0.3)	1.3	9.4
Dendrocoelidae	16.7 (4.5)	0.0	97.5	6.3 (1.0)	0.1	30.7
Dytiscidae	36.2 (4.2)	0.0	83.6	34.9 (1.8)	26.9	98.1
Elmidae	80.1 (4.4)	0.6	100.0	96.5 (2.2)	16.3	99.7
Ephemerellidae	38.3 (3.1)	5.3	95.2	31.0 (1.1)	13.1	41.9
Erpobdellidae	72.8 (5.1)	0.0	100.0	44.2 (3.3)	11.7	75.0
Gammaridae	93.4 (1.6)	57.6	100.0	82.6 (2.5)	11.2	96.5
Glossiphonidae	50.1 (4.7)	0.2	98.8	42.2 (2.8)	7.8	65.3
Gyrinidae	15.6 (4.8)	0.0	100.0	32.4 (2.5)	3.4	62.0
Haliplidae	5.9 (2.3)	0.0	79.7	17.8 (2.3)	1.9	87.8
Heptageniidae	90.5 (3.2)	11.2	100.0	87.9 (1.9)	27.0	97.8
Hydrobiidae	67.1 (4.3)	0.4	99.6	59.3 (2.5)	25.6	76.8
Hydrophilidae	29.1 (4.2)	0.0	82.1	45.9 (1.4)	31.1	81.4
Hydropsychidae	81.8 (3.9)	6.8	99.9	90.1 (2.1)	17.5	96.5
Hydroptilidae	28.0 (4.0)	0.0	86.5	26.6 (1.9)	5.9	41.3
Leptoceridae	38.4 (5.5)	0.0	100.0	30.4 (2.5)	4.7	60.5
Leptophlebiidae	37.2 (5.4)	0.0	95.4	25.8 (1.8)	13.1	82.5
Leuctridae	55.6 (5.0)	0.0	97.8	59.1 (2.3)	36.6	84.3
Limnephilidae	57.7 (4.3)	0.0	100.0	61.3 (3.0)	24.6	86.6
Lymnaeidae	53.9 (4.3)	9.8	100.0	43.8 (2.3)	27.0	91.0
Nemouridae	33.8 (3.9)	0.0	85.6	71.6 (2.2)	42.6	96.5
Oligochaeta	96.9 (1.0)	74.4	100.0	95.6 (1.7)	36.5	98.9
Perlidae	0.3 (0.2)	0.0	4.3	30.4 (2.3)	10.5	80.4
Perlodidae	38.8 (4.9)	0.0	100.0	69.4 (2.1)	1.7	82.5
Physidae	20.6 (4.2)	0.0	82.1	9.4 (1.4)	1.5	46.8
Planariidae	53.0 (6.2)	0.0	100.0	44.7 (1.5)	0.8	55.3
Planorbidae	17.8 (4.0)	0.0	98.1	11.1 (1.7)	0.8	52.0
Polycentropidae	27.7 (4.8)	0.0	100.0	48.5 (1.5)	30.4	89.6
Rhyacophilidae	88.7 (2.7)	26.0	100.0	86.9 (1.2)	53.5	93.7
Sericostomatidae	57.5 (5.3)	0.0	100.0	49.4 (1.5)	7.4	61.9
Sialidae	6.0 (2.7)	0.0	100.0	8.2 (1.9)	2.8	73.3
Simuliidae	84.8 (1.9)	58.3	100.0	80.3 (2.2)	6.0	90.2
Sphaeriidae	76.2 (2.9)	34.7	99.2	52.2 (2.2)	26.0	74.9
Taeniopterygidae	15.3 (2.6)	0.0	44.8	30.2 (0.8)	15.3	38.9
Tipulidae	66.5 (4.0)	7.9	100.0	82.8 (0.8)	70.6	89.5

4.3.4. Site community composition in 2006

For each of the 42 common families recorded from the River Clyde, the probability of occurrence for each family was calculated for each of the 37 sites showing a significant change in family richness. Each family showed a large range (0% to 100%) in probability of occurrence at a site (Table 4.1).

4.3.5 'Target' community composition

For the 37 sites showing a significant change in family richness, the RIVPACS 'target' community composition was produced based on the 2006 physical and environmental data. For the 42 common families recorded from the River Clyde, RIVPACS predictions for the probability ranged from 0% to 100.0% (Table 4.1).

4.3.6 Comparison of community composition

Paired t-tests revealed significant differences between the proportional probability of occurrence (logistic regression) and the probability of capture (RIVPACS predictions) for 17 of the 42 common families in the River Clyde (Table 4.2).

Six families (Sphaeridae, Asellidae, Baetidae, Gammaridae, Erpobdellidae and Ancylidae) had significantly higher probability of occurrence at a site than that predicted by RIVPACS software. Eleven families (Perlidae, Nemouridae, Corixidae, Taeniopterygidae, Haliplidae, Perlodidae, Gyrinidae, Hydrophilidae, Caenidae, Chloroperlidae and Polycentropodidae) had significantly lower probability of occurrence at a site than the probability of capture predicted by RIVPACS (Table 4.2).

A t-test of the BMWP score for those families with a lower observed probability of occurrence than predicted by RIVPACS was significantly ($p = 0.003$) higher (mean 7.4) than those with an higher observed probability of occurrence than predicted by RIVPACS (mean 4.2), thus indicating that RIVPACS was generally over-predicting pollution intolerant families and under predicting pollution tolerant families.

Table 4.2: p-value after Bonferroni correction (parenthesis) and BMWP score of family (square brackets) for macroinvertebrate families showing a statistically significant difference between site probability of occurrence and RIVPACS predicted probability of capture.

Higher probability at a site than RIVPACS predictions			**Lower probability at a site than RIVPACS predictions**		
Sphaeridae	(<0.001)	[3]	Perlidae	(<0.001)	[10]
Asellidae	(<0.001)	[3]	Nemouridae	(<0.001)	[7]
Baetidae	(<0.001)	[4]	Corixidae	(<0.001)	[5]
Gammaridae	(<0.001)	[6]	Taeniopterygidae	(<0.001)	[10]
Erpobdellidae	(<0.05)	[3]	Haliplidae	(<0.001)	[5]
Ancylidae	(<0.05)	[6]	Perlodidae	(<0.001)	[10]
			Gyrinidae	(<0.01)	[5]
			Hydrophilidae	(<0.01)	[5]
			Caenidae	(<0.01)	[7]
			Chloroperlidae	(<0.05)	[10]
			Polycentropodidae	(<0.05)	[7]

4.4 Discussion

Using only family groups which are known to be common in the River Clyde catchment I have shown that there are significant discrepancies between the macroinvertebrate fauna at recovering sites within the River Clyde compared with predictions of occurrence of ‘target’ fauna for these sites using RIVPACS III+ software. RIVPACS over predicted the probability of occurrence of eleven families in recovering sites (compared with the observed probability of occurrence) and significantly under predicted for six families. For 25 families there was no significant difference between observed and predicted family occurrence probability. Thus, the application of a simple comparison of a RIVPACS prediction of community composition with a collected sample would likely, significantly underestimate the actual recovery of that site in terms of BMWP score. Those families which had a higher probability of occurrence at a site than that predicted by RIVPACS were relatively pollution tolerant (BMWP score ranged from 3 to 6), while those with a lower probability of occurrence at a site than that predicted by RIVPACS were relatively less pollution tolerant.

There are several possible mechanisms that may explain this pattern of results. During the period of water quality degradation, community composition would have been dominated by pollution tolerant families (the basis of pollution indices). Following improvements to water quality, the pollution tolerant families resident in the community may influence endpoint community composition by occupying niches which, under more ‘natural’ conditions, would be occupied by other less pollution tolerant families. For example, the pollution tolerant family Asellidae in the River Clyde is represented by *Asellus aquaticus*. Food items for this isopod are diverse and include resource gathering via shredding, grazing, detrivorous, xylophagous and predatory feeding mechanisms (Moog, 2002). Initially the ability of this species to withstand poor water quality would have given it a competitive advantage and allowed it to persist. Following improvements to water quality, the diverse feeding strategies may have enabled *A. aquaticus* to occupy niche space, which would under more ‘natural’ conditions be occupied by other species (for example those families over predicted by RIVPACS software).

It is also likely that families over represented by RIVPACS predictions may have been unable to invade and establish within a community following water quality improvements as niche space under improved water quality conditions may now be occupied by other families adopting a similar niche space which recolonised first. For example, niche space for the active predatory family Perlidae may now be occupied by another actively foraging predator, like Rhyacophilidae (Elliott, 2005) or Erpobdellidae (Kreuter et al., 2008). Both Rhyacophilidae and Erpobdellidae are more tolerant of poor water quality than is the family Perlidae, possibly allowing them to establish within a community before water quality recovers enough to support Perlidae.

Fundamental changes to the landscape may also be hindering the colonisation and establishment of some groups as a result of increased urbanisation (Smith et al., 2009). For example, the presence of road culverts along river stretches has been shown to affect the upstream dispersal abilities of Trichoptera (Blakely et al., 2006). Changes to the physical structure of the river, in terms of riparian vegetation, substrate structure and flow modifications (Allan, 2004; Paul & Meyer, 2001), may be hindering the re-colonisation of some groups resulting in their over-prediction by the RIVPACS model.

Invasive species may also be influencing the disparity between site community composition and RIVPACS predictions. The over prediction of Gammaridae may be a result of the presence of the invasive North American freshwater amphipod *Crangonxy pseudogracilis* which is now widespread throughout the River Clyde catchment (pers. obs.). This invasive amphipod has been shown to tolerate complementary and contrasting physico-chemical regimes to the native *G. pulex* (MacNeil et al., 2000) possibly expanding the riverine distribution of the family Gammaridae in the River Clyde. This expanded distribution may result in increased detection rates of this family at sites which, under pristine (i.e. non-invaded) conditions would not support Gammaridae to the same degree.

The disparity between site observations and RIVPACS predictions may have serious implications for the assessment of recovery in running water systems. The results from the 2006 survey undertaken by SEPA (Scottish Environment Protection Agency) at the sites used in this study show that 18 of the 37 sites in this study have achieved ‘excellent’ status in terms of taxon richness. Of these 18 sites however, 16 were downgraded as a result of lower than predicted Average Score Per Taxon (ASPT). The ASPT is the average family pollution score for the sample (i.e. the BMWP score divided by number of scoring taxa), thus downgrading the community as a result of low average score suggested that the community may have recovered in terms of richness but is showing a significantly different community composition than that expected if the site had not been subjected to poor water quality. It is therefore likely that a large investment would be required to return community composition to that of the perceived ideal as it may involve culling certain species to allow others to re-establish (Persson et al., 2007).

The use of community traits and functionality has been suggested previously as a more accurate bio-monitoring assessment tool (Doledec et al., 1999). However it may be possible to resolve the disparity between RIVPACS predictions and contemporary community composition by readdressing the balance between the taxonomic and functional response of the recovering community, by changing the current banding for richness and ASPT categories. This is therefore likely to produce a more accurate assessment of community recovery using existing assessment mechanisms.

CHAPTER 5 Resource use of an invading predator is predicted by colonisation patterns

5.1 Introduction

Understanding the rules that govern community assembly is becoming increasingly important. Management of new species invasions, shifts in conservation direction from maintaining pristine to rehabilitating disturbed habitats and global efforts to restore damaged ecosystems all require an understanding of how communities are formed. Resource competition within a community is a fundamental mechanism involved in community structure and function. Much recent research has focussed on the effect invasive (i.e. non-native) species have on the invaded community (Ehrenfeld, 2010) and resultant resource competition with native species (Olsson et al., 2009; Suding et al., 2004). Restoration ecology has also provided some insights into the effects of resource competition but research in this field is mostly focused onplant communities. Here too, research into resource utilisation most often involves manipulating the interaction between invasive and native species as part of the recovery process (e.g. MacDougall & Turkington, 2005; but see Baer et al., 2004). Mechanisms governing resource use in a community reforming from a native species pool and subject to natural processes are less well understood.

The utilisation of resources following colonisation and establishment within a community has implications for both the coloniser and the colonised community. A colonising organism can affect community resource utilisation through multiple pathways. For example, direct competition for resources (Amarasekare, 2002; Maron & Marler, 2008;

Baer et al., 2004) competition for physical space (Erladsson et al., 2006) and changes to the physical habitat following colonisation (Kilronomos, 2002) can influence the quality and quantity of resources available and can ultimately effect ecosystem function (e.g. Persson et al., 2007).

The influence of the community on the resources used by the colonising species has implications for the future functioning of the community. Resource use affects the growth and reproduction of an organism (Naya et al., 2007; Browne et al., 2006) and its offspring (Kyneb & Toft, 2006), which may ultimately affect community functionality. Resource usage of colonising organisms may therefore provide insight into the future functionality of recovering or invaded communities.

Stable isotope analysis has provided a powerful tool to analyse the resource use of animals. Variation in the stable isotopes of nitrogen and carbon in tissue provides insights into long term diet as ^{15}N and ^{13}C isotopes are enriched relative to ^{14}N and ^{12}C isotopes, in consumer tissue compared to the resource consumed (DeNiro & Epstein, 1978; DeNiro & Epstein 1981). On average, the ^{15}N/^{14}N ratio increases by 3-4 ‰ (Post, 2002) per trophic level, while ^{13}C/^{12}C has a relatively smaller fractionation, increasing on average by 0.5-1‰ per trophic level (Post, 2002). Change in nitrogen isotope enrichment is frequently used to identify trophic position, while carbon isotopic enrichment is used to identify the utilised carbon source. Nitrogen and carbon stable isotope ratios can provide information about the long term resource utilisation of individual animals.

Rhyacophila dorsalis is a predatory Trichopteran (Moog, 2002) and, when present in riverine macroinvertebrate communities, is indicative of good water quality. Resource use of *R. dorsalis* within a river recovering from a period of water quality degradation may provide some insights into mechanisms governing community assembly. Using stable isotope ratios of resident and re-colonising *R. dorsalis* populations, here I investigated differences in resource utilisation between these two population types and attributed resource use differences to colonisation patterns. Specifically, I investigated whether competition, the richness of the colonised community, the rate at which colonisation proceeded and the time elapsed since colonisation, affected the resultant resource use of this colonising predator.

5.2 Methods

5.2.1 Study area and site selection

The River Clyde is located in West Central Scotland (between Lat: 56^{o} N & 55^{o} 30’ N and Long: 004^{o} 73’ W & 003^{o} 55’ W). The catchment covers an area of 3,125 km^{2} with a total river length of 4,165 km and 26 km^{2} of freshwater lochs and reservoirs. Landuse in the catchment is dominated by agriculture (45%) and natural and semi-natural habitats (37%) with urban landuse comprising 18%, the remaining 1% being lochs and reservoirs. Although urban landuse does not dominate, in 2006, 31% (1.6M) of the total population of Scotland lived within the catchment (General Register Office for Scotland Report, 2007). The River Clyde has been described in the past as one of the worst polluted river basins in Britain (Hammerton, 1986), but has in recent decades shown a marked improvement in water quality as a result of restoration efforts.

Sampling sites were chosen based on the presence of Rhyacophilidae in historic macroinvertebrate monitoring records collected between 1975 and 2006 by the Scottish Environmental Protection Agency (SEPA) and its predecessor organisations. Sites at which Rhyacophilidae had been recorded throughout the 32 year period (i.e. the Rhyacophilid population had always been resident) were defined as ‘resident sites’. Sites at which Rhyacophilidae had been initially absent or only recorded very occasionally in the monitoring records time series and then, had subsequently recolonised the site (i.e. in later years Rhyacophilidae were consistently recorded at the site) were defined as ‘colonisation sites’. Using these criteria, 5 ‘resident sites’ and 7 ‘colonisation sites’ were identified (Figure 5.1). Rhyacophilidae in the River Clyde are almost exclusively represented by *Rhyacophila dorsalis* (Curtis).

5.2.2 Colonisation patterns

Rhyacophilidae colonisation patterns at the 7 colonisation sites were determined using historic detection/non-detection records. To reduce the stochastic variation in the detection of Rhyacophilidae at a site, Rhyacophilidae detection/non-detection was regressed separately on both year and community richness using logistic regression (Figure 5.2). Community richness was defined as the number of macroinvertebrate Families recorded in each sample as determined from the list of 82 macroinvertebrate Families recorded as part of the BMWP system (not including Aphelocheridae, Brachycentridae, Goeridae, Lepidostomatidae, Odontoceridae, Psychimyiidae and Valvatidae, due to taxonomic and recording issues at the start of the study period) (Armitage et al., 1983). In the regressions of Rhyacophilidae occurrence on year and on community richness, Rhyacophilidae were defined as colonising a site when the probability of detection was 50%. Using this 50% detection probability from these two regressions, three site (i.e. community) specific measurements of colonisation pattern were defined.

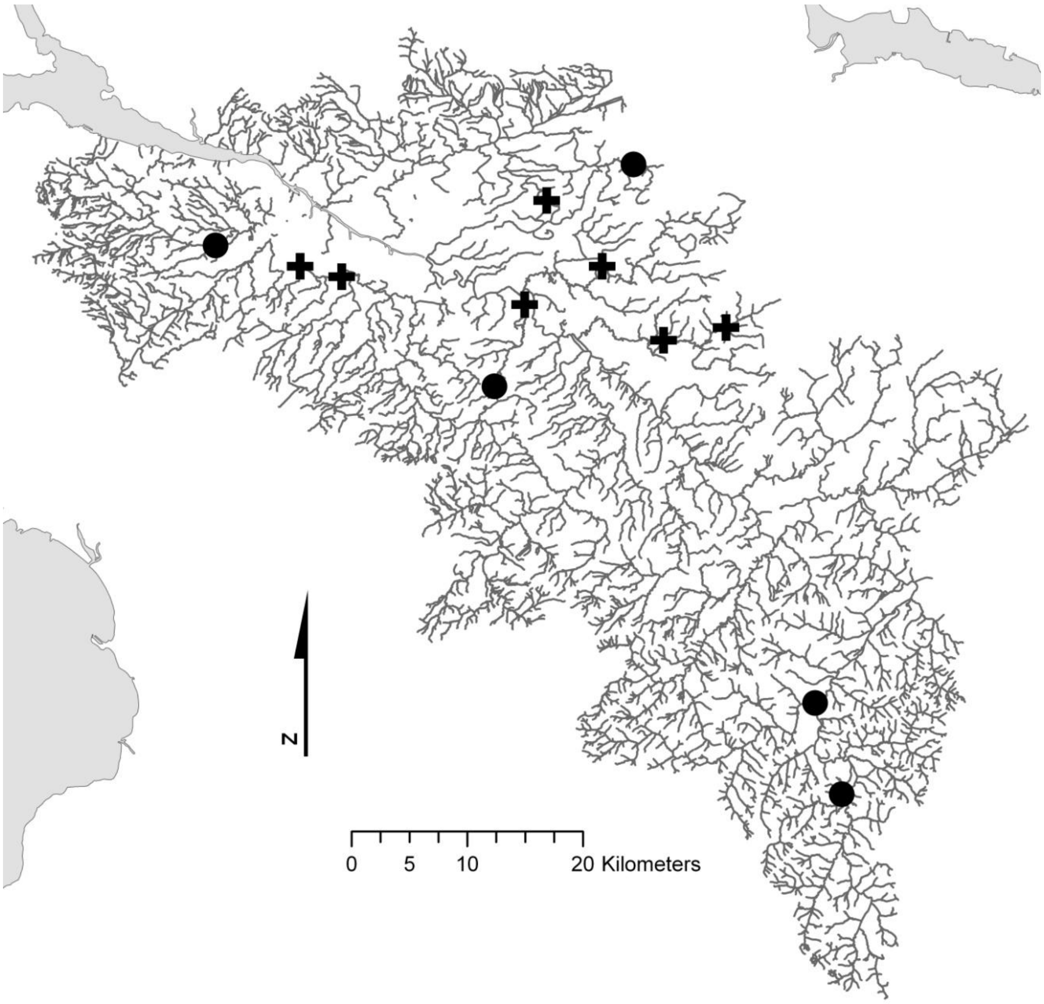
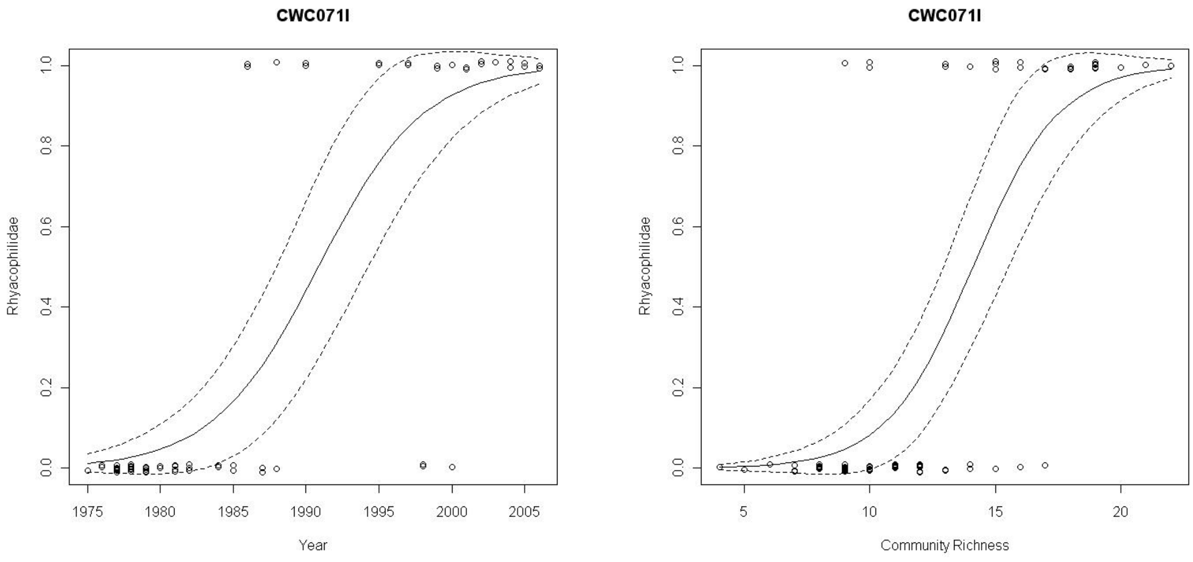


Figure 5.1: Location of the 5 resident (circles) and 7 colonising (crosses) populations of *Rhyacophila dorsalis* in the River Clyde.

Firstly, from the logistic regression of Rhyacophilidae detection/non-detection on year, the rate at which Rhyacophilidae had colonised the community was measured as the regression coefficient. Secondly, from the same logistic regression, the time elapsed since colonisation was defined as the time between the 50% probability of detection of Rhyacophilidae at a site and the sample collection in October 2009. Finally, from the regression of Rhyacophilidae detection/non-detection on community richness, the community richness of the site at which Rhyacophilidae colonised (i.e. 50% probability of detection) was determined.



(a) (b)

Figure 5.2: Colonisation pattern of Rhyacophilidae at site CWC071I. From the regression of Rhyacophilidae detection/non-detection on (a) year, the rate of colonisation (i.e. the regression coefficient) was 0.277, and the year in which there was a 50% (i.e. 0.5) probability of detection was 1990.9 (November 1990). From the regression of Rhyacophilidae on (b) community richness, the 50% probability of detection was when the community had a richness of 14.1 Families.

A simple measurement of competition was also determined from the historic records. Using the same logistic regression method, detection/non-detection records for other Families recorded at a site were individually regressed on year. Those Families with a greater than, or equal to 50% probability of occurrence in the year at which Rhyacophilidae had colonised the site, were defined as being established members of the community at the point of Rhyacophilidae colonisation. The functional feeding groups of these established community members were defined as per Moog (2002) and the number of other predatory Families at the time of Rhyacophilidae colonisation was determined, and provided a simple measurement of competition.

5.2.3 Stable isotope analysis

Stable isotope analysis was used to establish resource utilisation in both resident and colonising populations of *R. dorsalis*. In October 2009, 10 final instar *R. dorsalis* individuals were collected by kick-sampling using a 500 μm pond net at each of the 5 resident and 7 colonisation sites. To account for differences in basal nitrogen and carbon at each site (basal nitrogen and carbon have been shown to vary between sites (e.g. Dekar et al., 2009)), 10 individual Heptageniidae (scraper Ephemeropterans, Moog (1990)) were also collected from each site, to provide a measure of nitrogen and carbon signatures at this trophic position (Andersen & Cabanna, 2007).

For stable isotope analysis, *R. dorsalis* and the Heptageniidae samples were dried in an oven at 40°C to constant weight. Head capsules of the animals were removed and weighed into tin caps. Isotopic analysis of carbon and nitrogen were carried out at the NERC Life Sciences Mass Spectrometry Facility, East Kilbride, Scotland, by continuous flow isotope ratio mass spectrometry (CF-IRMS), using a Costech ECS 4010 elemental analyser interfaced with a ThermoFisher Scientific Delta XPPlus IRMS. Stable isotopes are expressed conventionally as parts per thousand (‰) delta values ($\delta^{13}C$ and $\delta^{15}N$), in relation to the international standards for carbon (PeeDee Belemnite) and nitrogen (atmospheric nitrogen). Precision, obtained from replicate analyses of internal gelatin standards was 0.13 ‰ (carbon) and 0.11 ‰ (nitrogen).

5.2.4 Isotopic baseline corrections

As basal resources have been shown to vary considerably in their $\delta^{15}N$ and $\delta^{13}C$ measurements between sites (e.g. Dekar et al., 2009), I corrected for these differences before analysis. To determine the trophic position (TP) of both resident and colonising *R. dorsalis*, corrections to the $\delta^{15}N$ were calculated using the following equation recommended by Anderson & Cabana (2007):

$$\mathrm{TP} = \left(\frac{\delta^{15}\mathrm{N}_{\mathrm{RD}} - \delta^{15}\mathrm{N}_{\mathrm{baseline}}}{3.4} \right) + 2$$

Where; TP = trophic position of either resident or colonising *R. dorsalis,* i.e. the corrected value of $\delta^{15}N$; $\delta^{15}N_{RD}$ = the measured N isotopic ratio of resident or colonising *R. dorsalis*; $\delta^{15}N_{baseline}$ = the isotopic N ratio of primary consumers; 3.4 = one trophic level fractionation increment of $\delta^{15}N$ (Post (2002); 2 = is the trophic position of the organism used to estimate the baseline (i.e. a primary consumer, here Heptageniidae). $\delta^{15}N_{baseline}$ was calculated using the mean nitrogen signals from primary consumers of the Family

Heptageniidae. Members of the Family Heptageniidae are algal scrapers, which have been shown to be effective as a measurement of baseline $\delta^{15}N$ (Andersen & Cabanna, 2007).

Basal carbon resources were corrected by the following method:

$$\text{Ccorr} = \delta^{13}C_{RD} - \delta^{13}C_{mean}$$

Where: Ccorr = the corrected carbon signature of either resident or colonising *R. dorsalis*; $\delta^{13}C_{RD}$ = the carbon isotope signal of either resident or colonising *R. dorsalis*; $\delta^{13}C_{mean}$ = is the mean primary consumer (Heptageniidae) carbon isotope signal.

Niche width (NW) was determined at the catchment scale (all sites combined) and at the population level (individual sites) for resident and colonising *R. dorsalis* using corrected $\delta^{15}N$ (TP) and $\delta^{13}C$ (Ccorr) values. NW was calculated as the area encompassed by the smallest polygon containing all the individuals from each population (individual sites) and all the individuals of resident or colonising *R. dorsalis* (resident or colonising sites combined) in $\delta^{15}N$ and $\delta^{13}C$ niche space (Layman et al., 2007). The area of each niche width polygon was calculated using ArcGIS (ESRI, 2007).

5.2.5 Statistical analysis

Differences between trophic position (TP), carbon signature (Ccorr) and niche width (NW) between resident and colonising populations of *R. dorsalis* were tested with ANOVA and variance ratio tests. To explore further whether TP, Ccorr or NW were affected by colonisation patterns (i.e. colonisation rate, time since colonisation, community richness at colonisation and competition) a combination of non-parametric (Spearman’s rank correlation) and parametric (linear regression) was employed. Spearman’s correlations initially established whether a real relationship existed between the independent (TP, Ccorr and NW) and dependent variables (colonisation patterns). Significant correlations were investigated further with individual linear regressions, with each independent variable (TP, Ccorr or NW) regressed separately. All statistical analyses were performed using SPSS version 13.0 (SPSS, 2004).

5.3 Results

5.3.1 Colonisation patterns

Colonisation patterns of Rhyacophilidae varied between sites (Table 5.1).

The coefficient from the logistic regression of Rhyacophilidae detection/non-detection on year, at each site, ranged from 0.147 to 0.277 and provided a measure of the rate at which Rhyacophilidae colonised a site. The value of the coefficient is an abstract number, but is indicative of colonisation rate, with a small number equating to a relatively slower colonisation compared to a high number indicative of a faster colonisation rate. For example, the site with the largest regression coefficient (ie the fastest colonisation rate) was CWC071I (regression coefficient = 0.277). Using the regression equation from this site it took 7.9 years for the probability of detection of Rhyacophilidae to increase from 25% to 75%. At the site with the slowest colonisation rate (i.e. smallest regression coefficient), CRC020I (regression coefficient = 0.147), the time taken for Rhyacophilidae detection to increase from 25% to 75% was 15 years, almost twice that of site CWC071I. From the same regressions (i.e. Rhyacophilidae detection/non-detection on year) the time elapsed since colonisation (i.e. number of years since 50% probability of detection and sampling date in October 2009) range from 6.2 to 21.2 years. From the regressions of Rhyacophilidae detection/non-detection on community richness at each site, the community richness at which Rhyacophilidae colonised a site (i.e. 50% probability of detection) ranged from a community richness of 10.8 to 19.5 Families present at colonisation (Table 5.1). The simple measurement of competition at each site ranged from the presence of 0 to 7 predatory Families established within the community (i.e. greater than or equal to 50% probability of detection in the year at which Rhyacophilidae had also a 50% probability of detection) range from 0 to 7 predatory Families present (Table 5.1).

Table 5.1: Regression coefficients from the logistic regressions of Rhyacophilidae detection/non-detection on year and community richness and the associated colonisation pattern measurements. Time elapsed is the time between the 50% probability of detection of Rhyacophilidae at a site and the sample collection in October 2009; richness is the community richness of the site at which Rhyacophilidae colonised (i.e. 50% probability of detection); competition is the number of other predatory Families at the time of Rhyacophilidae colonisation. The logistic regressions take the form $y = 1 / (1+ e^{-(\beta 0 + \beta 1x)})$.

Site	**Year**		**Community Richness**		**Rate**	**Time Elapsed**	**Richness**	**Competition**
	β0	**β1**	**β0**	**β1**				
CKE026I	-519.120	0.259	-10.028	0.5131	0.259	6.2	19.5	7
CNC004I	-519.3143	0.261	-8.088	0.6072	0.261	14.3	13.3	2
CRC020I	-291.609	0.147	-3.222	0.2997	0.147	20.6	10.8	0
CSC010I	-400.508	0.200	-7.634	0.5279	0.200	11.7	14.5	5
CSC013I	-323.810	0.163	-5.607	0.3526	0.163	18.6	15.9	5
CWC025I	-533.742	0.268	-4.055	0.25515	0.268	21.2	15.9	4
CWC071I	-551.531	0.277	-8.271	0.5862	0.277	18.9	14.1	1

5.3.2 Organisms

R. dorsalis individuals collected from all the sites belonged to instar 5 (head width range 1.06-1.39mm; mean=1.21±0.08 (St Dev)), apart from two animals collected at one site that were instar 4 (head capsule width 0.73 & 0.77mm) (Elliot, 1968). Ten *R. dorsalis* individuals were collected from each site (3 samples were lost during processing, thus reducing sample size to 9 and 8 for site CWC025I and site CWC071I respectively).

At each site 10 Heptageniidae were collected (apart from at site CSC010I where only 5 were collected). Of the Heptageniidae collected; at 7 sites the animals collected were all *Ecdyonurus* spp., at 2 sites the animals collected were *Rhithrogena semicolorata* and at one site both *Ecdyonurus* spp. and *Rhithrogena semicolorata* were collected. At the site where both species of Heptageniidae were present, 10 *Ecdyonurus* spp. and 10 *Rhithrogena semicolorata* were collected (i.e. 20 individual Heptageniidae in total). By collecting both species from this site I could establish whether significant differences existed when using different species to correct for basal ranges of δ^{15}N and δ^{13}C.

5.3.3 Isotopic baseline corrections

To ensure that the corrections for basal δ^{15}N and δ^{13}C did not differ according to the species used for baseline (i.e. differences between *Ecdyonurus* spp. and *R. semicolorata*), at the site where both species were present, the δ^{15}N and δ^{13}C ranges for *Ecdyonurus* spp. and *R. semicolorata* were compared using ANOVA. Significant differences (ANOVA; $p < 0.001$, $F_{(2,18)}=36.475$) were present in the δ^{15}N of the two species, however no significant differences were detected between the δ^{13}C values. As differences in δ^{15}N would affect the baseline corrections for the trophic position (TP) of *R. dorsalis*, at the two sites where only *R. semicolorata* was collected, TP of *R. dorsalis* at these sites was adjusted to account for this difference. At the site where both *Ecdyonurus* spp. and *R. semicolorata* were present, TP of *R.dorsalis* calculated using *R. semicolorata* was 0.66 higher than TP calculated using *Ecdyonurus* spp.. At the two sites where *R. semicolorata* was used to correct δ^{15}N the trophic position of *R. dorsalis* was thus reduced by 0.66.

5.3.4 Statistical analysis

5.3.4.1 Colonising and resident population differences

The total niche width (NW) of colonising *R. dorsalis* (all sites combined; $NW_{colonising}$ = 100.20) was 1.7 times that of the total niche width of resident *R. dorsalis* ($NW_{resident}$ =56.58) (Figure 5.3). At the population (site) level NW ranged from 1.11 to 19.24 for resident populations and from 2.71 to 26.76 for colonising populations (Table 5.2). There was no significant difference in mean niche width between resident and colonising populations (ANOVA; p = 0.885, $F_{(1,10)} = 0.022$) and there was no significant difference in the variance of niche width between resident and colonising populations (variance ratio F-test; $p > 0.05$; $F_{(6,4)} = 1.471$).

Across all sites, the trophic position of resident *R. dorsalis* ranged from 1.42 to 2.97 (mean = 1.95 ± 0.60 (S.E.)) and for colonising sites trophic position ranged from 0.83 to 3.33 (mean = 2.02 ± 0.84 (S.E.)) (Table 5.2). There was no significant difference in the mean trophic position (ANOVA; p = 0.502, $F_{(1,115)} = 0.453$) but colonising populations had a significantly higher variance in trophic position than resident populations (F-test; $p < 0.001$, $F_{(66,49)} = 2.641$). Colonising and resident populations were on average utilising the same trophic position, but the variation in trophic position was significantly different between the two population types.

Across all sites, the Ccorr for resident *R. dorsalis* ranged from −2.33 to −1.03 (mean = -0.45 ± 0.19 (S.E.)) and range from −3.08 to 3.41 (mean = 0.35 ± 0.16 (S.E.)) for colonising populations (Table 5.2). The difference in the mean Ccorr between colonising and resident populations was significantly different (ANOVA; p = 0.001, $F_{(1,115)} = 11.104$). There was no significant difference in the variance of Ccorr between colonising and resident population of *R. dorsalis* (variance ration F-test; $p > 0.05$, $F_{(49,66)} = 1.072$). Thus colonising populations of *R. dorsalis*, were on average using a more enriched carbon source than resident populations, however the variation in the carbon source used between the colonising and resident populations was similar.

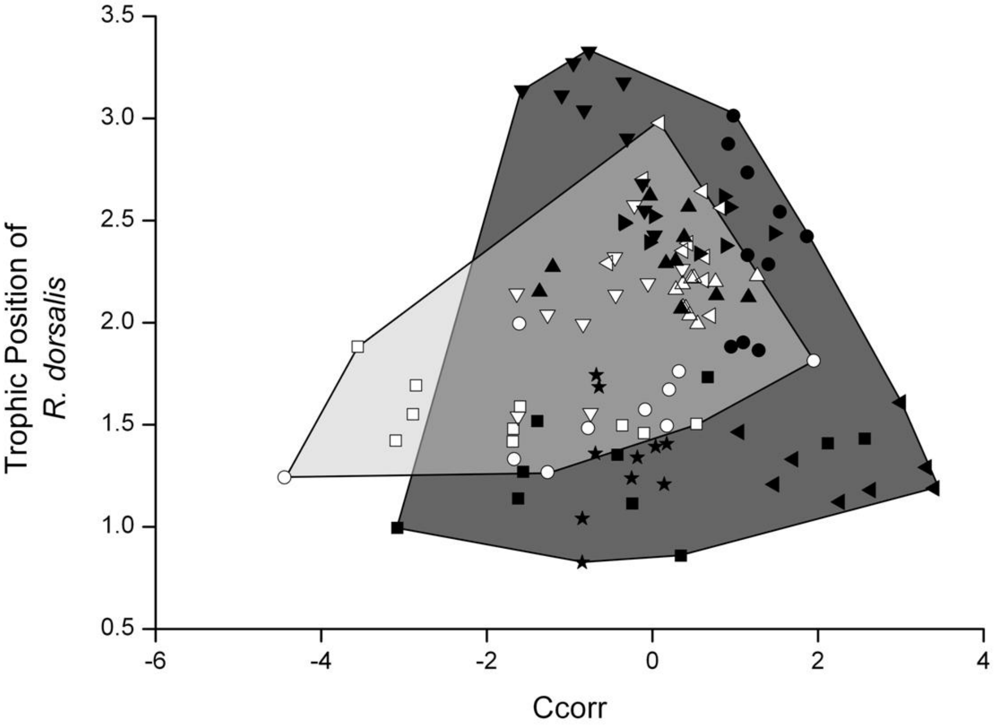


Figure 5.3: Total niche widths (polygon areas) at the species level using calculated trophic position and carbon range (corrected stable isotope ratios of $\delta^{15}N$ and $\delta^{13}C$ respectively) for resident (open shapes, light grey, $NW_{resident}$ =56.58) and colonising (solid shapes, dark grey, $NW_{colonising}$ = 100.20) *R. dorsalis*. Different shapes represent different populations (sites).

5.3.4.2 Colonisation patterns and trophic position

Non-parametric correlations and linear regressions revealed significant relationships between trophic position occupied and colonisation patterns of *R. dorsalis* populations (Table 5.3; Figure 5.4).

Richness of the community at colonisation significantly influenced the trophic position occupied by *R. dorsalis* (Table 5.3, Figure 5.4a). *R. dorsalis* colonising a relatively impoverished community (i.e. low community richness) occupied a significantly higher trophic position when compared to *R. dorsalis* populations which had colonised relatively rich (i.e. higher community richness) communities.

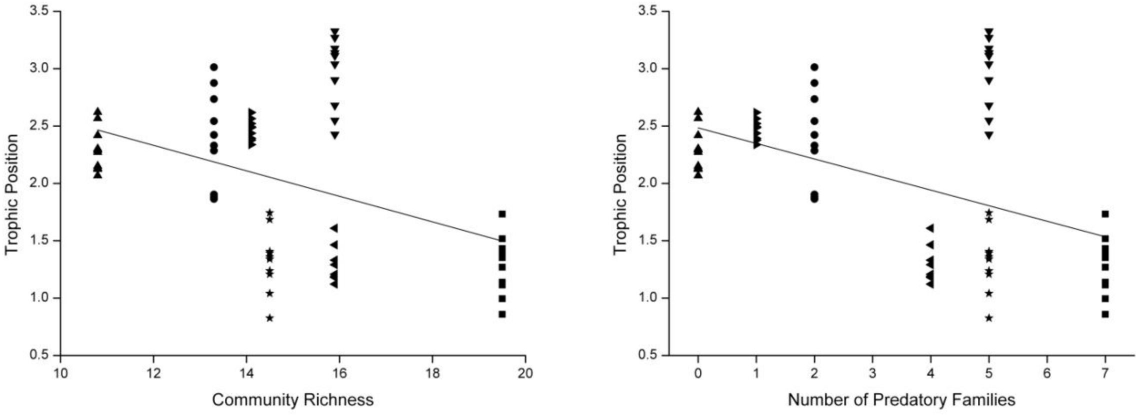
Table 5.2: Mean corrected isotopic values and niche width for resident and colonising populations of *R. dorsalis*. TP (trophic position) is the corrected δ^{15}N value; Ccorr is the corrected δ^{13}C value; NW is niche width (see text for explanation); numbers in parenthesis are standard deviation.

	TP	**Ccorr**	**NW**
Resident Populations			
CCL017I	1.55 (0.14)	-1.73 (1.39)	9.25
CDN007I	1.50 (0.21)	-0.72 (1.70)	19.24
CGY017I	2.14 (0.09)	0.54 (0.29)	1.11
CKE022I	2.08 (0.32)	-0.69 (0.67)	12.18
CRC017I	2.45 (0.28)	0.37 (0.43)	7.18
Colonising Populations			
CKE026I	1.28 (0.26)	-0.26 (1.75)	26.76
CNC004I	2.39 (0.42)	1.23 (0.30)	6.22
CRC020I	2.30 (0.19)	0.10 (0.80)	8.02
CSC010I	1.32 (0.27)	-0.38 (0.41)	5.24
CSC013I	2.96 (0.31)	-0.61 (0.52)	5.58
CWC025I	1.30 (0.17)	2.36 (0.88)	7.52
CWC071I	2.47 (0.09)	0.44 (0.65)	2.71

The number of predatory Families present in the community at the time of colonisation (i.e. my measure of competition) significantly influenced the trophic position occupied by *R. dorsalis* (Table 5.3, Figure 5.4b). Trophic position occupied by *R. dorsalis* populations which had colonised a community with a relatively low number of previously established predatory Families, was significantly higher than that occupied by *R. dorsalis* populations which had colonised a community with a relatively higher number of previously established predatory Families. The linear regression of trophic position on number of predatory Families provides a simple measurement of the effect increasing competition has on the resultant trophic position occupied by colonising populations of *R. dorsalis*. Using this equation, by increasing the number of predatory Families present from 0 present to 7 present, the trophic position occupied by *R. dorsalis* decreased by approximately 1 (0.94) level.

Table 5.3: Results from the significant Spearman correlations and individual linear regressions of trophic position on four colonisation variables.

	Correlation Results		Regression Results			
	p-value	ρ	p-value	r^2_{adj}	coefficient	intercept
Richness	0.002	-0.366	0.001	0.156	-0.111	3.667
Competition	0.001	-0.390	<0.001	0.204	-0.136	2.484



(a) (b)

Figure 5.4: Significant linear relationships between trophic positions occupied by colonising populations of *Rhyacophila dorsalis* and (a) richness of the colonised community; (b) number of established predatory Families in the community (different symbols represent different populations (sites)).

5.3.4.3 Colonisation patterns and carbon range

Non-parametric correlations and linear regressions revealed significant relationships between carbon source and colonisation patterns of *R. dorsalis* populations (Table 5.4; Figure 5.5). The rate at which *R. dorsalis* colonised a site was significantly related to the carbon source utilised (Table 5.4; Figure 5.5a). *R. dorsalis* with rapid colonisation rates were utilising a more enriched $\delta^{13}C$ source than those populations with slower colonisation rates.

The time that had elapsed since *R. dorsalis* colonisation significantly influenced the carbon source utilised (Table 5.4; Figure 5.5b). Populations of *R. dorsalis* which had been established for a relatively long time were utilising a significantly more enriched $\delta^{13}C$ source when compared to those populations which had only recently colonised a site.

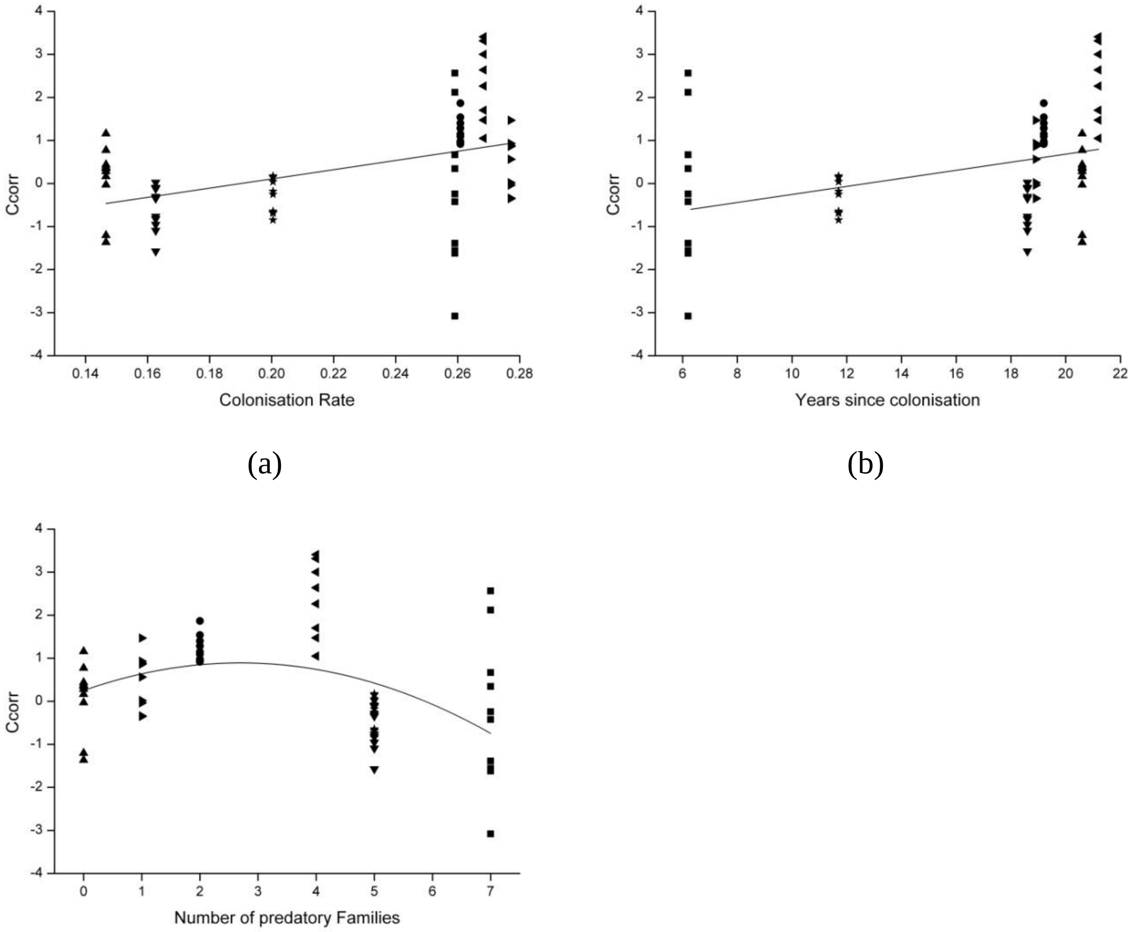
Table 5.4: Results from the significant Spearman correlations and individual linear regressions of carbon range (Ccorr) position on three colonisation variables. The linear relationship between Ccorr and competition is not significant at the $p < 0.05$ level but does indicate a trend (i.e. $p < 0.10$).

	Correlation Results		Regression Results			
	p-value	ρ	p-value	r^2_{adj}	coefficient	intercept
Rate	<0.001	0.477	<0.001	0.172	10.723	-2.037
Time Elapsed	<0.001	0.574	0.001	0.135	0.094	-1.191
Competition	0.006	-0.330	*0.064*	*0.037*	*-0.122*	*0.772*

The relationship between carbon range and the number of predatory Families established in the community at the time of *R. dorsalis* colonisation was not significant as a simple linear relationship (Table 5.4). Further investigation of the relationship between Ccorr and number of predatory Families was significant as a second order function (quadratic; p = 0.004, $r^2 = 0.157$) function (Figure 5.5c). The relationship between enriched $\delta^{13}C$ source use and the measurement of competition used in this study is clearly complex.

5.4 Discussion

Clear and consistent patterns in the mechanisms controlling resource utilisation of a coloniser have been shown. At the catchment level (i.e. all sites combined), colonising *R. dorsalis* had a larger niche width when compared to that of resident *R. dorsalis*. A difference in niche width following colonisation is often attributed to an increased competitive plasticity of the colonising species for resources, to my knowledge this has only been demonstrated with invasive species (e.g. Olsson et al., 2009). As it is highly likely that the species colonising in this study have arisen from a common pool for the species, differences highlighted here are likely to be shaped by the composition and structure of the community to which colonisation has occurred, rather than competitive plasticity.



(a)

(b)

(c)

Figure 5.5: Significant linear relationships between corrected carbon source (Ccorr) of colonising populations of *R. dorsalis* and (a) colonisation rate of *R. dorsalis*; (b) time elapsed since colonisation. (c) Significant quadratic relationship between Ccorr of colonising *R. dorsalis* and competition community (different symbols represent different populations (sites)).

The trophic position of colonising *R. dorsalis* was significantly affected by the richness and composition of the community to which colonisation occurred. In low richness communities and communities containing fewer predatory Families (i.e. low competition) colonising *R. dorsalis* occupied a significantly higher trophic position. Resource utilisation is effected by interspecific competition, with competition for resources resulting in trophic position changes in a species (Vander Zanden et al., 1999). With an increasing number of predatory Families in a community utilising resources, the availability of resource space for colonisers will possibly decrease. It is also likely that the resident predatory Families have become adapted to defending the optimum resources available to them, thus resource niche space available to novel colonisers will be at the fringes of existing predatory Families recourse niches. It is therefore likely that in a community with an increased number of resident predatory Families, the resource niche available for colonisation will be suboptimal for a novel colonising predator, resulting in a lowering in the trophic position occupied by the colonising predator, as seen here.

The maximum time elapsed since colonisation in this study is just over 20 years, and as time elapsed did not show a significant relationship with trophic position occupied, it is likely that the competitive forces controlling resource utilisation in these colonisers have remained consistent throughout the study period. This contradicts findings from other studies where trophic position has been shown to change following the colonisation of an invasive species (Vander Zarden et al., 1999). This contradiction may have arisen due to either, the length of time elapsed in this study has not been long enough to detect significant temporal change or, there may be different temporal controls influencing trophic position development during native species recolonisation.

The significant relationship between time elapsed and the carbon signature (Ccorr) of *R. dorsalis* utilised may have arisen as a result of the progression of the community to which colonisation had occurred. In this study, the communities under investigation have all undergone, or are currently undergoing the process of recovery from a period of water quality degradation. It is therefore likely that the basal carbon signatures of these communities have changed during the recovery process as a result of improving water quality. For example, in a study from New Zealand, Rogers (2003) demonstrated that the isotopic carbon signatures of biota surrounding a sewage outfall were shown to become more $\delta^{13}C$ enriched following the cessation of the discharge, which arose as a result of the reduction in the input of relatively isotopically light sewage detritus. The biota in the study showed a differential response to this change in carbon input, with the primary producer (seaweed, *Ulva lactuca*) showing a much more rapid response to the change in basal carbon source (i.e. faster increase in $\delta^{13}C$ tissue values), compared to the relatively slower change in $\delta^{13}C$ values in the tissue of primary consumers (blue mussels, *Mytilus galloprovincalis* and limpets, *Callana dendiculata*). Although difficult to make direct comparisons, there may be similar mechanisms underlying the temporal change in the carbon signature of *R. dorsalis* in the recovering communities in this study. The increase in the carbon signature of *R. dorsalis* with increasing time since colonisation may be a result of the improvements in the water quality and the resultant changes to basal carbon source at a site.

The relationship between carbon signature and the numbers of predatory Families at the point of *R. dorsalis* colonisation is complex. It is possible that the mechanisms underlying this are an interaction between the changes to the basal carbon as a result of improving water quality, the differential rate at which members of the community respond to the change in basal carbon (Rogers, 2003) and the inter-specific effects of competition.

Comparisons of the trophic position estimates for the resident and colonising populations in this study have shown significantly higher variation in the trophic position occupied by colonising populations of *R. dorsalis*. Multiple individuals from three colonising populations are exploiting a trophic position lower compared to that of resident populations; individuals from another colonising population are exploiting a higher trophic position; and the remaining colonising populations show considerable overlap with resident populations trophic positions. Variation in both trophic position and utilised carbon source of the colonising populations has been significantly linked with colonisation patterns. Changes in resource utilisation may have implications for life history strategies, growth and disease resistance, which have been shown to be influenced by diet quality (Naya et al., 2007; Olsson et al., 2008; Browne et al., 2006). Diet quality has been shown to influence offspring fitness (Kyneb & Toft, 2006), affecting subsequent generations. If we assume that increased fitness and disease resistance of community members promote community stability, it is likely that colonisation patterns influencing resource use may have direct implications for the functionality and hence the stability of a community. This has major implications for restoration ecology, as the ability of a community to withstand future environmental fluctuations may have arisen through the colonisation mechanisms which restructured the community.

CHAPTER 6 Long-term changes to species distribution in the River Endrick

6.1 Introduction

Species distribution changes are occurring at rapidly increasing rates (Vitousek et al., 1997; Mack et al., 2000; Walther et al., 2002). Documenting changes in distribution is important to provide a mechanism through which research can be targeted to (hopefully) yield pertinent insights into factors contributing to distributional changes. Generally, studies in this area of science are primarily concerned with the movement of non-native species or changes to longitudinal limits often associated with climate change. There are some long term monitoring programmes which have been designed to track long term change without targeting specific species or specific mechanisms. The data accumulated from these studies has provided insights into population change for a host of organism groups. Long-term records gathered through the Continuous Plankton Recorder survey has documented plankton species distribution (Warner & Hays, 1994) providing information which has been used to track the impacts of climate change (e.g. Beaugrand & Ried, 2003) and changes to commercially important fish stocks (e.g. Reid et al., 2001). Monitoring of British bird and moth populations have provided data with which to assess long term population changes and infer mechanisms underlying the observed long-term trends (e.g. Peach *et al*., 1999; Salma et al., 2007; Conrad et al., 2004).

Long-term studies on freshwater systems are more scarce (Jackson & Füreder, 2006). This is surprising for two reasons. Firstly, streams are a major route through which minerals and materials are cycled (Vannote et al., 1980) and their physical structure results in a highly varied habitat mosaic. As a consequence of the variety of available recourses and habitats, the macroinvertebrate fauna inhabiting these systems is varied, in terms of species richness and functional diversity. Secondly, fresh waters have been highlighted as being under the greatest threat from global climate change and are now recognised as one of the most threatened ecosystems globally (Vörösmarty et al., 2010). Both this variety in species richness and their sensitivity to changing climate make river systems an exceptional ecosystem to document species distribution changes.

Historic records of species from river systems can be sporadic (sample location and date undefined), vague (no details of collection method) and unreliable (taxonomic identification problems) meaning, the comparison of historic species distribution with contemporary records can be problematic or impossible. Some suitable datasets are however available. Using material I collected in 2010 and historic data collected during a PhD undertaken between 1959 and 1963 (Maitland, 1963), I assessed distributional changes of macroinvertebrate species in a river system after a 50 year period.

6.2 Methods

6.2.1 Study area

The River Endrick is located in West Central Scotland, between Lat: 56^{o} 06’ N & 55^{o} 58’ N and Long: 004^{o} 07’ W & 004^{o} 31’ W (Figure 6.1). The watershed of the river lies entirely in the midland valley of Scotland which is dominated by soft (old red sandstone) solid geology. The river rises at a height of 495m and flows in a generally westerly direction for 49 km where it enters Loch Lomond (a large (71 km^2) lake). Landuse within the catchment is dominated by agriculture but four settlements are also likely to influence the river (Maitland, 1966a) (Figure 6.1).

6.2.2 Historic studies of the River Endrick fauna

Two major studies of the macroinvertebrate fauna of the River Endrick have been undertaken previously.

6.2.2.1 1960 study

An ecological study of the invertebrate and vertebrate fauna of River Endrick between 1959 and 1963 was undertaken by P.S. Maitland as a PhD thesis through the University of Glasgow (Maitland, 1963). Part of this thesis was to establish a reliable check-list of the species of invertebrates found in the River Endrick. Twelve sampling sites were chosen along the main river channel from the river source (defined here as the "start of the highest rising tributary" (Maitland, 1966a)) to the mouth (the point at which the river enters Loch Lomond (Figure 6.1). "The twelve stations [sites] were selected more or less at random along the length of the river, though care was taken not to site any where fauna might be influenced by unnatural factors – e.g. near a sewage works or a ford" (Maitland, 1966a). Samples were collected at these 12 sites in October 1959, February 1960 and June 1961. These samples are referred to as the 1960 study period.

6.2.2.2 1990 study

The 12 sampling sites on the River Endrick were resampled in 1990 by Doughty and Maitland (1994). Due to differences in sampling months (samples were collected in March/April and August 1990) and sampling technique (multiple standard kick samples), direct comparisons of invertebrate assemblages in 1990 with the 1960 study are not possible. Notwithstanding this disparity in sample collection, reference will be made to these samples if biologically appropriate (Doughty & Maitland, unpublished data).

6.2.3 2010 study

6.2.3.1 Site selection

Of the original 12 sites in the 1960 study, 7 were re-sampled in February, June and October 2010, using the same timing and method employed in the 1960 study, providing comparable samples from the two study periods. Two of the original 12 sites were not included in the 2010 study for biological reasons. The site at the mouth of the river was not included as it was likely that it would have been influenced to a greater degree by changes within the lake and thus samples collected here may not reflect riverine change. The changed location of the effluent discharge from the sewage works at Balfron meant that the study site there was now located downstream of this discharge and no longer appropriate. The site at Drymen Bridge included 7 possible habitats to be sampled. Following the original protocol, this would result in 70 mins of collected material in each of the three months, a total of 3.5 hours of collected material and was discounted due to time constraints. Of the remaining 9 sampling sites 7 were chosen to provide an even spread of sampling sites along the main channel of the river (Figure 6.1).

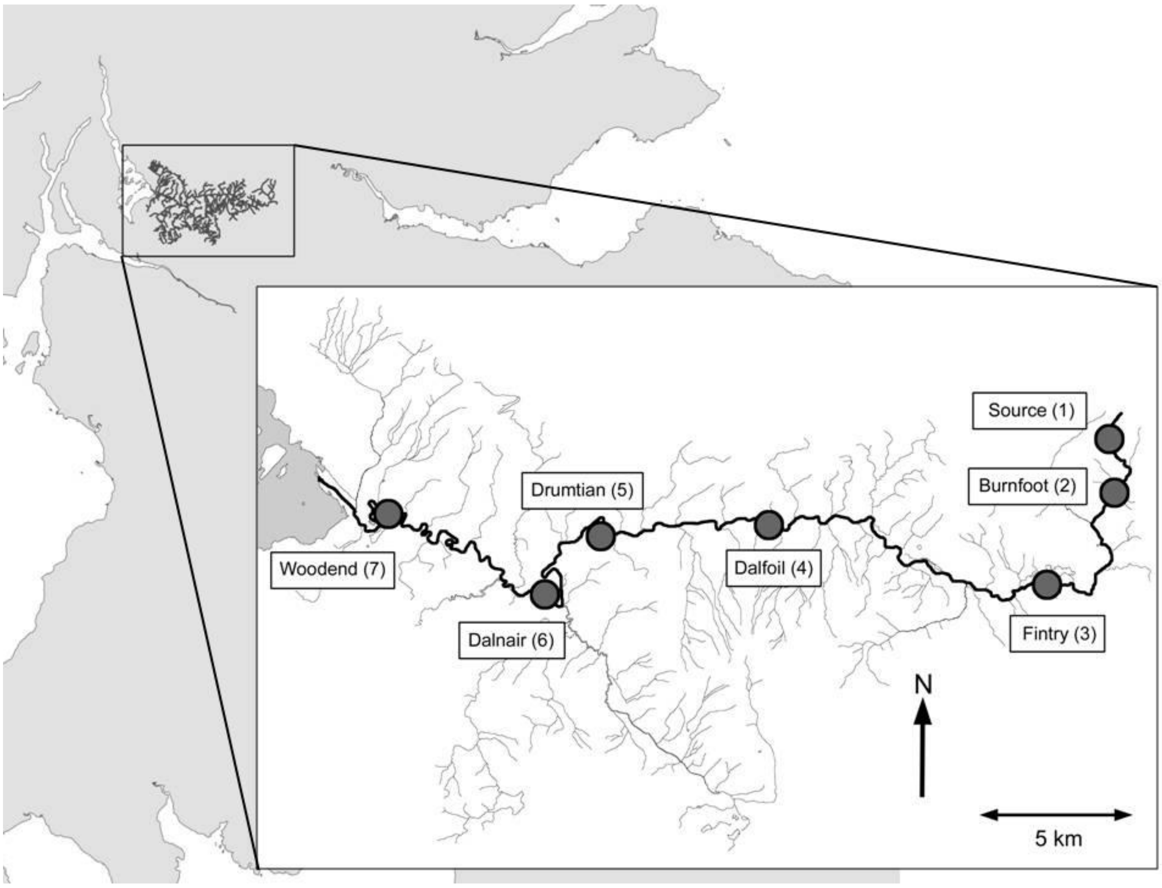


Figure 6.1: Location of the 12 sampling sites on the main channel of the River Endrick from the 1960 study period and the 7 sites (solid circles) re-sampled in the 2010 study period; four settlements in the catchment are detailed as hatched ovals.

6.2.3.2 2010 sample collection

Samples were collected at the 7 sites in 2010 except from one sample which was collected in February 2011 (Table 6.1). Due to extreme weather in February 2010 sampling on the river was problematic due to ice cover. Nominal February samples were collected between 15th February 2010 and 16th March 2010, and one collected on 14th February 2011. These samples will be referred to as ‘spring samples’. Samples collected in June 2010 were collected within one week (between 9th and 15th June) and will be referred to as ‘summer samples’, and samples collected in October were collected within one week (between 11th to 15th October) and will be referred to as ‘autumn samples’.

Material was collected using the same method employed in the 1960 study (Maitland, 1966a) using the semi-quantitative survey techniques recommended by Macan (1958) and Hynes (1961). Confirmation of the exact sampling technique employed in 1960 was achieved through discussion with P. S. Maitland. At each site, material was collected for 10 minutes in each distinct habitat, “using whatever method of collecting seemed to be most suitable for the habitat in question” (Maitland, 1966a), using a standard pond net (1mm mesh; bag depth 0.2m; 25x25 cm frame). The distinct habitats at each site were the same as those defined in the 1960 study (Table 6.1). Each collection was placed individually in a plastic bag with a label.

In the laboratory, the soft bodied animals (i.e. Hirudinea and Tricladida) were removed and identified before preservation due to identification difficulties with preserved material. The remaining material was then placed in a plastic bag with a label, 70% industrial methylated spirit (IMS) added and then stored in a fridge for future sorting and identification.

Sorting and identification was carried out in the laboratory. The content of each bag was washed through a 500µm sieve to remove the IMS and fine silts. Material was then examined over white and black backgrounds in small quantities and all animals removed. Animals were then identified to species using the appropriate identification key (see Appendix D for full list of keys used) and numbers of each species recorded. Species identification was completed for; Tricladida, Hirudinea, Crustacea, Ephemeroptera, Plecoptera, Hemiptera, Neuroptera, Trichoptera, Lepidoptera and Coleoptera.

6.2.4 Species abundance and distribution

For each species, three unique pieces of information were used to assess distributional change.

6.2.4.1 Occupied site changes

Changes to the number and location of the sites occupied by each species were determined from the detection / non-detection of each species at each of the 7 site in each study period.

6.2.4.2 Site abundance

As the time spent within each site varied between sites (although was constant sampling seasons and years) depending on the number of habitats sampled (Table 6.1), the number of individuals collected at a site were standardised to the number of individuals collected at a site per hour (for all seasons combined). This will be referred to as a standard sample. This allowed for direct comparison with the numbers collected during the 1960 study period, which had been standardised in the same way (Maitland, 1966a).

Original numbers were not available for the 1960 study period. The number of individuals of each species collected at a site in a standard sample (i.e. number of individuals per one hour sampling at a site) was derived from the charts presented in Maitland (1966a). The charts were scanned at high resolution. The scanned images were then imported into ArcGIS (ESRI, 2007) and the numbers at each of the 7 sites were derived using the “measure” function. These derived numbers were also used to calculate the total number of each species collected during the 1960 survey.

At each of the 7 sites, for both study periods, there was a measurement of individual species abundance in the form of number of individuals collected in a standard sample (i.e. number of individuals of a species collected in one hour at a site), and total number collected during the study period.

6.2.4.3 Frequency of occurrence

The number of individuals of a species collected at a site (in a standard sample) was converted to a frequency of the total number of individuals of that species collected from the River Endrick (i.e. total number of all 7 standard samples), for each study period separately. This provided a measurement of frequency of occurrence of each species in each study period along the main channel of the river. A visual analysis of an x-y plot of study frequency of occurrence against site distance from the source of the river allowed a simple assessment of abundance distribution change in each study period.

Table 6.1: Details of location (Easting & Northing), sampled habitat, sampling dates (yyyy.mm.dd) and total sample time for each of the 7 sites in this study. Sampled locations, habitats and times are identical to those of the 1960 study.

Site	**Location:** Easting Northing	**Sampled Habitats (10 min in each)**	**Sample Dates**	**Total Sample Time**
Source (1)	268162 688929	(1) Gravel and peat in riffle (2) Moss growing over gravel and peat	2011.02.14 2010.06.13 2010.10.15	60 min
Burnfoot (2)	268162 688929	(1) Boulders in riffle (2) Stones in pool (3) Moss growing on solid rock	2010.03.14 2010.06.15 2010.10.14	90 min
Fintry (3)	266102 686200	(1) Stones in riffle (2) Stones in pool (3) Moss growing on stones	2010.03.11 2010.06.12 2010.10.12	90 min
Dalfoil (4)	257000 688100	(1) Stones in riffle (2) Stones in pool	2010.02.19 2010.06.11 2010.10.12	60 min
Drumtian (5)	251646 687845	(1) Stones in riffle	2010.02.18 2010.06.10 2010.10.12	30 min
Dalnair (6)	249791 685920	(1) Stones in riffle (2) Silted stones at edge of river (3) Partly emergent weed in silt at river edge	2010.03.01 2010.06.09 2010.10.11	80 min[§]
Woodend (7)	244677 688531	(1) Sand in mid-stream (2) Partly emergent weed in silt at river edge	2010.02.15 2010.06.09 2010.10.11	50 min[‡]

[§] 10 min sample in thick weed not collected on 2010.03.01 due to non-existence of habitat,
[‡] 10 min sample in mid-stream sand not collected on 2010.10.11 due to high river levels preventing access to this habitat

6.2.5 Distribution analysis

Using the species abundance and distribution information from the 1960 and 2010 study periods, changes in the distribution of species within the River Endrick would fall into 6 general categories:

(a) *Similar distribution in both study periods*. This is in terms of both spatial distribution (i.e. distribution along the length of the river) and abundance distribution (i.e. site abundance).

(b) *Possible local extinction of a species.* The detection of a species in the 1960 study but no detection in the 2010 study would represent a possible loss of a species from the river fauna.

(c) *Species previously unrecorded.* The detection of a species in the 2010 study but no detection in the 1960 study would represent an addition to the river fauna.

(d) *Different distribution in the 2010 study compared with the 1960 study*. Here the distribution of a species has changed in terms of spatial distribution and/or abundance distribution.

In the case of situation (b) and (c) special attention will be paid to improvements in the identification keys which may influence these results. As 5 of the original 12 sites were not surveyed in 2010, in the case of situation (c), a non-detection in the 1960 study will be confirmed with the inclusion of these additional sites (i.e. a species may not have been recorded in 1960 at one of the seven sites used in this study, but may have been detected at one of the other sites, thus not truly absent from the river in 1960).

6.2.6 Statistical analysis

To determine whether distributional changes (both spatial and abundance) in situations (d) were significant a combination of Fisher's exact test and the Kendall coefficient of concordance test was used.

In situation (d) where site occupancy was similar in both study periods, the Kendall test was used to test whether differences in the abundance (i.e. number of individuals of the species collected in one hour sampling) along the length of the river had changed. For each species individually, the total number collected in one hour of sampling (i.e. a standard sample) at each of the 7 sites were ranked for each study period (i.e. 1960 and 2010) separately, the ranks of the 7 sites in each study period were then compared using Kendall's test of concordance, following the method in Siegel (1956). The significance of Kendall's coefficient, W, provides an indication of the concordance (i.e. similarity) of the rank of the sites between the two study periods. The larger the p-value associated with W indicates an increasing dissimilarity between the two study periods in terms of site abundance. While Kendall's test does not test the significance of the difference (Kendall's method tests for similarity) in the rank of site abundance between the two study periods, large p-values associated with W could be interpreted as highly dissimilar abundance distributions. Chi-squared tests were not employed for testing species abundance distribution change here, due to the large number of sites at which either no individuals or very low number of individuals, were recorded.

In situation (d) where there is a change in site occupancy, Fisher's exact test was used to test whether the detection of a species outwith the historic distribution (i.e. 1960 study period) was significant. In order to compare similar samples, the number of species collected in a standard sample (i.e. in one hour of sampling at a site, for all seasons combined) were used in Fisher's exact test. The contingency table for Fisher's exact test took the form:

	New Sites	Historic Sites
1960	a	b
2010	c	d

where; new sites were the sites at which the species had been recorded in 2010 but not in 1960; historic sites were the sites at which the species had been recorded in 1960, a = 0 (i.e. no individuals were recorded at the new sites in 1960); b = the total number of individuals collected during the 1960 study (i.e. the total number collected in standard samples from the 7 sites); c = the total number of individuals collected at the new sites in the 2010 study (i.e. the total number collected in standard samples from the new sites); d = the total number of individuals collected from the same sites in both 2010 and 1960. A two-sided test was employed as the null hypothesis of detection was not directional (i.e. no a priori knowledge of the detection of a species at a new site). Kendall's test of concordance was then used to assess possible differences in the abundance distribution of the species between the two study periods.

Differences in the total number of each species collected in each study period were investigated using χ^2 (with Yates correction for small sample size) (Zar, 1999):

$$\chi_c^2 = \left(\frac{(|\exp - \text{obs}| - 0.5)^2}{\exp} \right)$$

where, 'exp' is the total number of species collected in 1960, 'obs' is the total number collected in 2010. χ^2 may produce spurious significance when either 'exp' or 'obs' in the above equation is 0 or very low (i.e. less than 5) thus, if the number collected in 1960 (i.e. 'obs') or 2010 (i.e. 'exp') was 0 or <5 then the value was either replaced with 5 as recommended by Quinn & Keough (2002). This χ^2_c was used to test for significant differences in total number of individuals of each species collected in each study period and whether an extinction or collection of a new species was likely to be significant.

Fisher's exact test was performed using R version 2.11.1 (R Development Core Team, 2010), and Kendall's W and χ^2 and the associated p-values were calculated manually using Microsoft Excel version 2007.

6.3 Results

122 species (48,834 individuals) were identified from material collected during the 2010 study period and are detailed in Appendix B.

Distribution analysis was only undertaken for species where reliable identification in both study periods could be made. Distribution of the Tricladida, Hirudinea, Malacostraca, Ephemeroptera, Plecoptera, Hemiptera, Trichoptera (not including the Families Beraeidae, Brachycentridae, Goeridae, Hydroptilidae, Lepidostomatidae, Leptoceridae, and Odontoceridae due to identification issues in the 1960 study period), and Coleoptera (7 common species) were compared between the two study periods. From this group of invertebrate orders, the distribution of 81 species was investigated further.

Thirteen species showed a significant change in spatial distribution (i.e. site occupancy) with an associated change in abundance distribution (i.e. category d, above), 13 species had possible (i.e. a high p-value associated with the W statistic from Kendall's test) changes in abundance distribution (i.e. category d), 8 species previously unrecorded were recorded in the River Endrick in 2010 (i.e. category c), 4 species have possibly been lost from the river since 1960 (i.e. category b) and 43 species show similar spatial and abundance distribution in the two study periods (i.e. category a). Distributional details of the 43 species which had similar distribution in each study period are summarised in Appendix C.

6.3.1 Invertebrata

The distribution of each of the 81 species is reported in a standard format. Each species is assessed separately under the criteria of the distribution analysis (i.e. belonging to one of the 4 categories, a-d). The spatial distribution (i.e. site occupancy) is represented as a simple distributional map where contiguous distribution along the watercourse is representative of species detection at adjoining sites. The abundance distribution is represented in graphical form, with distance from the river source (i.e. site location) as the x-axis and frequency of occurrence (see methods) as the y-axis. Each table summarises the numerical details of each species collection during each study period, the numbers for the 1960 period are derived from charts. Each table details: the total number of individuals collected in each study period (Total); the total river mean (± standard deviation) corrected for sampling effort for each study period separately was calculated as the mean number of individuals collected in a standard sample (i.e. 1 hour sample) for the 7 sites combined for each study period separately; and the number of sites at which the species was collected in each study period. Those species which have not undergone any significant distributional change are detailed in Appendix C. Species are ordered phyletically at the level of Class and Order and then alphabetically from genus.

6.3.1.1 Tricladida

Five species of Tricladida were identified from the River Endrick in the 2010 study, one species fewer than the 1960 study, indicating a possible local extinction of one species (*Crenobia alpina*) from the River Endrick. Peaks in Tricladida species abundance remain similar between the two study periods (Figure 6.2) with peak abundance for Tricladida at two distinct points along the length of the river (9 km and 44 km from the river source). These two peaks are representative of two different Tricladida assemblages; *Polycelis felina* found exclusively in the upper reaches of the river and the remaining four species found only in the lower reaches of the river.

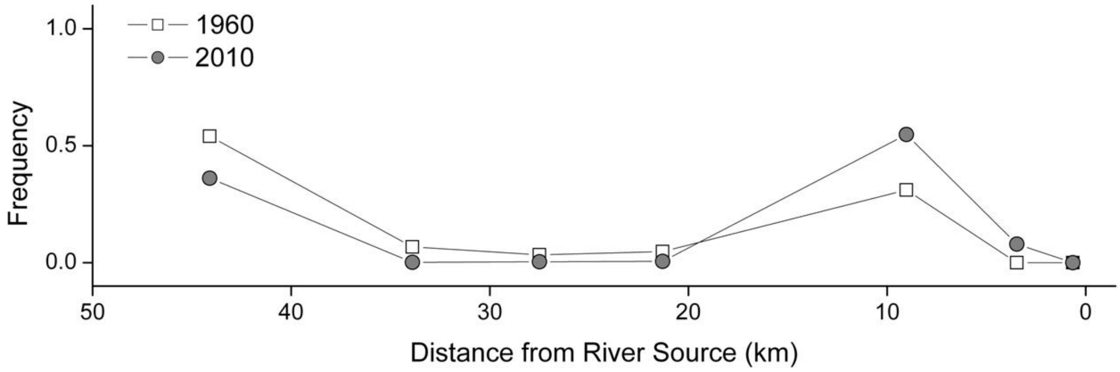


Figure 6.2: Frequency of occurrence of Tricladida at each of the 7 sites during the 1960 and 2010 study of the River Endrick.

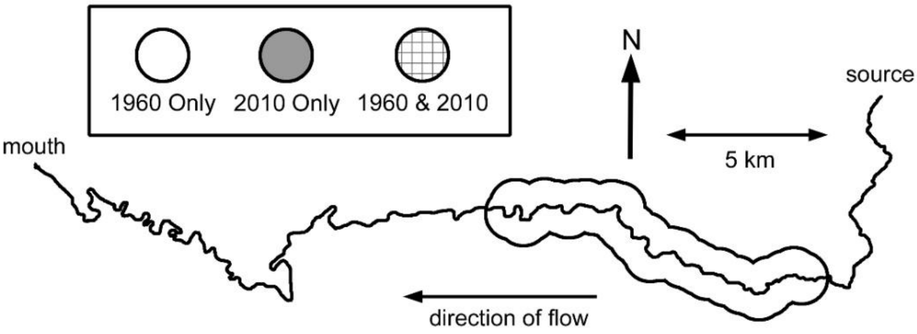
Table 6.2: Species of Tricladida with similar distribution patterns in both study periods (i.e. *(a) Similar distribution in both study periods*. above); species distributions are detailed in Appendix 7.C.

Species
Dugesia lugubris
Polycelis felina
Polycelis nigra
Polycelis tenuis

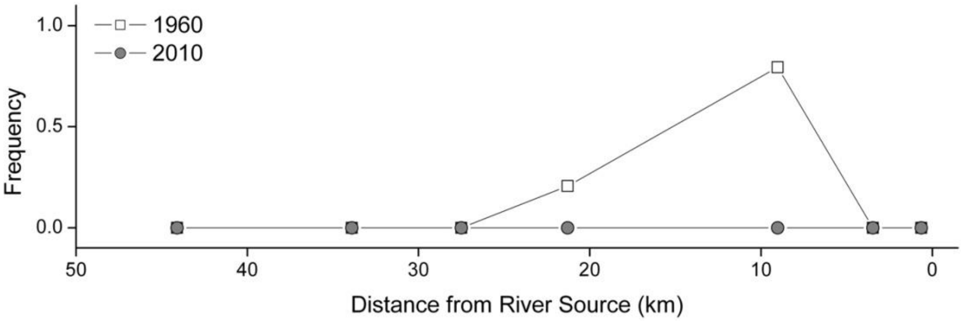
Crenobia alpina was relatively common in the 1960 study period but was not detected in any sample collected in the River Endrick in 2010 (Table 6.3; Figure 6.3). The non-detection of this species was significant ($\chi^2_c = 37.630$, $p < 0.0001$) and it is therefore highly likely that *C. alpina* has been lost from the River Endrick (Figure 6.3). *(b) Possible local extinction of a species*

Table 6.3: Numerical summary of *C. alpina* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	48	4.86 (± 10.11)	2
2010	0	0	0



(a)



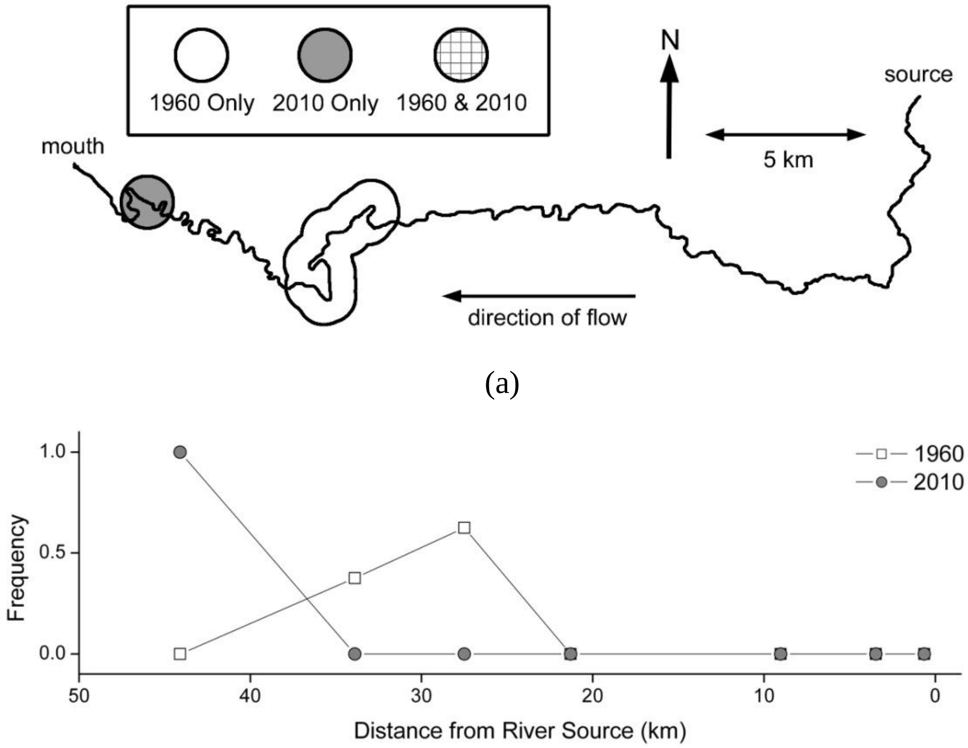
(b)

Figure 6.3: Distribution of *C. alpina* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *C. alpina* in each study period.

Dendrocoelum lacteum was relatively uncommon in both 1960 and 2010 (Table 6.4). *D. lacteum* is found exclusively in the lower reaches of the river (Figure 6.4), but site occupancy differed significantly (Fisher's test (spatial distribution), p = 0.0003) between years with *D. lacteum* now occupying a location further downstream in 2010 compared with 1960 (Figure 6.4a). Distribution of relative abundance changed (Kendall's test (distribution of species abundance); 0.192, p = 0.890; Figure 6.4b) but absolute abundance was not significantly different (χ^2_c = 0.0357, p = 0.850) between 1960 and 2010 (Table 6.4). *(d) Different distribution in 2010 compared with 1960.*

Table 6.4: Numerical summary of *D. lacteum* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	7	1.14 (± 2.04)	2
2010	6	0.86 (± 2.27)	1



(a)

(b)

Figure 6.4: Distribution of *D. lacteum* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *D. lacteum* in each study period.

6.3.1.2 Hirudinea

Six species of Hirudinea were identified from the River Endrick in the 2010 study. This is less than that recorded in the 1960 study, however those species not detected in 2010 were recorded as rare in the 1960 study and it is likely that the reduced number of sample locations has resulted in the non-detection of *Theromyzon tessulatum*, *Hemiclepsis marginata* and *Dina lineata* in the 2010 study. Distribution of the Hirudinea has changed between the two study periods (Figure 6.5). Peak abundance appears to have moved upstream and the length of the river occupied by Hirudinea appears to have increased in an upstream direction, (Figure 6.5).

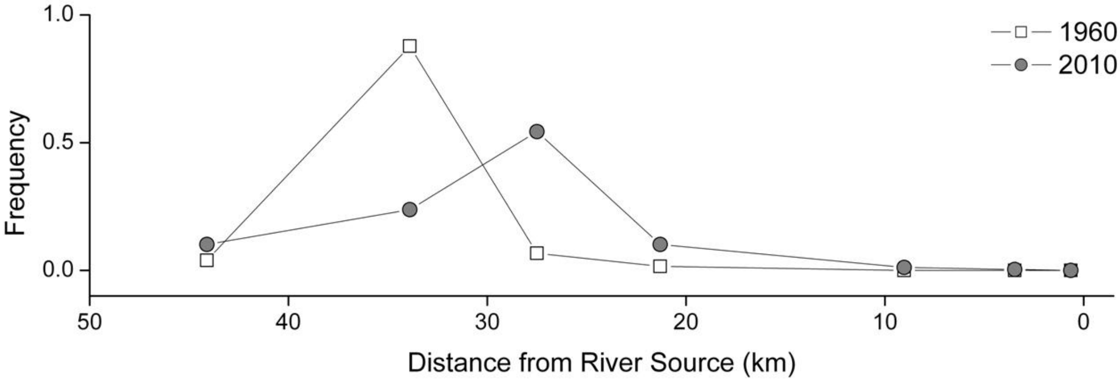


Figure 6.5: Frequency of occurrence of Hirudinea at each of the 7 sites during the 1960 and 2010 study of the River Endrick.

Table 6.5: Sporadic occurrences of Hirudinea species in both study periods (identification to be confirmed.

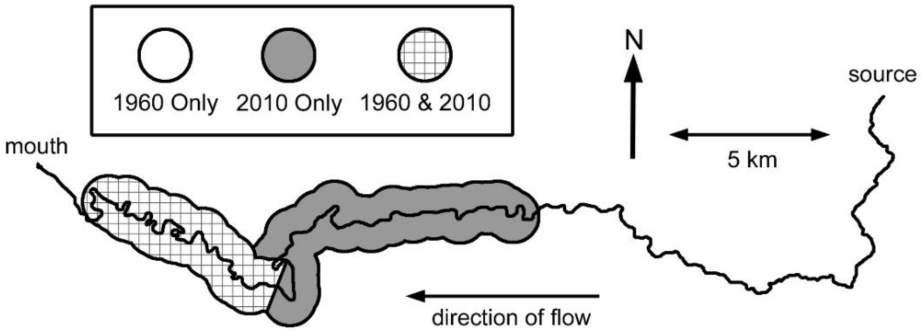
Species
Batracobdella paludosa *Glossiphonia heteroclita*

In the 2010 study, one individual of the species *Batracobdella paludosa* and two individuals of the species *Glossiphonia heteroclita* were collected from the site at Fintry (site 3), and one individual of the species *Erpobdella testacea* was collected from Dalnair (site 6). The identification of these species has not been confirmed and are not discussed further.

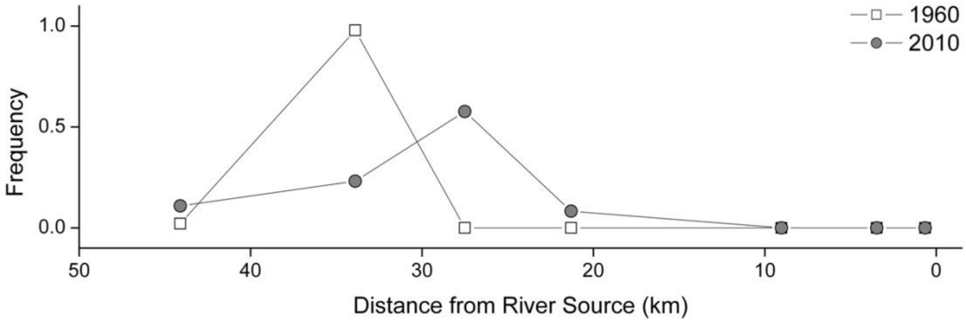
Erpobdella octoculata was abundant in both 1960 and 2010 (Table 6.6). *E. octoculata* is found in the lower middle reaches of the river (Figure 6.6) but site occupancy has significantly increased upstream in 2010 (Fisher's test; p = 0.001) from the 1960 range (Figure 6.6a). Distribution of relative abundance changed (Kendall's test; W = 0.589, p = 0.314; Figure 6.6b) and absolute abundance has significantly decreased (χ^2_c = 6.992, p = 0.008) between 1960 and 2010 (Table 6.6). Peak abundance for this species has moved upstream in 2010 compared with 1960. *(d) Different distribution in 2010 compared with 1960.*

Table 6.6: Numerical summary of *E. octoculata* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	212	20.29 (± 52.36)	2
2010	173	32.71 (± 47.83)	4



(a)



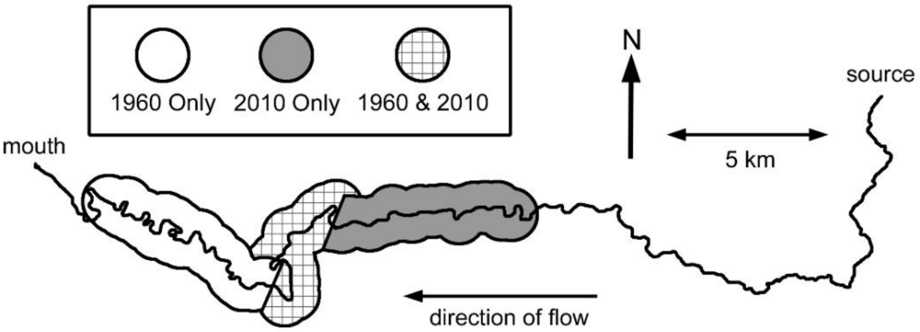
(b)

Figure 6.6: Distribution of *E. octoculata* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *E. octoculata* in each study period.

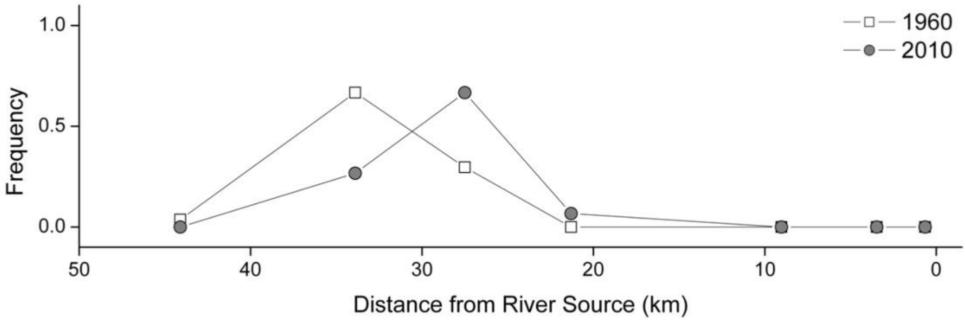
Glossiphonia complanata was common in both 1960 and 2010 (Table 6.7). *G. complanata* is generally found in the middles reaches of the river (Figure 6.7), but the detection of *G. complanata* upstream of the 1960 range was not significant (Fisher's exact test, p = 0.357). Distribution of relative abundance changed (Kendall's test; W = 0.692, p = 0.217; Figure 6.7b) and absolute abundance has decreased significantly (χ^2_c = 13.133, p = 0.0003) between 1960 and 2010 (Table 6.7). Peak abundance for this species has moved upstream in 2010 compared with 1960. *(d) Different distribution in 2010 compared with 1960.*

Table 6.7: Numerical summary of *G. complanata* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	32	3.86 (± 6.89)	3
2010	11	2.14 (± 3.76)	3



(a)



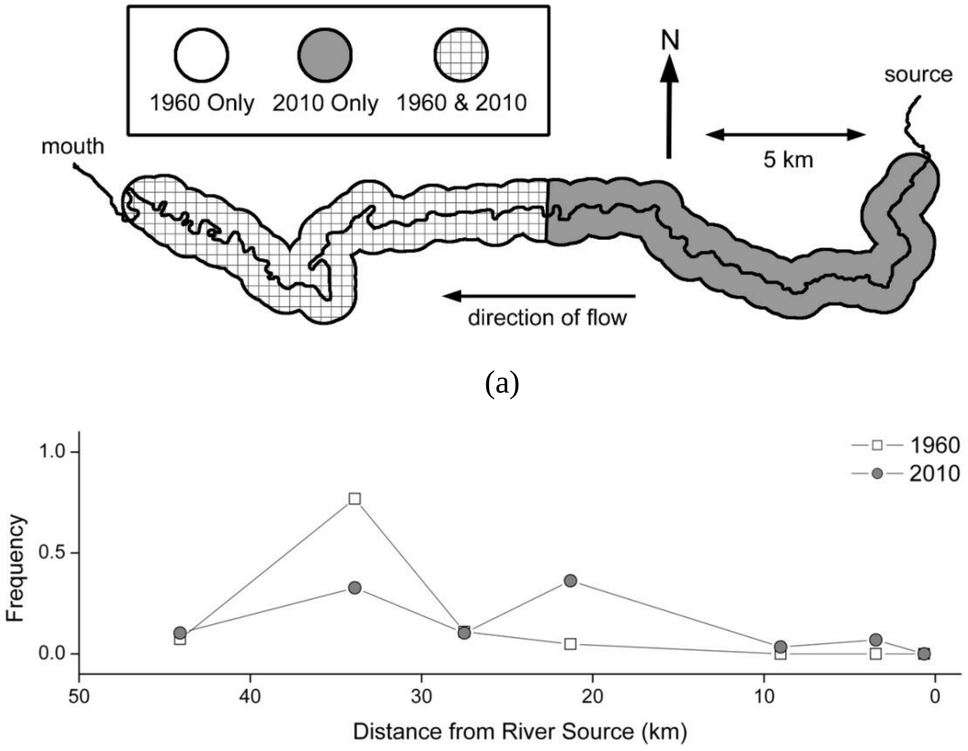
(b)

Figure 6.7: Distribution of *G. complanata* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *G. complanata* in each study period.

Helobdella stagnalis was common in the lower half of the river in 1960 but appears to have undergone an extreme range expansion and is now found along the length of the River Endrick (Table 6.8; Figure 6.8). The detection of *H. stagnalis* upstream of the 1960 spatial limit was significant (Fisher's exact test; p = 0.033; Figure 6.8a). Distribution of relative abundance changed (Kendall's test; W = 0.821, p = 0.131; Figure 6.8b) and absolute abundance has significantly decreased ($\chi^2_c = 78.856$, $p < 0.0001$) between 1960 and 2010 (Table 6.8). *(d) Different distribution in 2010 compared with 1960.*

Table 6.8: Numerical summary of *H. stagnalis* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	109	311.71 (± 22.88)	4
2010	20	2.71 (± 2.69)	6



(a)

(b)

Figure 6.8: Distribution of *H. stagnalis* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *H. stagnalis* in each study period.

6.3.1.3 Crustacea

Only the Malacostraca were considered in the 2010 study. Three species were recorded in the 2010 study, representing an increase of one species of Malacostraca (*Crangonyx pseudogracilis*) in the River Endrick since 1960. Abundance distribution of Malacostraca within the River Endrick may have changed in 2010 compared with the 1960 study period (W = 0.404; p = 0.138; Figure 6.9).

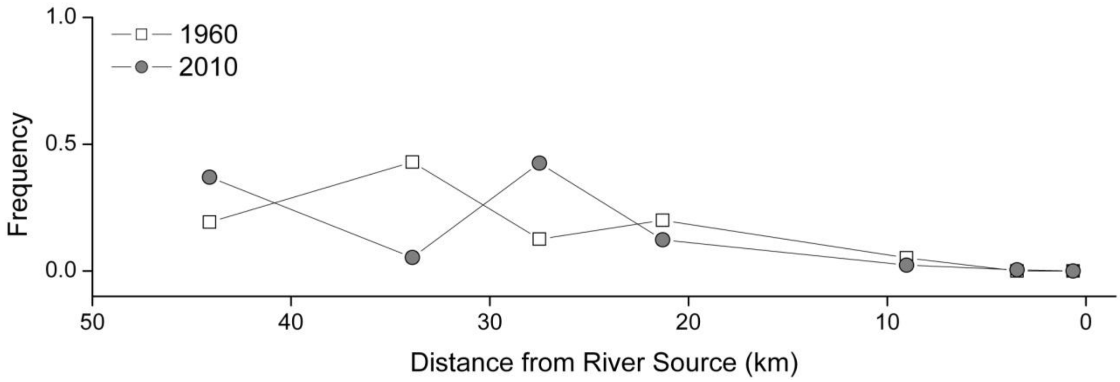


Figure 6.9: Frequency of occurrence of all Malocostraca at each of the 7 sites during the 1960 and 2010 study of the River Endrick.

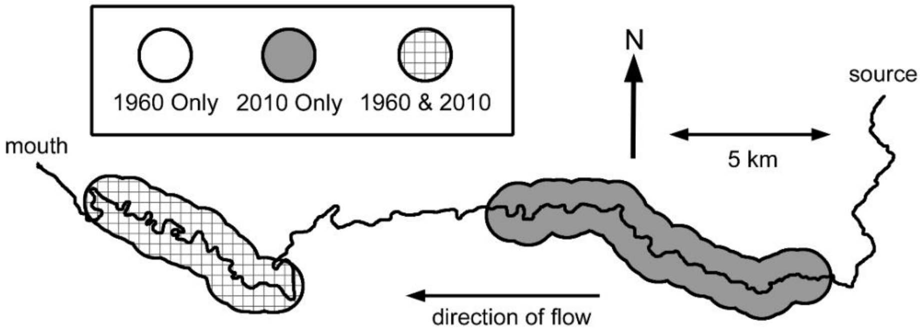
Table 6.9: Species of Crustacea with similar distribution patterns in both study periods (i.e. *(a) Similar distribution in both study periods*. above); species distributions are detailed in Appendix 7.C.

Species
Gammarus pulex

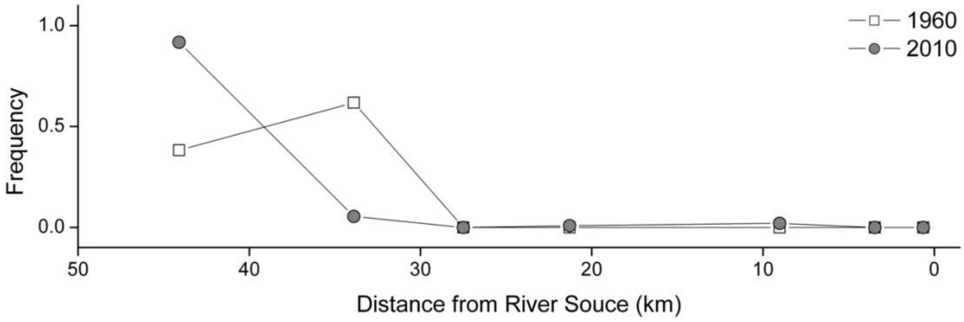
Asellus aquaticus was common in both 1960 and 2010 (Table 6.10). *A. aquaticus* was common in the lower reaches of the river in 1960 but was recorded upstream of this limit in 2010 (Figure 6.10a). The lack of continuous distribution is likely due to no pool habitat sampled in either study period at site 5 (all *A. aquaticus* were collected in pool habitat at the new upstream sites) it is therefore likely that the distribution is contiguous (Figure 6.10a). Due to significantly higher abundance in 2010 ($\chi^2_c = 288.151$, $p < 0.0001$) and the low numbers collected from the new upstream sites, the detection at these sites is not significant (Fisher's test; $p = 0.127$). Although the range of this species may have increased upstream the peak in abundance appears to have moved downstream (Kendall's test, $W = 0.696$, $p = 0.213$) (Figure 6.10b). *(d) Different distribution in 2010 c.f. 1960.*

Table 6.10: Numerical summary of *A. aquaticus* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	134	14.57 (± 25.83)	2
2010	331	52.14 (± 124.93)	4



(a)



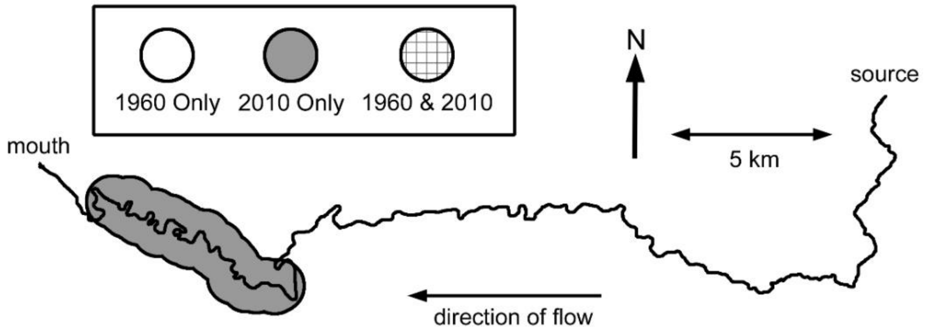
(b)

Figure 6.10: Distribution of *A. aquaticus* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *A. aquaticus* in each study period.

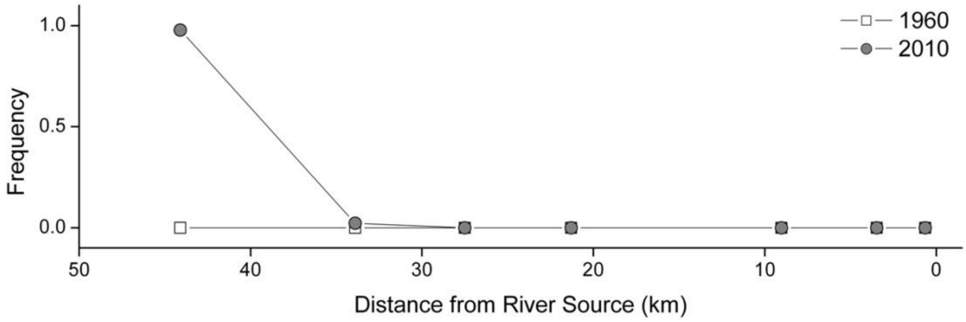
Crangonyx pseudogracilis is a new species to the River Endrick since the 1960 study period (Table 6.11; Figure 6.11b). The collection of this species in the River Endrick is highly significant ($\chi^2_c = 3.6e^4$, $p < 0.0001$). *C. pseudogracilis* is a non-native gammaridean amphipod, which was first recorded in Britain in the 1930s and is now widespread throughout the UK (Sutcliffe, 1991). Individuals of this species were collected solely from habitats with a slow current (pool and emergent macrophyte), except one individual collected from riffle habitat at Dalnair (site 6). (c) *Species previously unrecorded.*

Table 6.11: Numerical summary of *C. pseudogracilis* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	0	0	0
2010	434	75.86 (± 195.89)	2



(a)



(b)

Figure 6.11: Distribution of *C .pseudogracilis* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *C. pseudogracilis* in each study period.

6.3.1.4 Ephemeroptera

22 species of Ephemeroptera were identified from the River Endrick during the 2010 study period. This is a similar number to that found in 1960 (21), but there has been some loss and gains of some species. *Cloeon simile* and *Baetis vernus* were recorded in the 1960 study but not in the 2010 study. *Baetis niger*, *Baetis scambus*, *Cloeon dipterum* and *Leptophlebia vespertina* were recorded in 2010 but not in 1960. Due to difficulties in the separation of *Ecdyonurus insignis* and *E. torrentis*, analysis of these species has been combined. Distribution of the Ephemeroptera has remained consistent between the two study periods (Figure 6.12).

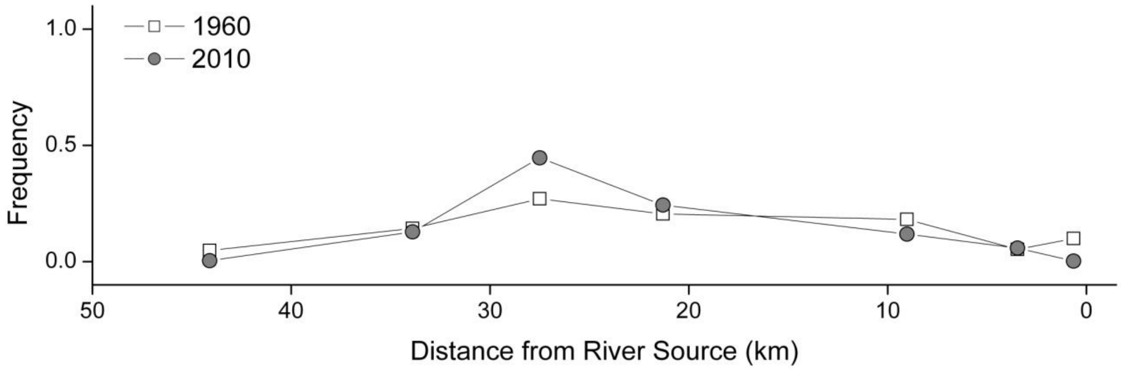


Figure 6.12: Frequency of occurrence of Ephemeroptera at each of the 7 sites during the 1960 and 2010 study of the River Endrick.

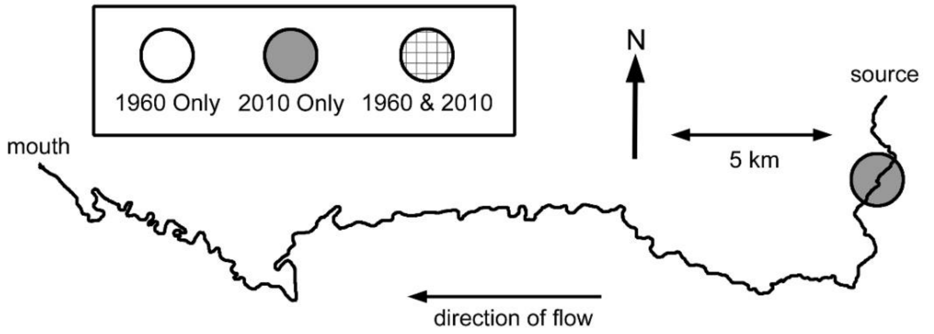
Table 6.12: Species of Ephemeroptera with similar distribution patterns in both study periods (i.e. *(a) Similar distribution in both study periods*. above); species distributions are detailed in Appendix 7.C.

Species
Ameletus inopinatus
Baetis muticus
Baetis rhodani
Caenis rivulorum
Centroptilum luteolum
E torrentis/insignis
Ecdyonurus venosus
Habrophlebia fusca
Leptophlebia marginata
Paraleptophlebia cincta
Rhithrogena semicolorata
Serratella ignita
Siphlonurus lacustris

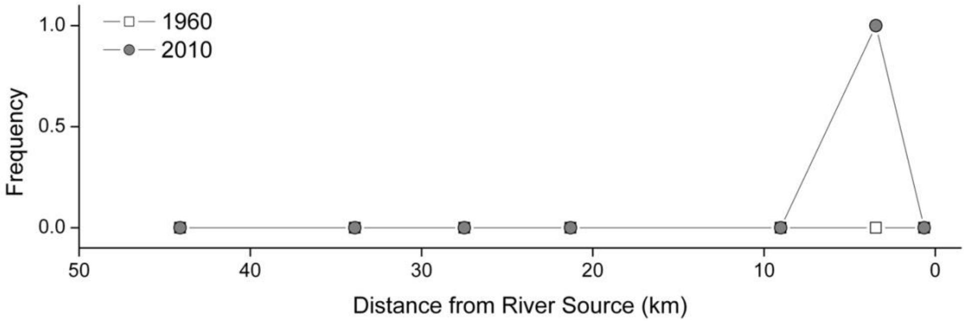
Baetis niger was collected from site 2 (Burnfoot) in 2010 (Table 6.13; Figure 6.13). Two individuals were collected from moss habitat in the autumn collection, but the detection of this species from the 2010 survey was not significant ($\chi^2_c = 0.05$, $p = 0.823$). Identification of these two individuals needs to be confirmed, this species was collected from this site during the 1990 study (Doughty & Maitland, unpublished data) but was not collected during the 1960 study. *(c) Species previously unrecorded.*

Table 6.13: Numerical summary of *B. niger* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	0	0	0
2010	2	0.19 (± 0.50)	1



(a)



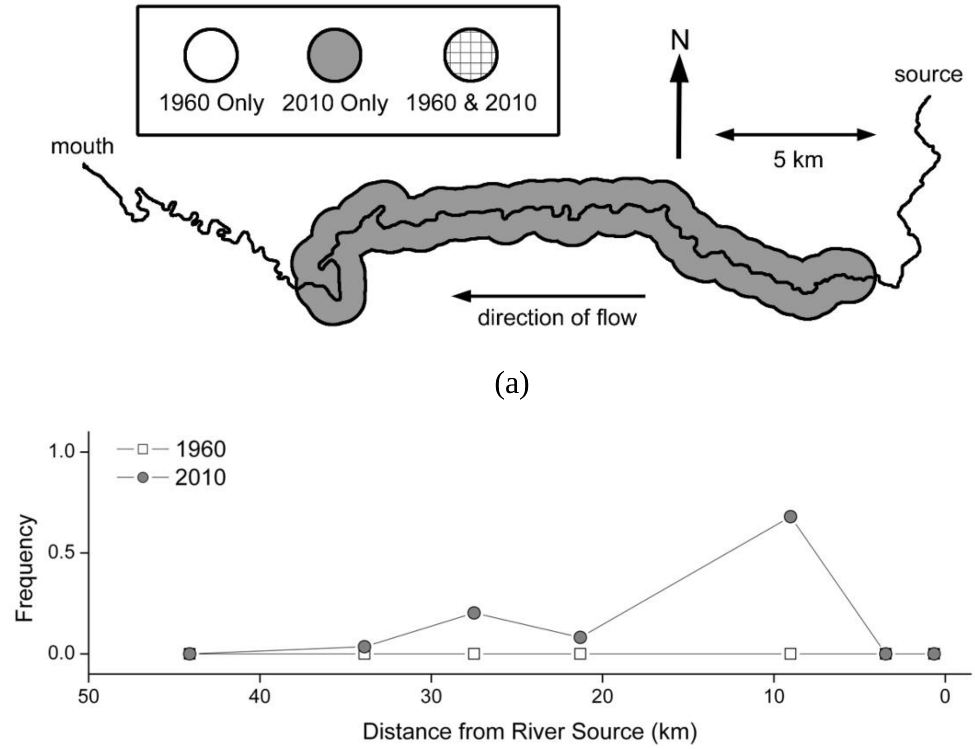
(b)

Figure 6.13: Distribution of *B. niger* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *B. niger* in each study period.

Baetis scambus is a new species to the River Endrick since the 1960 study period (Figure 6.14) and was recorded in significantly large numbers ($\chi^2_c = 5.3e^4$, $p < 0.0001$) during the summer 2010 study period (Table 6.14). 521 individuals were collected almost exclusively in summer months (3 individuals were collected in the autumn sample at Dalnair (site 6)) during the 2010 study. Individuals of this species were almost always collected from habitat in fast flow conditions (i.e. riffle and moss on rock). Of the 521 individuals collected, 516 were collected from riffle or moss habitat. *(c) Species previously unrecorded.*

Table 6.14: Numerical summary of *B. scambus* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	0	0	0
2010	521	59.29 (± 102.76)	4



(a)

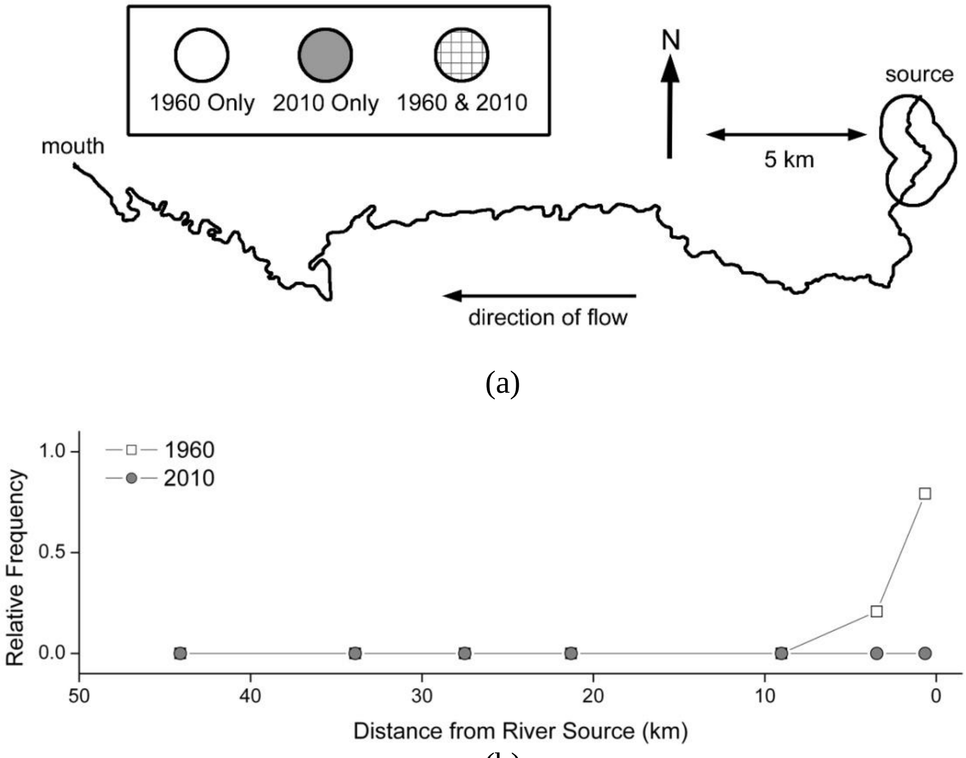
(b)

Figure 6.14: Distribution of *B. scambus* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *B. scambus* in each study period.

Baetis vernus was abundant in the 1960 study period but was not detected in any sample collected in the River Endrick in 2010 (Table 6.15; Figure 6.15). The non-detection of this species was highly significant ($\chi^2_c = 4.8e^2$, $p = 4.7e^{-97}$) and it is therefore highly likely that *B. vernus* has been lost from the River Endrick (Figure 6.15). *(b) Possible local extinction of a species*

Table 6.15: Numerical summary of *B. vernus* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	488	422.0 (± 63.14)	2
2010	0	0	0



(a)

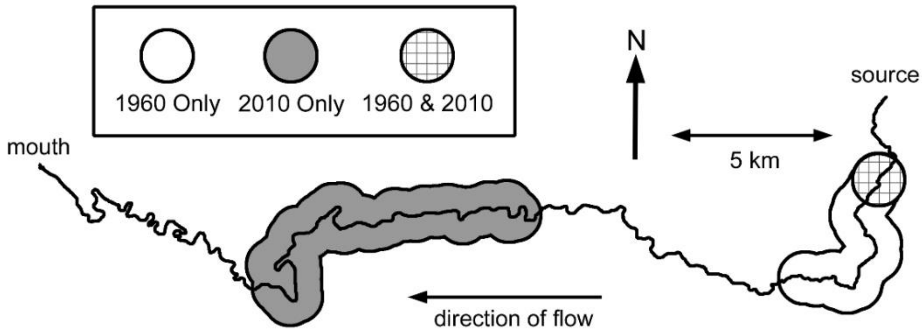
(b)

Figure 6.15: Distribution of *B. vernus* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *C. alpina* in each study period.

Electrogena lateralis was collected from the River Endrick in 1960 and 2010 but the distribution of this species has changed (Table 6.16; Figure 6.16). *E. lateralis* was collected from the upper reaches in both 1960 and 2010 but the species was also collected downstream of the 1960 range in 2010 (Figure 6.16a). The detection of *E. lateralis* at the new sites downstream of the 1960 range was significant (Fisher's test; $p < 0.001$; Figure 6.16a). Distribution of relative abundance changed (Kendall's test; $W = 0.272$, $p = 0.775$; Figure 6.16b) and absolute abundance has reduced significantly ($\chi^2_c = 85.454$, $p < 0.0001$) between 1960 and 2010 (Table 6.16). Peak abundance for this species has moved downstream in 2010 compared with 1960. *(d) Different distribution in 2010 compared with 1960.*

Table 6.16: Numerical summary of *E. lateralis* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	140	13.29 (± 29.81)	2
2010	32	5.86 (± 8.47)	4



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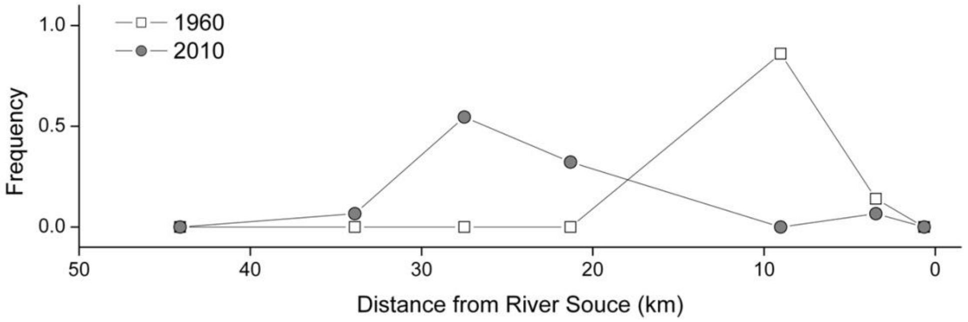


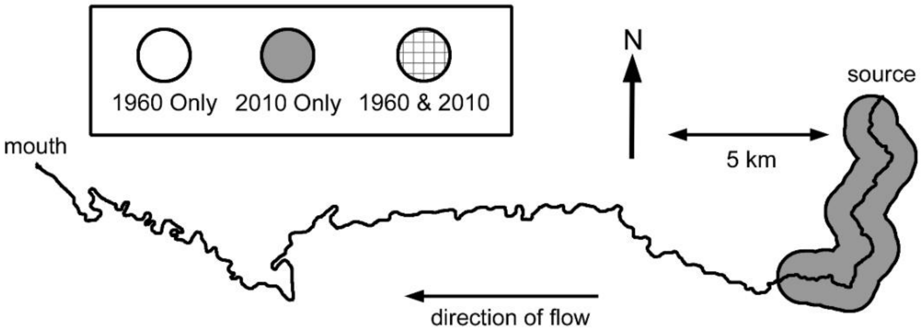
(b)

Figure 6.16: Distribution of *E. lateralis* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *E. lateralis* in each study period.

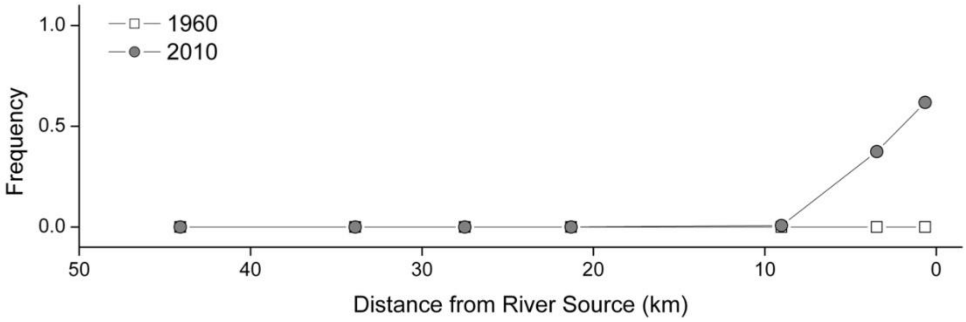
Leptophlebia vespertina is a new species to the River Endrick since the 1960 study period and was recorded from 3 sites in the upper part of the river in 2010 (Table 6.17; Figure 6.17). The collection of this species in the River Endrick is highly significant ($\chi^2_c = 1.9e^3$, $p < 0.0001$). *L. vespertina* was recorded at the source site (site 1) in the 1990 study (Doughty & Maitland, unpublished data). *(c) Species previously unrecorded.*

Table 6.17: Numerical summary of *L. vespertina* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	0	0	0
2010	104	12.57 (± 21.98)	3



(a)



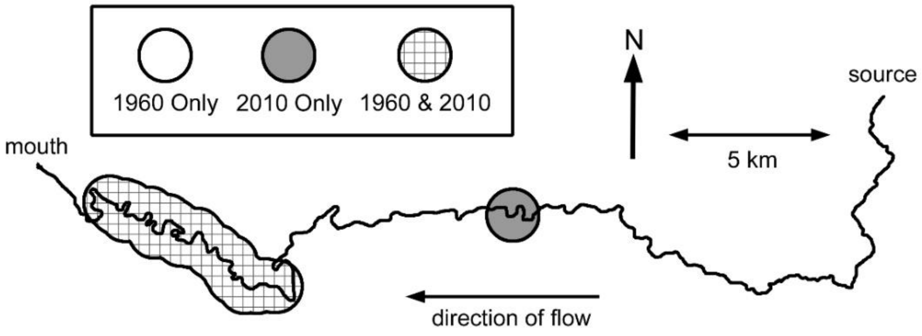
(b)

Figure 6.17: Distribution of *L. vespertina* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *L. vespertina* in each study period.

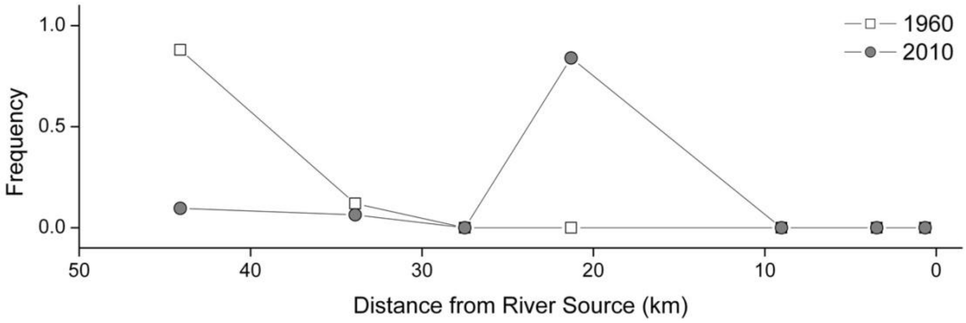
Procloeon pennulatum was common in both 1960 and 2010 (Table 6.18). *P. pennulatum* was collected from the lower reaches in both 1960 and 2010 but the species was also collected upstream of the 1960 range in 2010 (Figure 6.18a). The detection of *P. pennulatum* at the new site upstream of the 1960 range was significant (Fisher's test; $p < 0.001$; Figure 6.18a). Distribution of relative abundance changed (Kendall's test; $W = 0.563$, $p = 0.345$; Figure 6.18b) and absolute abundance has increased significantly ($\chi^2_c = 6.75$, $p = 0.009$) between 1960 and 2010 (Table 6.18). Peak abundance for this species has moved upstream in 2010 compared with 1960. *(d) Different distribution in 2010 compared with 1960.*

Table 6.18: Numerical summary of *P. pennulatum* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	27	3.57 (± 8.20)	2
2010	41	6.00 (± 12.90)	3



(a)



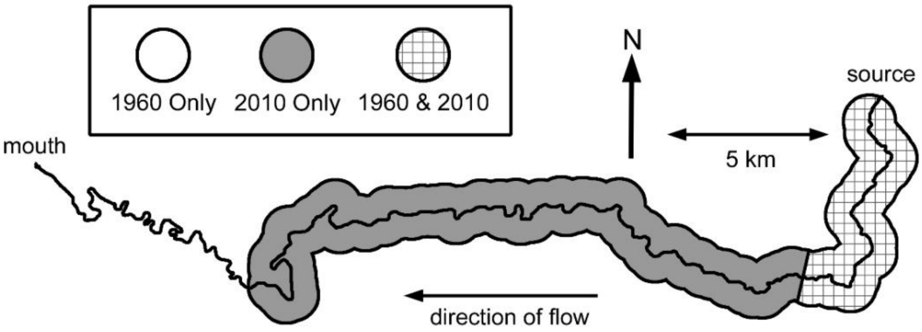
(b)

Figure 6.18: Distribution of *P. pennualtum* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *P. pennualtum* in each study period.

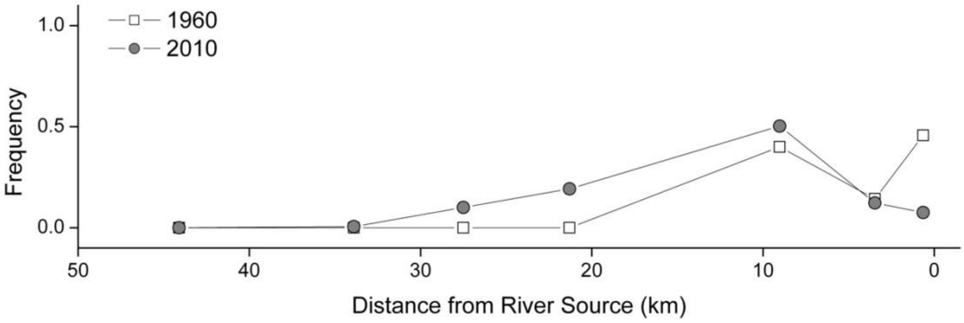
Paraleptophlebia submarginata was collected from the River Endrick in 1960 and 2010 but the distribution of this species has changed (Table 6.19; Figure 6.19). *P. submarginata* was collected from the upper reaches in both 1960 and 2010 but the species was also collected downstream of the 1960 range in 2010 (Figure 6.19a). The detection of *P. submarginata* at the new sites downstream of the 1960 range was significant (Fisher's test; $p < 0.001$; Figure 6.19a). Distribution of relative abundance changed (Kendall's test; W = 0. .607, p = 0.295; Figure 6.19b) and absolute abundance increased significantly (χ^2_c = 220.006, $p < 0.0001$) between 1960 and 2010 (Table 6.19). *(d) Different distribution in 2010 compared with 1960.*

Table 6.19: Numerical summary of *P. submarginata* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	45	5.00 (± 7.09)	3
2010	145	17.14 (± 20.51)	6



(a)



(b)

Figure 6.19: Distribution of *P. submarginata* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *P. submarginata* in each study period.

6.3.1.5 Plecoptera

20 species of Plecoptera were identified from the River Endrick during the 2010 study period. This is the same number of species recorded during the 1960 study period, but the composition of the Plecoperan fauna has changed. During the 2010 study period, three species were not detected (*Taeniopteryx nebulosa*, *Amphinemura standfussi* and *Chloroperla tripunctata*) and three novel species were detected (*Diura bicaudata*, *Nemourella picteti* and *Nemoura cinerea*). Distribution of the Plecoptera has remained consistent between the two study periods (Figure 6.20).

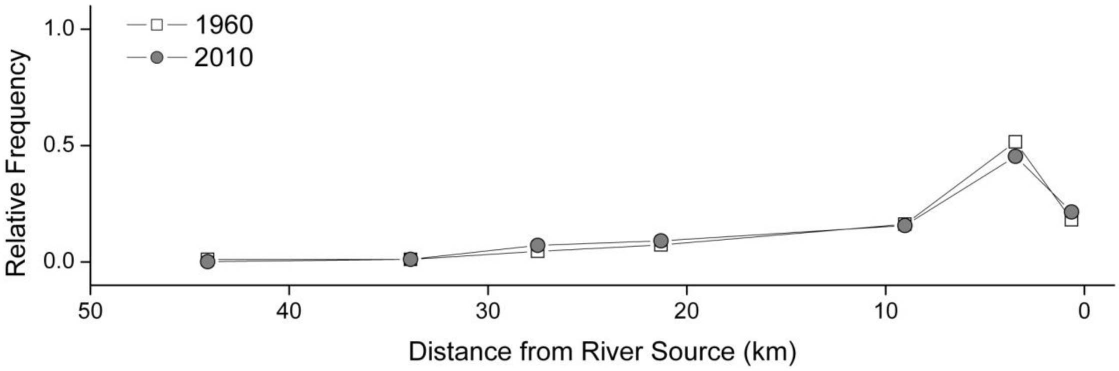


Figure 6.20: Frequency of occurrence of Plecoptera at each of the 7 sites during the 1960 and 2010 study of the River Endrick.

Table 6.20: Species of Ephemeroptera with similar distribution patterns in both study periods (i.e. *(a) Similar distribution in both study periods*. above); species distributions are detailed in Appendix 7.C.

Species
Amphinemura sulcicollis
Brachyptera risi
Capnia bifrons
Dinocras cephalotes
Euleuctra geniculata
Isoperla grammatica
Leuctra hippopus
Leuctra nigra
Leutra inermis
Nemoura avicularis
Siphonoperla torrentium

Amphinemura standfussi was not detected in the River Endrick during the 2010 study period but was recorded, but was found at one site in low abundance in 1960 (Table 6.21; Figure 6.21). Due to the low number recorded in 1960 the non detection of this species from the River Endrick in 2010 is not significant ($\chi^2_c = 0.05$, $p = 0.823$). *A. standfussi* was not collected during the 1990 study (Doughty & Maitland, unpublished data). *(b) Possible local extinction of a species*

Table 6.21: Numerical summary of *A. standfussi* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	4	4.00 (± 0.57)	1
2010	0	0	0

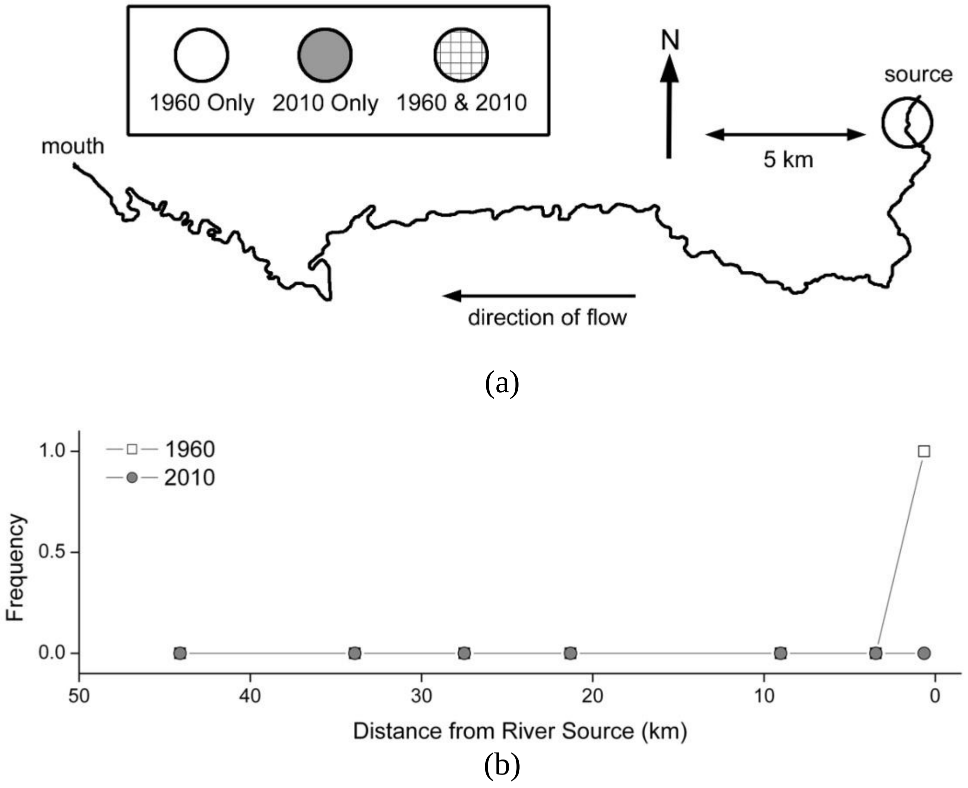


Figure 6.21: Distribution of *A. standfuusi* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *A. standfuusi* in each study period.

Diura bicaudata is a new species to the River Endrick since the 1960 study period and was recorded at low abundance from 1 site at the source of the river in 2010 (Table 6.22; Figure 6.22). Three individuals were collected from moss habitat in the spring collection, but the detection of this species from the 2010 survey was not significant ($\chi^2_c = 0.05$, $p = 0.823$). This species was collected from this site during the 1990 study (Doughty & Maitland, unpublished data) but was not collected during the 1960 study. *(c) Species previously unrecorded.*

Table 6.22: Numerical summary of *D. bicaudata* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	0	0	0
2010	3	0.43 (± 1.13)	1

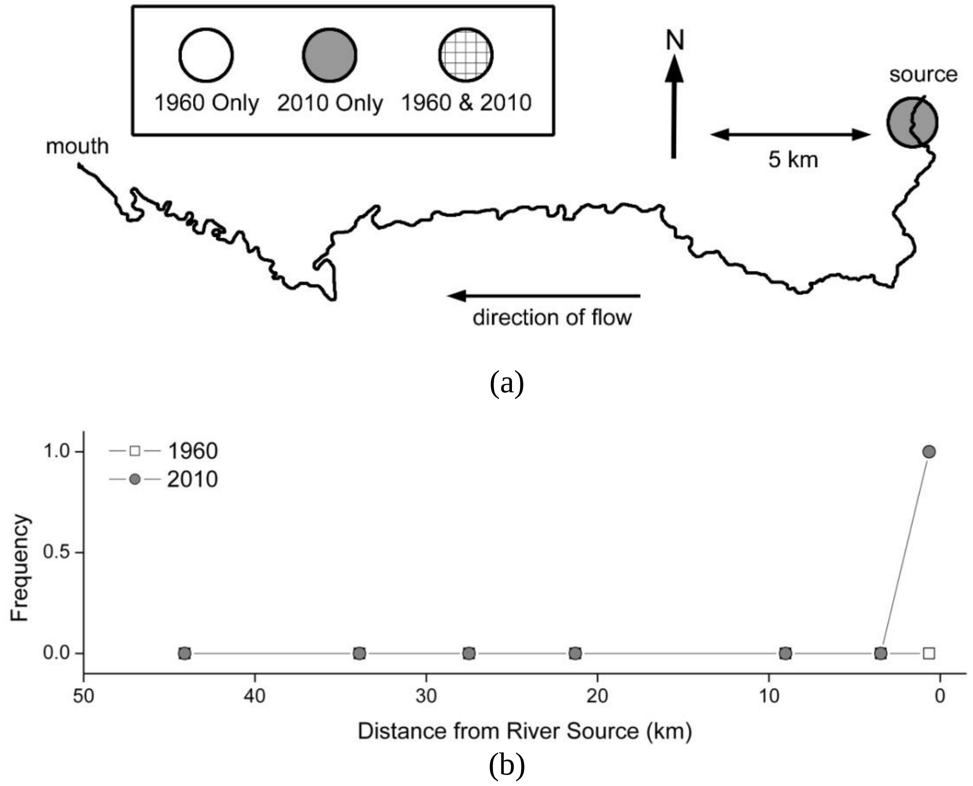
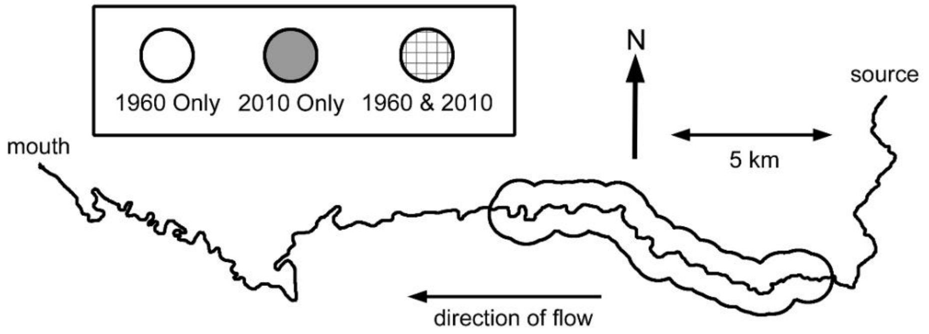


Figure 6.22: Distribution of *D. bicaudata* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *D. bicaudata* in each study period.

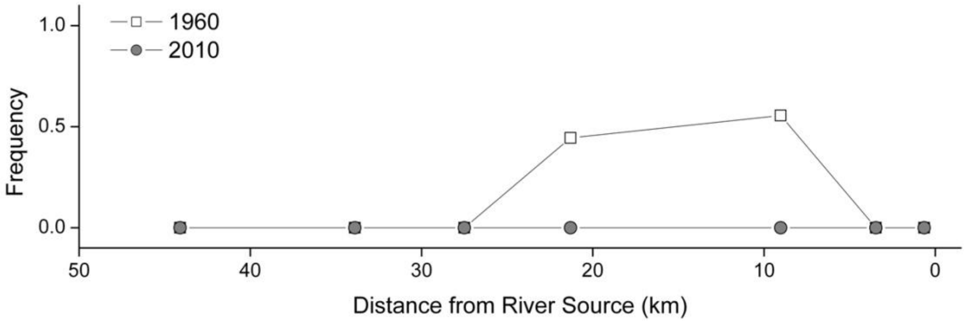
Chloroperla tripunctata was relatively common in the 1960 study period but was not detected in any sample collected in the River Endrick in 2010 (Table 6.23; Figure 6.23). Due to the low number recorded in 1960 the non detection of this species from the River Endrick in 2010 is not significant ($\chi^2_c = 3.521$, p = 0.061). 17 individuals of *C. tripunctata* were collected during the 1990 study at the same sites this species was recorded from in 1960 (Doughty & Maitland, unpublished data). *(b) Possible local extinction of a species*

Table 6.23: Numerical summary of *C. tripunctata* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	12	1.29 (± 2.22)	2
2010	0	0	0



(a)



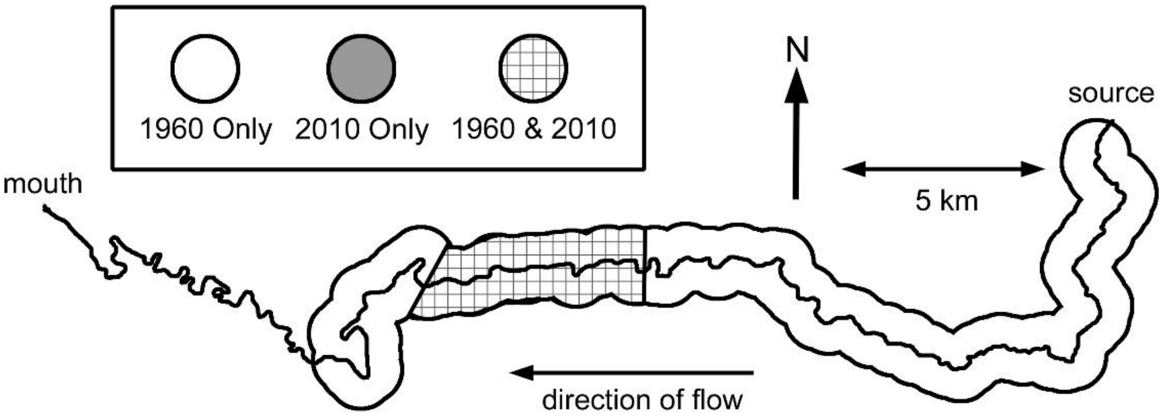
(b)

Figure 6.23: Distribution of *C. tripunctata* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *P. bipunctata* in each study period.

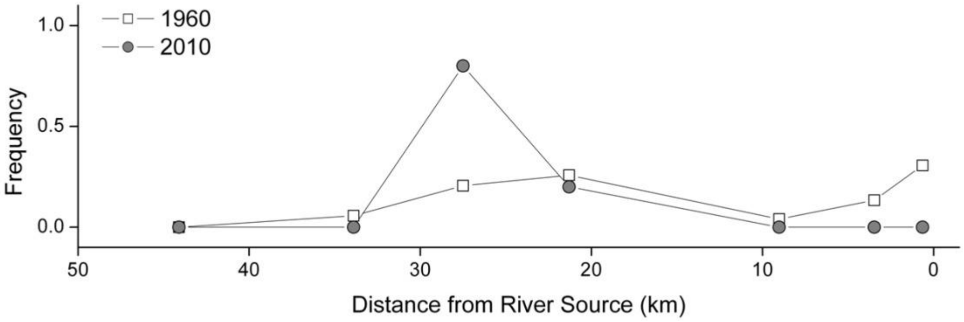
Leuctra fusca was collected from the River Endrick in 1960 and 2010 but the distribution of this species has changed (Table 6.24; Figure 6.24). The range of this species appears to have contracted to the middle reaches of the river in 2010 compared to a more widespread distribution in 1960. Distribution of relative abundance changed (Kendall's test; W = 0.589; p = 0.314; Figure 6.24b) and absolute abundance has decreased significantly (χ^2_c = 575.397, $p < 0.0001$) between 1960 and 2010 (Table 6.24). *(d) Different distribution in 2010 compared with 1960.*

Table 6.24: Numerical summary of *L. fusca* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	606	85.43 (± 69.98)	6
2010	15	4.29 (± 8.98)	2



(a)



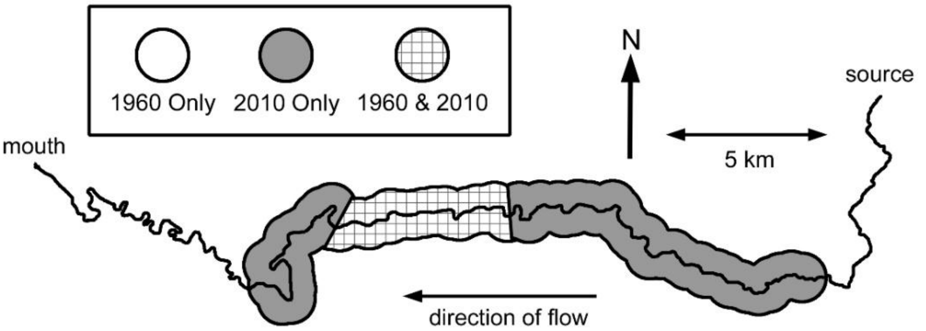
(b)

Figure 6.24: Distribution of *L. fusca* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *L. fusca* in each study period.

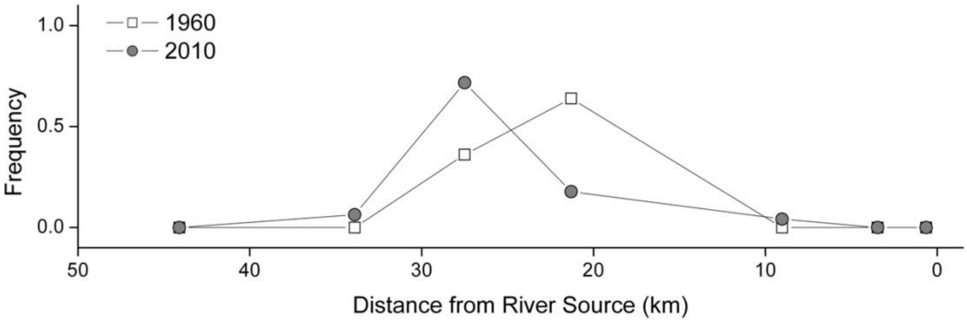
Leuctra moselyi was collected from the River Endrick in 1960 and 2010 but the distribution of this species has changed (Table 6.25; Figure 6.25). The range of this species appears to have expanded from a range confined to the middle reaches in 1960 to a range covering a larger length of the river in 2010 (Figure 6.25a). Site occupancy differed significantly between years (Fisher's test; $p = 0.042$). Distribution of relative abundance changed (Kendall test; $W = 0.696$, $p = 0.213$) and absolute abundance increased significantly ($\chi^2_c = 9.4e^3$, $p < 0.0001$) between 1960 and 2010 (Figure 6.25b). *(d) Different distribution in 2010 compared with 1960.*

Table 6.25: Numerical summary of *L. moselyi* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	30	5.14 (± 9.25)	2
2010	563	115.86 (± 211.84)	4



(a)



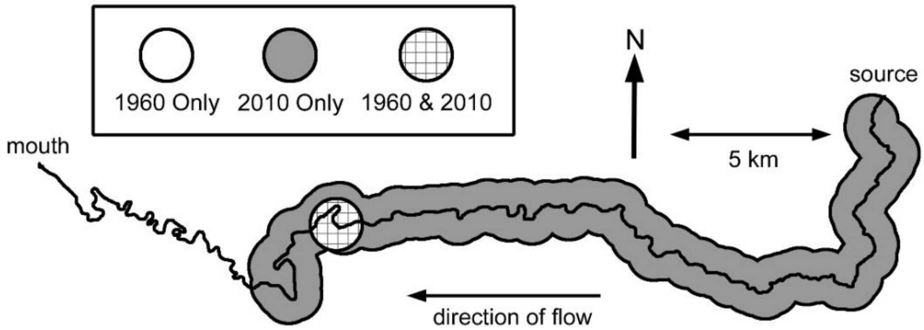
(b)

Figure 6.25: Distribution of *L. moselyi* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *L. moselyi* in each study period.

Nemoura cambrica was collected from the River Endrick in 1960 and 2010 but the distribution of this species has changed (Table 6.26; Figure 6.26). *N. cambrica* was collected from the middle reaches in both 1960 and 2010 but the species was also collected upstream and downstream of the 1960 range in 2010 (Figure 6.26a). During the 1960 this species was recorded from 4 of the 12 study sites, but always in low numbers. The detection of this species in 2010 outwith the historic range in 1960 was significant (Fisher's exact test; $p = 0.003$; Figure 6.26a). Distribution of relative abundance changed (Kendall's test; $W = 0.401$, $p = 0.567$; Figure 6.26b) and absolute abundance has increased significantly ($\chi^2_c = 1.4e^3$, $p < 0.0001$) between 1960 and 2010 (Table 6.26). *(d) Different distribution in 2010 compared with 1960.*

Table 6.26: Numerical summary of *N. cambrica* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	2	0.57 (± 1.51)	1
2010	91	16.00 (± 19.00)	6



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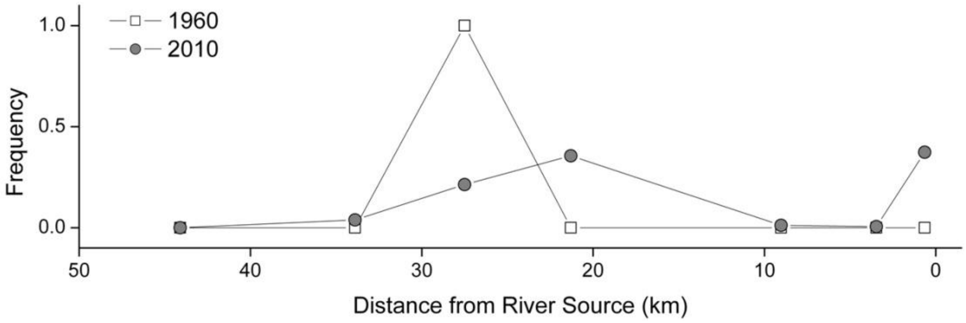


(b)

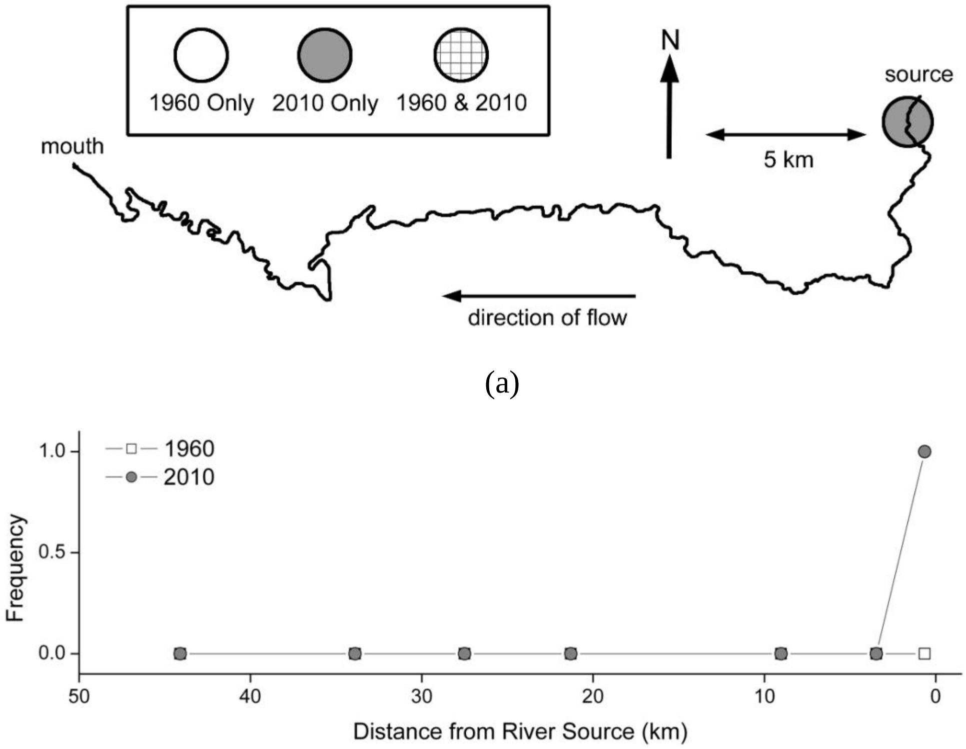
Figure 6.26: Distribution of *N. cambrica* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *N. cambrica* in each study period.

Nemoura cinerea is a new species to the River Endrick since the 1960 study period and was recorded from 1 site at the source of the river in 2010 significantly large numbers ($\chi^2_c = 1.8e^4$, $p < 0.0001$) (Table 6.27; Figure 6.27). *N. cinerea* was also recorded at the site at the source of the river (site 1) in the 1990 study (Doughty & Maitland, unpublished data).

(c) Species previously unrecorded.

Table 6.27: Numerical summary of *N. cinerea* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	0	0	0
2010	306	43.7 (± 115.66)	1



(a)

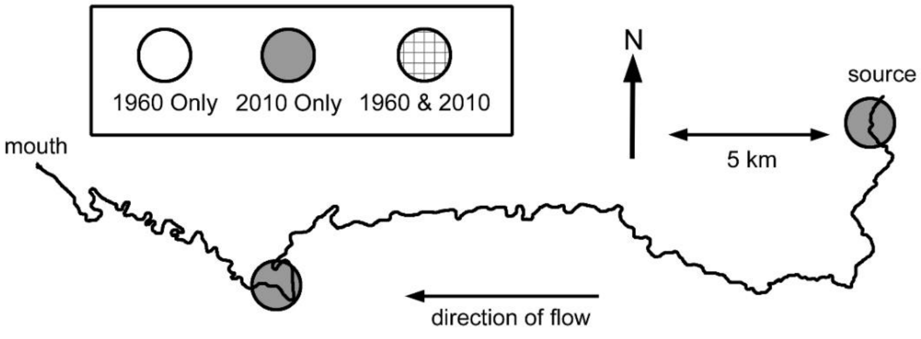
(b)

Figure 6.27: Distribution of *N. cinerea* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *N. cinerea* in each study period.

Nemurella pictetii is a new species to the River Endrick since the 1960 study period and was recorded from 2 sites on the River Endrick in 2010 significantly large numbers ($\chi^2_c = 2.2e^4$, $p < 0.0001$) (Table 6.28; Figure 6.28). 334 individuals were collected in all seasons at the site located near the source of the river and one individual was collected during the summer collected at Dalnair (site 6). The individual collected at Dalniar was a larger well developed nymph. *(c) Species previously unrecorded.*

Table 6.28: Numerical summary of *N. pictetii* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	0	0	0
2010	334	47.71 (± 125.80)	2



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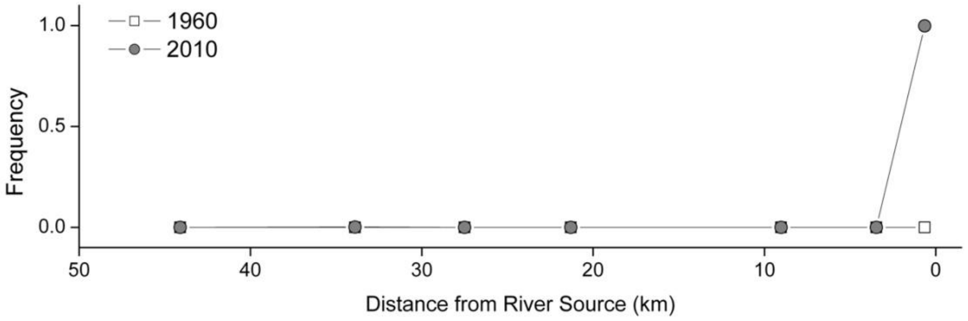


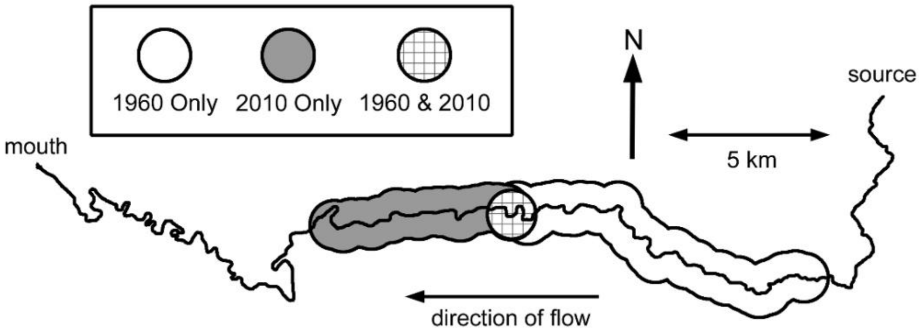
(b)

Figure 6.28: Distribution of *N. pictetii* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *N. pictetii* in each study period.

Perla bipunctata was collected from the River Endrick in 1960 and 2010 but the distribution of this species has changed (Table 6.29; Figure 6.29). The range of this species appears to have expanded from a range in the upper middle reaches in 1960 to a range occupying a position further downstream in 2010 (Figure 6.29a). Site occupancy differed significantly between years (Fisher's test; $p < 0.001$). Distribution of relative abundance changed (Kendall's test; $W = 0.357$, $p = 0.638$; Figure 6.29b) and absolute abundance increased significantly ($\chi^2_c = 13.556$, $p = 0.0002$) between 1960 and 2010 (Figure 6.29b). Peak abundance for this species has moved downstream in 2010 compared with 1960. *(d) Different distribution in 2010 compared with 1960.*

Table 6.29: Numerical summary of *P. bipunctata* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	31	3.14 (± 3.72)	2
2010	10	2.77 (± 5.26)	2



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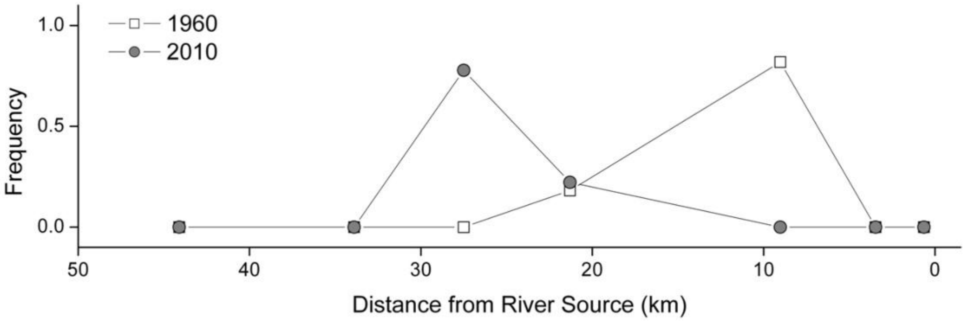


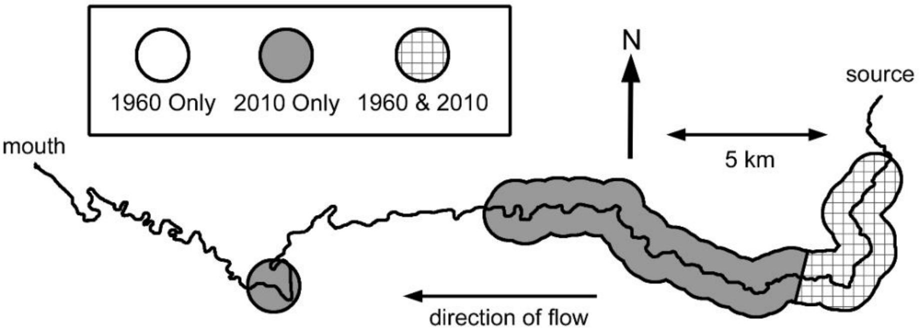
(b)

Figure 6.29: Distribution of *P. bipunctata* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *P. bipunctata* in each study period.

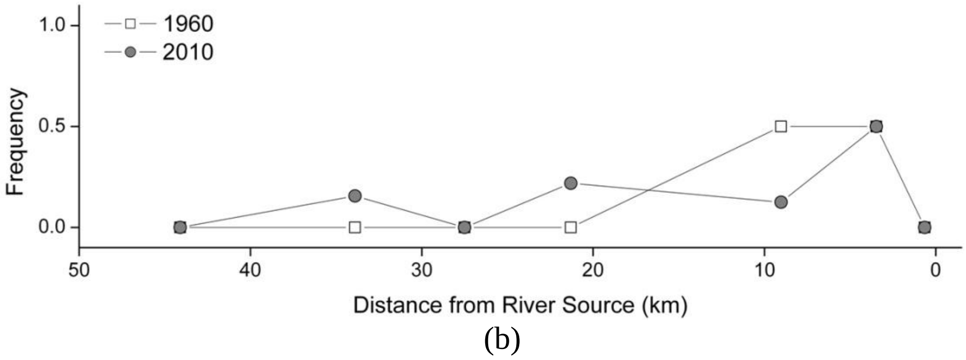
Perlodes microcephala was collected from the River Endrick in 1960 and 2010 but the distribution of this species has changed (Table 6.30; Figure 6.30). *P. microcephala* was collected from the upper reaches in both 1960 and 2010 but the species was also collected downstream of the 1960 range in 2010 (Figure 6.30a), although the detection downstream is equivocal (Fisher's exact test; p = 0.079). Distribution of relative abundance changed (Kendall's test; W = 0.576, p = 0.329; Figure 6.30b) and absolute abundance increased significantly (χ^2_c = 77.521, $p < 0.0001$) between 1960 and 2010 (Figure 6.30b). *(d) Different distribution in 2010 compared with 1960.*

Table 6.30: Numerical summary of *P. microcephala* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	12	1.14 (± 1.95)	2
2010	43	4.57 (± 5.77)	4



(a)



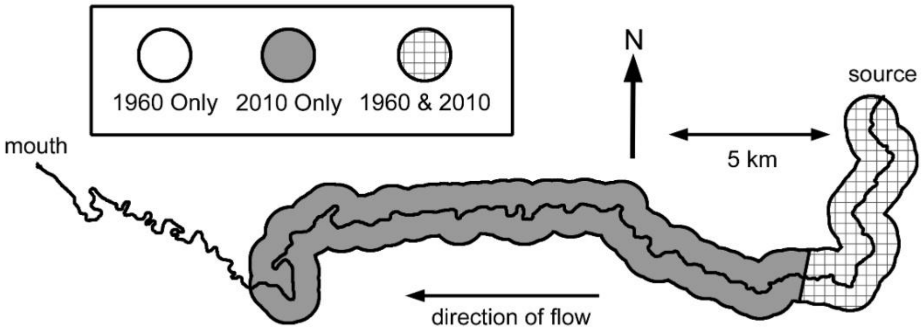
(b)

Figure 6.30: Distribution of *P. microcephala* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *P. microcephala* in each study period.

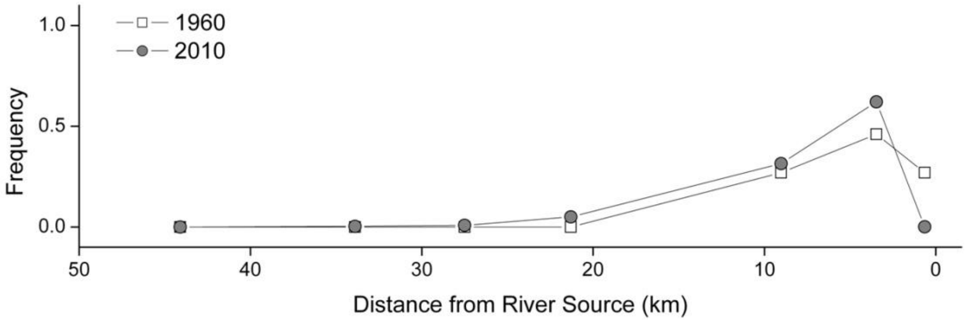
Protonemura meyeri was collected from the River Endrick in 1960 and 2010 but the distribution of this species has changed (Table 6.31; Figure 6.31). *P. meyeri* was collected from the upper reaches in both 1960 and 2010 but the species was also collected downstream of the 1960 range in 2010 (Figure 6.31a). The detection of *P. meyeri* at the new sites downstream of the 1960 range was significant (Fisher's test; $p < 0.001$; Figure 6.31a). Distribution of relative abundance changed (Kendall's test; $W = 0.692$, $p = 0.217$; Figure 6.31b) and absolute abundance has increased significantly ($\chi^2_c = 1.5e^3$, $p < 0.0001$) between 1960 and 2010 (Table 6.31). *(d) Different distribution in 2010 compared with 1960.*

Table 6.31: Numerical summary of *P. meyeri* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	466	48.71 (± 64.51)	3
2010	1328	130.00 (± 218.13)	6



(a)



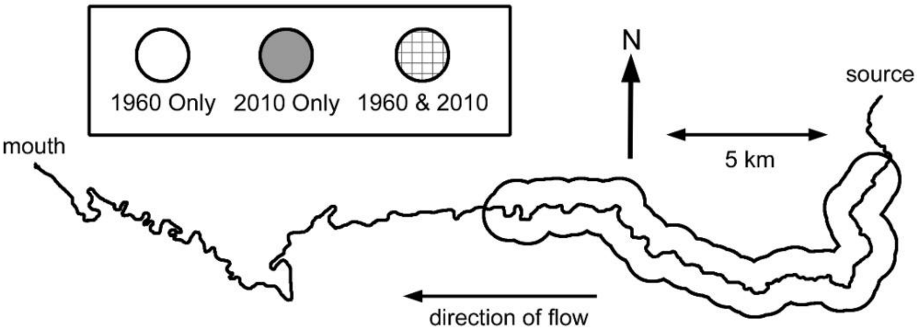
(b)

Figure 6.31: Distribution of *P. meyeri* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *P. meyeri* in each study period.

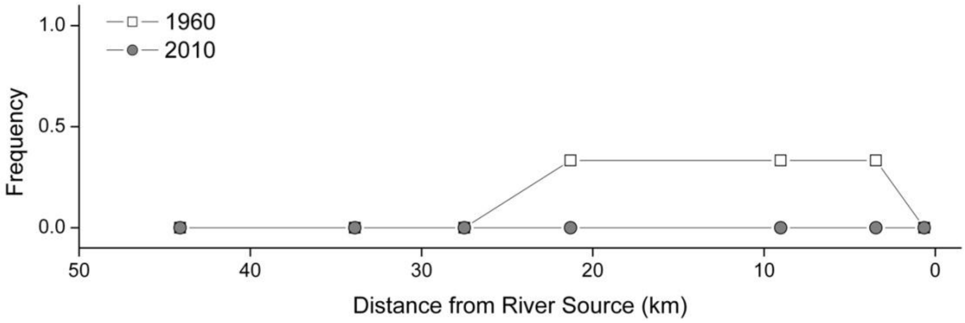
Taeniopteryx nebulosa was not detected in the River Endrick during the 2010 study period but was recorded, although not in abundance, from 3 sites in 1960 (Table 6.32; Figure 6.32). The non-detection of this species was significant (χ^2_c = 6.891, p = 0.009) and it is therefore highly likely that *T. nebulosa* has been lost from the River Endrick (Table 6.32; Figure 6.32). *(b) Possible local extinction of a species*

Table 6.32: Numerical summary of *T. nebulosa* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	16	1.71 (± 2.13)	3
2010	0	0	0



(a)



(b)

Figure 6.32: Distribution of *T. nebulosa* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *T. nebulosa* in each study period.

6.3.1.6 Hemiptera

The majority of this group, both in terms of number of species and abundance, remain confined to the lower reaches of the River Endrick (Figure 6.33). Seven species of Hemiptera were recorded during the 2010 study period. From the 7 study sites, nine species were recorded during the 1960 study period, seven of which were also recorded in the 2010 study period. *Velia caprai*, *Nepa cinerea*, *Hesperocorxia sahlbergi*, *Sigara distincta* and *Micronecta poweri* were not recorded during the 2010 study period. One individual of *Paracorixia concinna* was recorded from the River Endrick in the 2010 study.

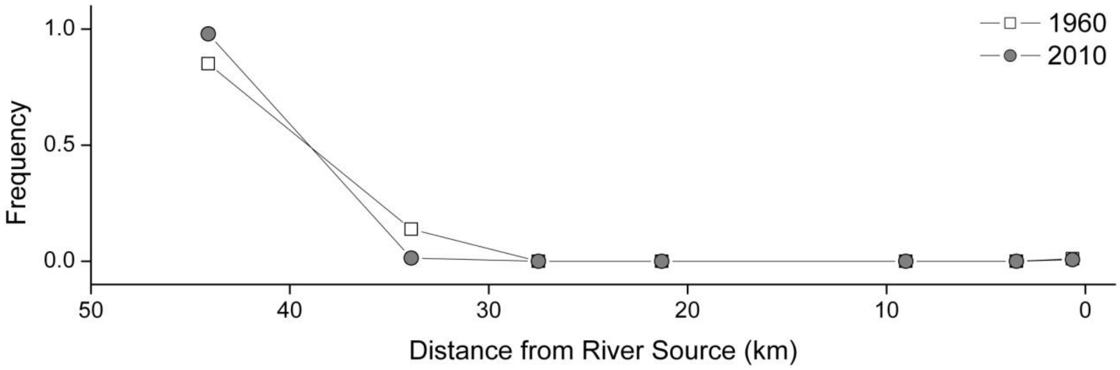


Figure 6.33: Frequency of occurrence of Hemiptera at each of the 7 sites during the 1960 and 2010 study of the River Endrick.

Table 6.33: All six species of Hemiptera recorded in both study periods had similar distribution patterns in both study periods (i.e. *(a) Similar distribution in both study periods*. above); species distributions are detailed in Appendix C.

Species
Gerris costai
Gerris lacustris
Notonecta glauca
Sigara dorsalis
Sigara falleni
Sigara fossarum

6.3.1.7 Trichoptera

Due to significant identification issues associated with this order (particularly with the Family Limnephilidae), the Trichopteran fauna of the River Endrick will not include detailed analysis of species from the Families, Beraeidae, Brachycentridae, Goeridae, Hydroptilidae, Lepidostomatidae, Leptoceridae, Limnephilidae and Odontoceridae. A full list of the Trichopteran species recorded during the 2010 study can be found in Appendix B. Distribution of the Trichoptera has remained consistent between the two study periods (Figure 6.34).

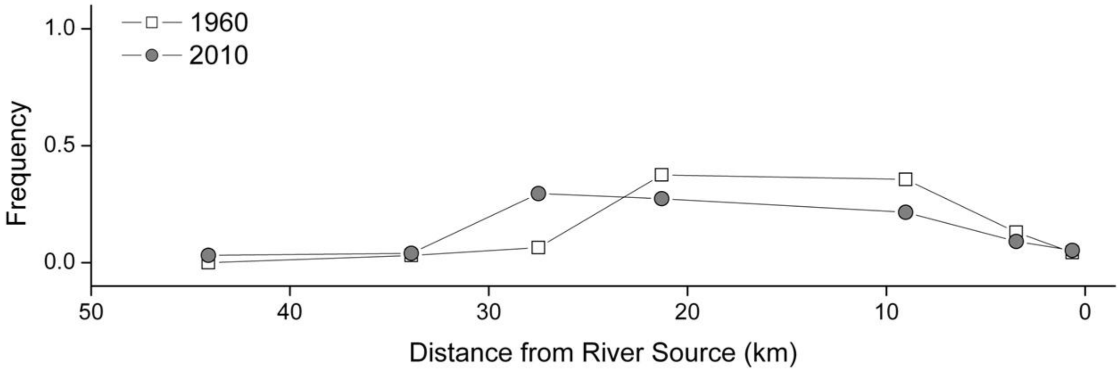


Figure 6.34: Frequency of occurrence of Trichoptera at each of the 7 sites during the 1960 and 2010 study of the River Endrick.

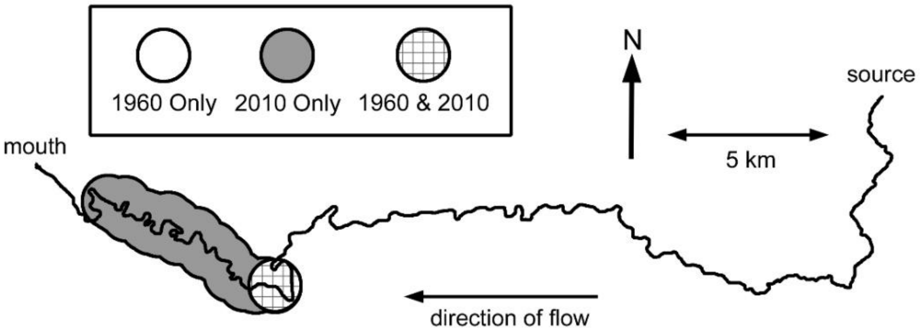
Table 6.34: Species of Trichoptera with similar distribution patterns in both study periods (i.e. *(a) Similar distribution in both study periods*. above); species distributions are detailed in Appendix C.

Species
Hydropsyche pelluidula
Hydropsyche siltalai
Lype phaeopa
Plectrocnemia conspersa
Polycentropus flavomaculatus
Polycentropus irroratus
Rhyacophila dorsalis

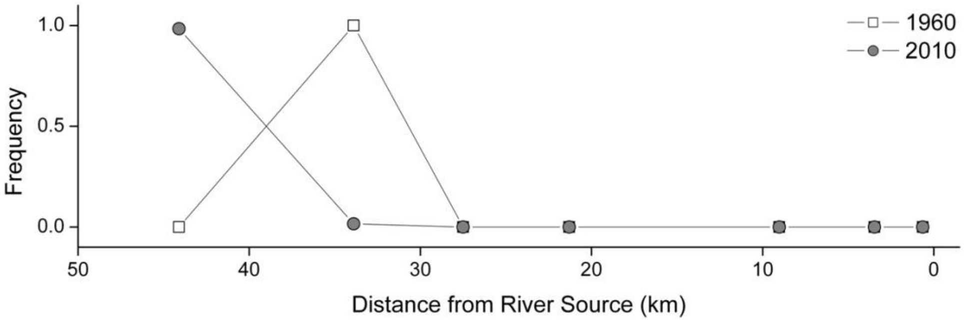
Cyrnus trimaculatus was collected from the River Endrick in 1960 and 2010 but the distribution of this species has changed (Table 6.35; Figure 6.35). *C. trimaculatus* is found exclusively in the lower reaches of the river (Figure 6.35a) but site occupancy differed significantly (Fisher's test, $p < 0.001$) between years with *C. trimaculatus* now occupying a location further downstream in 2010 compared with 1960 (Figure 6.35a). Distribution of relative abundance changed (Kendall's test; $W = 0.380$, $p = 0.602$; Figure 6.35b) and absolute abundance increased significantly ($\chi^2_c = 858.05$, $p< 0.0001$) between 1960 and 2010 (Table 6.35). Peak abundance for this species has moved downstream in 2010 compared with 1960. *(d) Different distribution in 2010 compared with 1960.*

Table 6.35: Numerical summary of *C. trimaculatus* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	5	0.43 (± 1.13)	1
2010	71	11.86 (± 30.93)	2



(a)



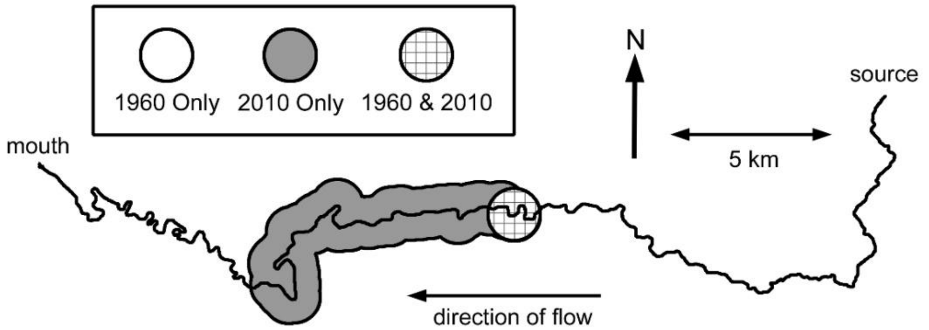
(b)

Figure 6.35: Distribution of *C. trimaculatus* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *C. trimaculatus* in each study period.

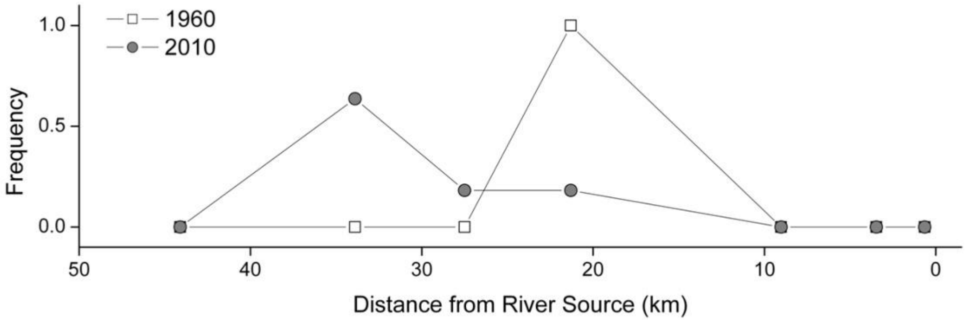
Glossosoma boltoni was collected from the River Endrick in 1960 and 2010 but the distribution of this species has changed (Table 6.36; Figure 6.36). *G. boltoni* was collected from the site 4 (Dalfoil) in 1960 and 2010 but the species was also collected downstream of the 1960 range in 2010 (Figure 6.36a). Site occupancy differed significantly between years (Fisher's test; $p < 0.001$). Distribution of relative abundance changed (Kendall's test; $W = 0.388$, $p = 0.588$; Figure 6.36b) and absolute abundance was not significantly different ($\chi^2_c = 0.019$, $p = 0.890$) between 1960 and 2010 (Table 6.36). Peak abundance for this species has moved downstream in 2010 compared with 1960. *(d) Different distribution in 2010 compared with 1960.*

Table 6.36: Numerical summary of *G. boltoni* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	12	1.71 (± 4.54)	1
2010	13	1.57 (± 2.57)	3



(a)



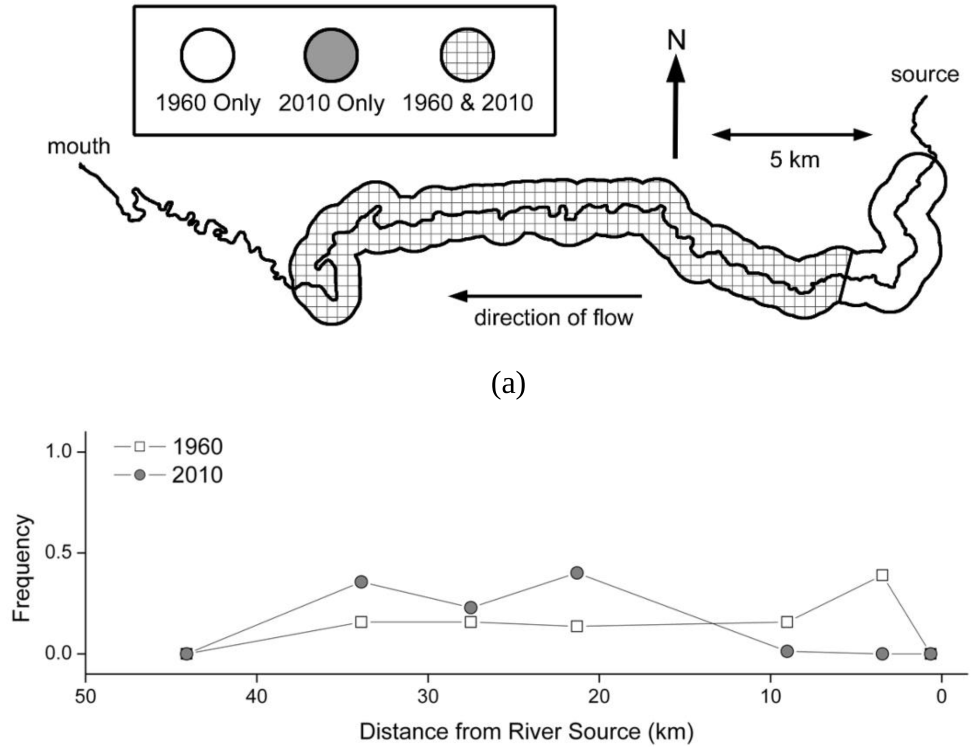
(b)

Figure 6.36: Distribution of *G. boltoni* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *G. boltoni* in each study period.

Psychomyia pusilla was collected from the River Endrick in 1960 and 2010 but the distribution of this species has changed (Table 6.37; Figure 6.37). Distribution of relative abundance changed (Kendall's test; W = 0.531, p = 0.383; Figure 6.37b) and absolute abundance decreased significantly (χ^2_c = 34.382, $p < 0.0001$) between 1960 and 2010 (Table 6.37). Peak abundance for this species has moved upstream in 2010 compared with 1960. *(d) Different distribution in 2010 compared with 1960.*

Table 6.37: Numerical summary of *P. pusilla* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	121	13.57 (± 12.41)	5
2010	56	7.57 (± 9.54)	4



(a)

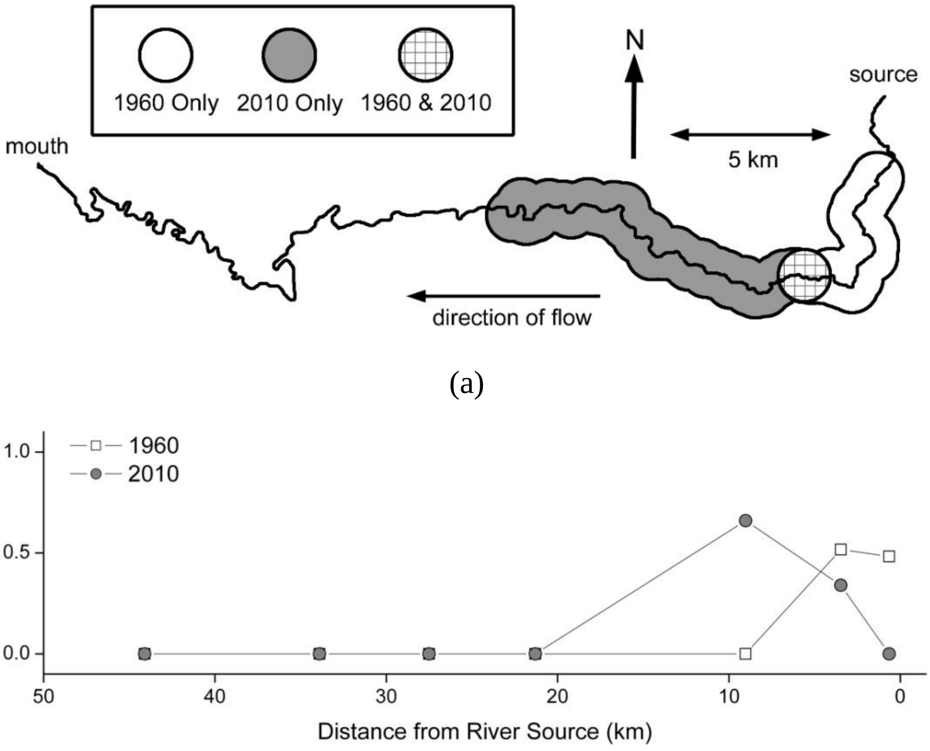
(b)

Figure 6.37: Distribution of *P. pusilla* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *P. pusilla* in each study period.

Rhyacophila munda was collected from the River Endrick in 1960 and 2010 but the distribution of this species has changed (Table 6.38; Figure 6.38). The range of this species appears to have moved downstream from a range in the upper reaches of the river in 1960, to a range occupying a position further downstream in 2010 (Figure 6.38a). Site occupancy differed significantly between years (Fisher's test; $p < 0.001$). Distribution of relative abundance changed (Kendall's test; $W = 0.411$, $p = 0.553$; Figure 6.38b) and absolute abundance increased significantly ($\chi^2_c = 115.953$, $p < 0.0001$) between 1960 and 2010 (Table 6.38). Peak abundance for this species has moved downstream in 2010 compared with 1960. *(d) Different distribution in 2010 compared with 1960.*

Table 6.38: Numerical summary of *R. munda* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	37	4.14 (± 7.08)	2
2010	103	9.71 (± 17.76)	2



(a)

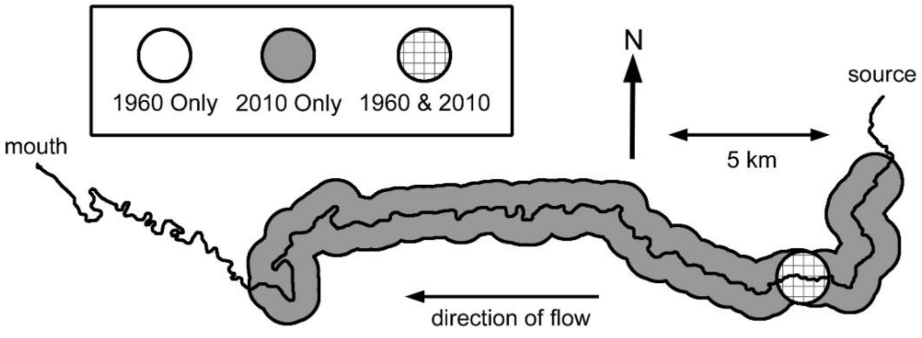
(b)

Figure 6.38: Distribution of *R. munda* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *R. munda* in each study period.

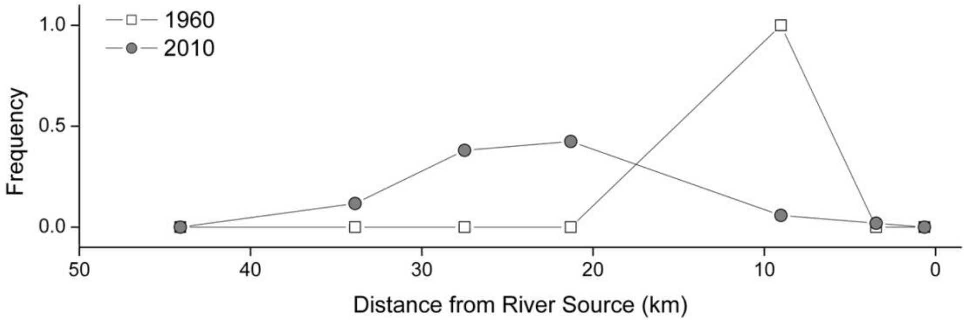
Sericostoma personatum was collected from the River Endrick in 1960 and 2010 but the distribution of this species has changed (Table 6.39; Figure 6.39). The range of this species appears to have expanded from a range confined to the upper middle reaches in 1960 to a range covering a larger length of the river in 2010 (Figure 6.39a). Site occupancy differed significantly between years (Fisher's test; $p < 0.001$). Distribution of relative abundance changed (Kendall's test; $W = 0.339$, $p = 0.667$; Figure 6.39b) and absolute abundance increased significantly ($\chi^2_c = 616.05$, $p < 0.0001$) between 1960 and 2010 (Figure 6.39b). Peak abundance for this species has moved downstream in 2010 compared with 1960. *(d) Different distribution in 2010 compared with 1960.*

Table 6.39: Numerical summary of *S. personatum* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	5	0.43 (± 1.14)	1
2010	61	9.71 (± 12.50)	5



(a)



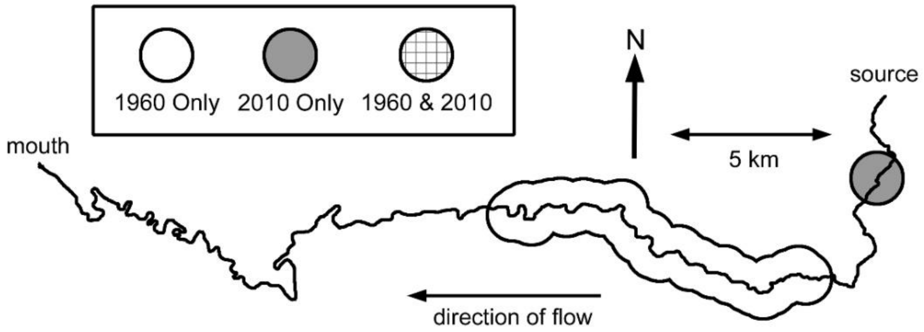
(b)

Figure 6.39: Distribution of *S. personatum* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *S. personatum* in each study period.

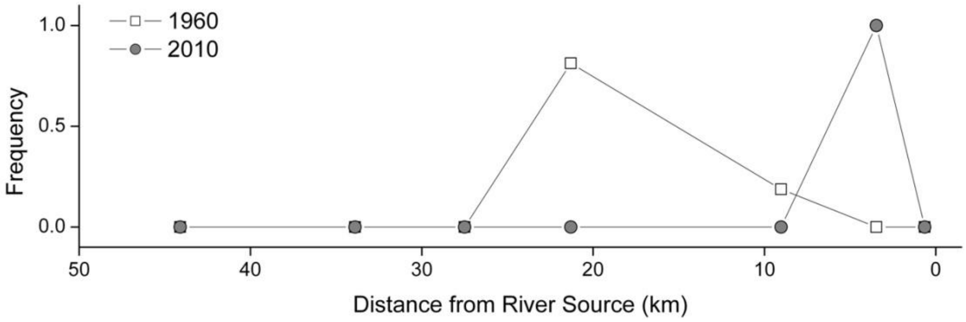
Tinodes waeneri was collected from the River Endrick in 1960 and 2010 but the distribution of this species has changed (Table 6.40; Figure 6.40). *T. waeneri* was collected only from the middle reaches of the river in 1960, but the species was collected only from the upper reaches of the river in 2010 (Figure 6.40a). The detection of *T. waeneri* at the new site upstream of the 1960 range was significant (Fisher's test; $p < 0.002$). Distribution of relative abundance changed (Kendall's test; $W = 0.192$, $p = 0.889$; Figure 6.40b) and absolute abundance decreased significantly ($\chi^2_c = 7.347$, $p = 0.0067$) between 1960 and 2010 (Table 6.40). Peak abundance for this species has moved upstream. *(d) Different distribution in 2010 compared with 1960.*

Table 6.40: Numerical summary of *T. waeneri* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	18	2.29 (± 4.86)	2
2010	6	0.57 (± 1.51)	1



(a)



(b)

Figure 6.40: Distribution of *T. waeneri* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *T. waeneri* in each study period.

6.3.1.8 Coleoptera

Due to the sporadic occurrence of this group within the River Endrick system ('some forty species have been recorded, though many of them on only one or two occasions' Maitland (1966a)) only seven species common to both study periods will be investigated further. A full species list recorded from the study periods is detailed in Appendix B. The combined distribution of these seven species of Coleoptera as a group has remained consistent between the two study periods (Figure 6.41).

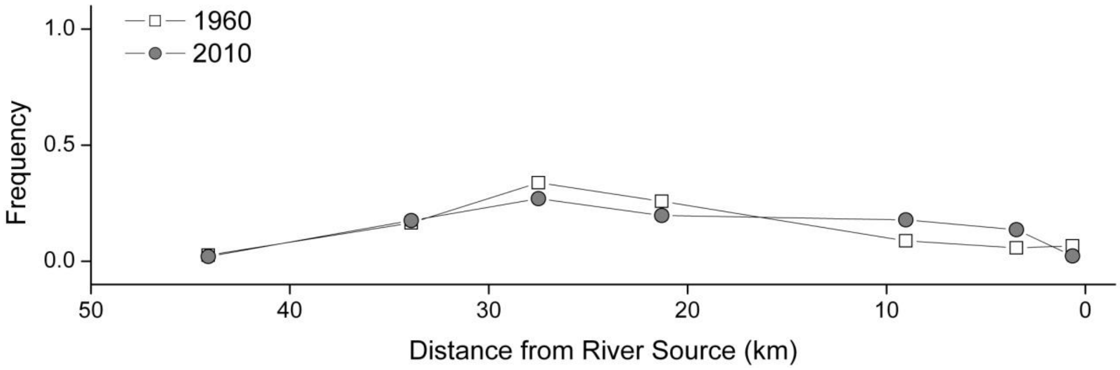


Figure 6.41: Combined frequency of occurrence of 7 species Coleoptera at each of the 7 sites during the 1960 and 2010 study of the River Endrick.

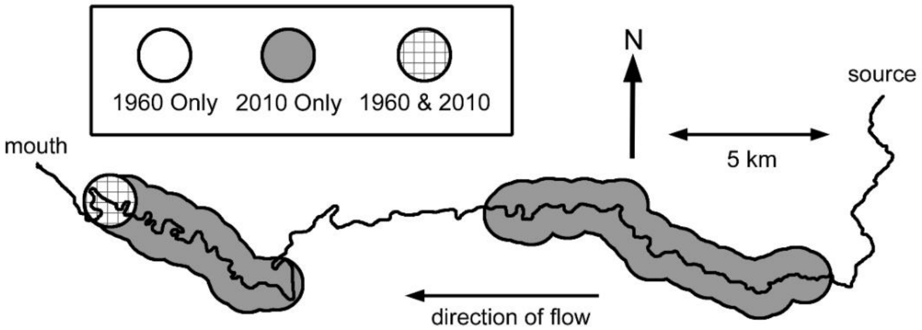
Table 6.41: Species of Coleoptera with similar distribution patterns in both study periods (i.e. *(a) Similar distribution in both study periods*. above); species distributions are detailed in Appendix C.

Species
Elmis aenea
Esolus parallelopipedus
Hydraena gracilis
Limnius volkmari
Oulimnius tuberculatus

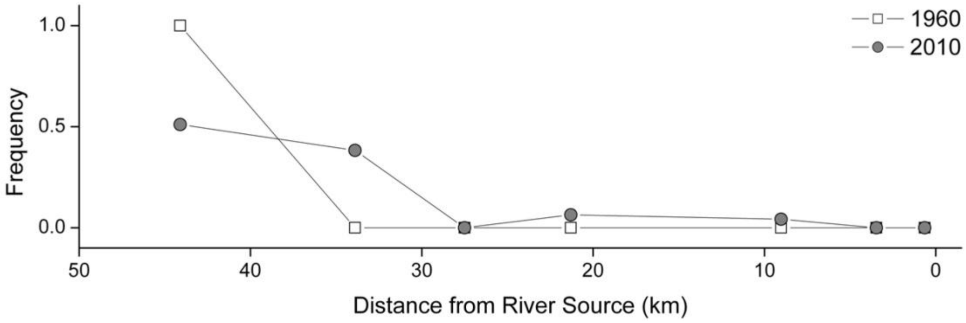
Haliplus wehnckei was collected from the River Endrick in 1960 and 2010 but the distribution of this species has changed (Table 6.42; Figure 6.42). *H. wehnckei* was collected only from the lower reaches in 1960, but was collected at 3 new upstream sites in 2010 (Figure 6.42a). The detection of this species in 2010 outwith the historic range in 1960 was significant (Fisher's exact test; p = 0.008). Distribution of relative abundance changed (Kendall's test; W = 0.509, p = 0.411; Figure 6.42b) and absolute abundance was not significantly different (χ^2_c = 1.841, p = 0.175) between 1960 and 2010 (Table 6.42). *(d) Different distribution in 2010 compared with 1960.*

Table 6.42: Numerical summary of *H. wehnckei* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	11	2.29 (± 3.30)	1
2010	16	1.57 (± 4.16)	4



(a)



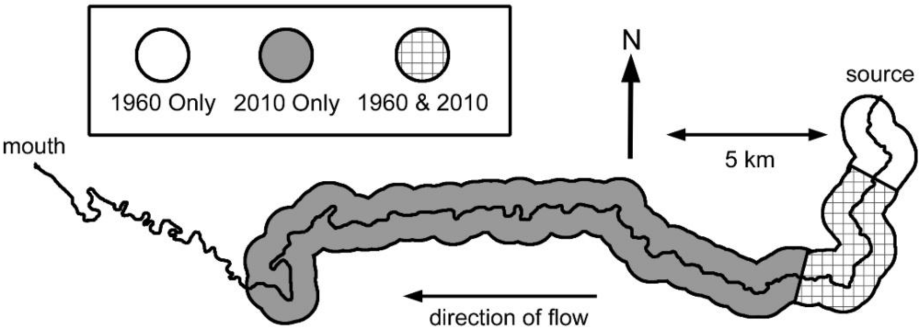
(b)

Figure 6.42: Distribution of *H. wehnckei* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *H. wehnckei* in each study period.

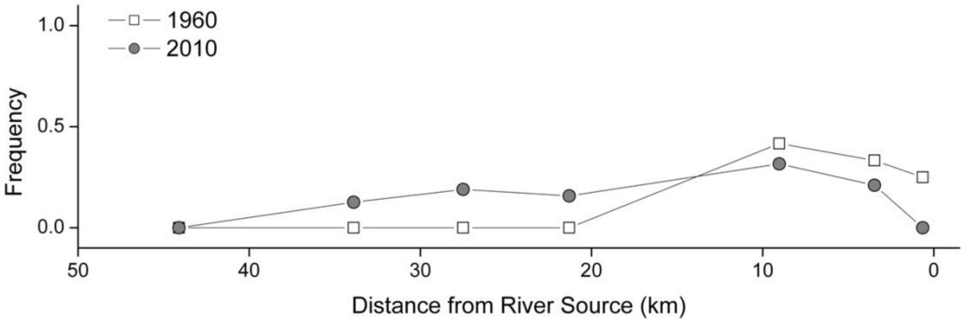
Oreodytes sanmarki was collected from the River Endrick in 1960 and 2010 but the distribution of this species has changed (Table 6.43; Figure 6.43). The range of this species has extended downstream from a range in the upper reaches of the river in 1960, to a range occupying a position further downstream in 2010 (Figure 6.43a). Site occupancy differed significantly between years (Fisher's test; p =0.003). Distribution of relative abundance changed (Kendall's test; W = 0.705, p = 0.206; Figure 6.43b) and absolute abundance increased significantly (χ^2_c = 27.191, p < 0.0001) between 1960 and 2010 (Table 6.43). *(d) Different distribution in 2010 compared with 1960.*

Table 6.43: Numerical summary of *O. sanmarki* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	17	1.71 (± 2.21)	3
2010	39	4.57 (± 3.64)	5



(a)



(b)

Figure 6.43: Distribution of *O. sanmarki* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *O. sanmarki* in each study period.

6.4 Discussion

The riverine macroinvertebrate fauna of the River Endrick has changed significantly in the last 50 years. Of the 78 species examined in this study there has been a possible local extinction of five species, the addition of 7 new species (not previously recorded) to the river system, one of which is non-native, and 22 have undergone a significant change in spatial and abundance distribution (Table 6.44).

Table 6.44: Species showing significant distributional change.

Local Extinctions
TRICLADIDA
- *Crenobia alpina*

EPHEMEROPTERA
- *Baetis vernus*

PLECOPTERA
- *Taeniopteryx nebulosa*
- *Amphinemura standfussi* [*]
- *Chloroperla tripunctata* [*]

New Additions
CRUSTACEA
- *Crangonyx pseudogracilis*

EPHEMEROPTERA
- *Baetis scambus*
- *Baetis niger*
- *Leptophlebia vespertina*

PLECOPTERA
- *Nemoura cinerea*
- *Nemurella pictetii*
- *Diura bicaudata*

Range Changes
TRICLADIDA
- *Dendrocoelum lacteum*

HIRUDINEA
- *Glossiphonia complanata*

CRUSTACEA
- *Asellus aquaticus*

PLECOPTERA
- *Nemoura cambrica*
- *Perla bipuncata*

TRICHOPTERA
- *Tinodes waeneri*
- *Rhyacophila munda*

Range Extensions
HIRUDINEA
- *Helobdella stagnalis*
- *Erpobdella octoculata*

EPHEMEROPTERA
- *Procloeon pennulatum*
- *Electrogena lateralis*
- *Paraleptophlebia submarginata*

PLECOPTERA
- *Protonemura meyeri*
- *Leuctra moselyi*
- *Perlodes microcephala*

TRICHOPTERA
- *Sericostoma personatum*
- *Cyrnus trimaculatus*
- *Glossosoma boltoni*

COLEOPTERA
- *Haliplus wehckei*
- *Oreodytes sanmarki*

Range Contractions
PLECOPTERA
- *Leuctra fusca*

TRICHOPTERA
- *Psychomyia pusilla*

[*] Results equivocal

6.4.1 Local extinctions

Crenobia alpina appears now to be locally extinct in the River Endrick. *C. alpina* is a stenothermic cold water species and the loss of this species has been noted from another British west coast river system, the Llyn Brianne (Durnace & Ormerod, 2010). In this study the loss of this species was linked to changes in large scale weather patterns (the North Atlantic Oscillation) which had a combined effect of disturbing both prey availability and the competitive interaction of *C. alpina* with a sympatrically associated Planarian, *Phagocata vitta*. These combined effects resulted in the local extinction of *C. alpina* and an increase in the numbers of *P. vitta* in the Llyn Brianne. In the River Endrick, the local extinction of *C. alpina* was accompanied by a significant increase in the total number of *Polycelis felina* collected in the 2010 compared with total numbers in 1960. It is likely that *P. felina* is responding in a similar way to *P. vitta* in the Llyn Brianne system (*P. vitta* has never been recorded from the River Endrick) and, the mechanisms contributing to the local extinction of *C. alpina* in the River Endrick are likely similar to those detailed by Durance & Ormerod (2010).

The loss of the previously substantial population (16 individuals were collected in the 1960 study) of *Taeniopteryx nebulosa* represents a major loss for the River Endrick, as this species is a threatened endemic in the Red Book Data (RBD).

No individuals of *Baetis vernus* were collected from the upper reaches of the river in 2010, compared with the 488 individuals of this species collected in 1960, and may represent a substantial loss from the headwaters of the River Endrick. *B. vernus* has been classified as using grazer/detrivorous feeding mechanisms, moderately saprobically tolerant and shows a preference for moderate flow regimes (Moog, 2002). Possible reasons for the loss of this unremarkable species are not apparent however, the appearance of *Baetis scambus* during the 2010 survey (*B. scambus* was not recorded during the 1960) suggests that there may have been identifications issues of these two species during either or both survey periods.

There is also evidence of the local extinction of the Chloroperlid, *Chloroperla tripunctata* and the Plecopteran *Amphinemura standfussi* but the loss of these species from the River Endrick are not statistically robust and require further investigation. All four species which have possibly been lost from the River Endrick (*C. alpina*, *T. nebulosa*, *A. standfussi* and

C. tripunctata) were historically collected from the middle upper to upper reaches of the River Endrick.

6.4.2 New species

Crangonyx pseudogracilis, an invasive species of North American Malacostraca, was recorded from the lower reaches of the River Endrick in 2010. This species was first recorded in Britain in the 1930's and is now widespread throughout the UK (Sutcliffe, 1991). *C. pseudogracilis* was first recorded in Loch Lomond in 1992 (Adams, pers. comm.), although it may have been established there some time before this. It was almost certainly not present at detectable levels pre 1990 in the River Endrick as the 1990 study did not record its presence (Doughty & Maitland, unpublished data) and the taxonomists from the 1990 study were aware of its presence at that time from an adjacent river, the River Clyde (Doughty, 1992). The range of *C. pseudogracilis* now extends approximately 15km upstream from the entry of the River Endrick to Loch Lomond. At the upper limit of the distribution of *C. pseudogracilis*, 10 individuals were found in pool habitat and 1 individual in riffle, suggesting that these animals show some preference for slower flow, which is likely to be limiting their distribution to the lower reaches in the River Endrick.

Six species native to Scotland were also recorded in 2010, which were not recorded in 1960. *Baetis scambus* was abundant during the 2010 study period and was recorded from throughout the length of the River Endrick. The other five new species (*Baetis niger*, *Leptophlebia vespertina*, *Nemurella picteti*, *Nemoura cinerea* and *Diura bicaudata*) were generally recorded from the upper reaches of the river. All six of these species were also recorded during the study undertaken in 1990 (Doughty & Maitland, unpublished data).

6.4.3 Range extensions

The significant upstream increase in the distribution and peak abundance of *Erpobdella octoculata* is counterintuitive. During the 1960 study period, the upstream limit of this species coincided with the inflow of the Blane Water, (Maitland, pers. comms.) a moderately polluted (at that time) tributary joining the river 800m upstream of the sampling site at Dalnair. Since the 1960 study period, the Blane Water has improved in quality (possibly accounting for the reduction in numbers of this pollution tolerant species at Dalnair in the 2010 study), and against this improvement in water quality, this species has expanded into relatively cleaner water. The mechanisms controlling the expansion of this species approximately 12.5 km upstream are not possible to explain within the scope of the data collected so far.

Another Hirudinea, *Helobdella stagnalis*, also appears to have undergone a range expansion, although results from the 2010 study are equivocal. During the 1990 study, 35 individuals of this species were collected in 12 minutes of sampling from the site at the source (site 1) (Doughty & Maitland, unpublished data) in March and August, it is therefore highly likely that this species has significantly increased the upstream limit of its distribution approximately 12 km to the source of the river.

Procloeon pennulatum has a changed distribution in 2010 compared to the distribution in 1960 with a significant increase in abundance upstream of its historic limit. This species is uncommon in Scotland, and is found more often in southern English rivers (Macadam & Bennett, 2010). The relatively large numbers collected in 2010 (compared with numbers collected during the 1960 study) indicate a possible northerly expansions and refuge for this species in the River Endrick.

Historically restricted to the upper/upper middle reaches of the river, *Electrogena lateralis*, *Paraleptophlebia submarginata*, *Protonemura meyeri*, *Perlodes microcephala* and *Sericostoma personatum* have all shown significant changes in their abundance and distribution downstream in the 2010 study period. These species show a wide range in tolerance to the different effects of changing weather patterns (Durnace & Ormerod, 2007). *P. submarginata*, and *S. personatum* have been highlighted as species intolerant of warm wet winters associated with changes in the North Atlantic Oscillation, while, *P. microcephala* has been shown to be tolerant of similar warm wet conditions (Durance & Ormerod, 2007). Often changes in the distribution of a species is attributed to changes in global climate, it is clear from species distribution changes in the middle reaches of the River Endrick that more complex interactions within the riverine community are contributing to changes in these species distributions.

Drivers of the shift in peak distribution of *Cyrnus trimaculatus* to approximately 10 km downstream of the historic (1960) peak distribution are not clear. *C. trimaculatus* is a net-spinning Polycentropodid predator (Edington & Hildrew, 1995; Moog, 2002), and the distribution change shown here may be a result of this species responding to changes in community structure and the availability of prey. Changes in the distribution of *C. trimaculatus* may also be linked with changes in flow patterns within the river. Different species of the net spinning Polycentropids have been shown to have distinct longitudinal distribution along the course of a river which has been linked to flow patterns (Edington & Hildrew, 1995).

6.4.4 Range contractions

Leuctra fusca and *Psychomyia pusilla* have both contracted their range towards the middle reaches of the River Endrick. Competition for resources arising from the number of species that have expanded their range into the middle reaches of the river (see above) may be affecting the distribution of these two species.

6.4.5 Range changes

The significant change in spatial and abundance distribution of, *Dendroceolum lacteum* may be linked to the change in abundance distribution of *Asellus aquaticus*. Peak abundance of the populations of both these species now occupy a similar location, further downstream of their historic distribution recorded in the 1960 study. To survive successfully, when living in symparty with other Tricladidas (as is the case on the River Encrick), *D. lacteum*, requires the presence of *A. aquaticus* as a food resource (Reynoldson & Young, 1966). It is likely that factors driving peak abundance of *A. aquaticus* downstream has resulted in a corresponding downstream shift in *D. lacteum*.

Perla bipunctata and *Rhyacophila munda* have both shown significant changes in their abundance and distribution downstream in the 2010 study period. Both these species have opposing tolerances to changing weather patterns (Durnace & Ormerod, 2007). *R. munda* has been shown to be intolerant of warm wet winters associated with changes in the North Atlantic Oscillation, while, *P. bipunctata* has been shown to be tolerant of similar warm wet conditions (Durance & Ormerod, 2007). The similarity in the range changes of these two species coupled with their differential response to large scale climate indicates a complex mechanism resulting in distributional change, where other environmental and biotic interaction are involved.

6.4.6 Abundance changes

Despite showing a general stasis in distribution between the 1960 and 2010 study periods (i.e. category (a), Appendix C), 37 species had significant differences in absolute abundance recorded (i.e. total number of individuals collected) in each study period (Table 6.44). The reasons surrounding abundance changes for those species listed in Table 6.44 are not immediately apparent and require further investigation although general theories for some species have been made.

The significant increase in the Tricladida, *P. felina*, has already been explained above in relation to the local extinction of *C. alpina*.

At the site located at the source of the river, *Ameletus inopinatus* has shown a significant reduction in abundance in 2010 compared with 1960. In 1960 and 1990 a total of 19 and 42 individuals of this species were collected respectively. The single individual collected during the 2010 study period represents a significant decline in number of this species at the source of the River Endrick. In contrast to this possible species decline another Siphlonurid, *Siphlonurus lacustris,* was first recorded at the site at the source of the river during the 2010 study period. These species share similar feeding requirements and life histories, but in contrast to *A. inopinatus* (a cold water stenothermic species (Gledhill, 1958)), *S. lacustris* can tolerate a broader range of temperatures. It is possible that a taxonomic replacement of the Siphlonuridae is progressing at the source of the River Endrick.

The significant increase in the abundance of *Seratella ignita* in the River Endrick in 2010 contradicts findings from the River Test in Hampshire which has shown a decline in the abundance of this species over a 10 year period between 1995 and 2004 (Bennett & Gilchrist, 2010). *S. ignita* is generally thought to be univoltine in cold waters (Elliot et al., 1988) but there is some evidence that in warmer waters in southern England there may be both summer and winter generations (Langford & Bray, 1969). In the 1960 study period all nymphs of *S. ignita* were collected in the summer samples (Maitland, 1965). In 2010, 11 nymphs were collected in autumn samples at sites 4 and 5. It may be likely that changes in the River Endrick are facilitating a change in generation time of this species more similar to that which occurs in southern British rivers, which may in turn be influencing abundance patterns.

The significant reduction in the abundance of *Amphinemura sulcicollis* in the River Endrick may be linked to similar mechanisms that have influenced the increased abundance of *S. ignita*. Nymphal growth of *A. sulcicollis* occurs during winter and spring (in the 1960 study period the nymphal growth occurred between September and May (Maitland, 1966b)), thus collections of nymphs in the summer samples in the 1960 study period were very low (Maitland, 1966b), as these samples coincided with the adult flight period. During the 2010 study, 36 and 32 individuals were collected from sites 2 and 3 respectively during summer sampling. This represents an increase in the abundance of this species in summer months in the River Endrick (c.f. Figure 1 in Maitland, 1966b). It may be likely that changes in the River Endrick are facilitating changes in the life history of this species which is influencing abundance patterns.

6.5 Conclusions

In the last 50 years, the macroinvertebrate fauna of the River Endrick has changed significantly. Changes to the distribution of some species, and the loss and gain of others have resulted in complex changes to distribution patterns. Some of these changes are a likely result of changes to large scale weather patterns and associated temperature shifts (e.g. the loss of *C. alpina* and changes to the Siphlonuridae at the source of the river), while other changes appear more complex. The middle reaches of the river have undergone considerable colonisation from species historically confined to the upper reaches of the river system. This increase in downstream distribution is significant and the resultant changes in community structure require further investigation. Changes to the lower reaches of the river have been explained in terms of species interactions and predator prey relationships and changes in abundance patterns have been linked with possible changes in life history strategies.

The primary cause(s) of species distribution and abundance changes in the River Endrick are unclear. No specific mechanism could account for the mosaic of shifting species distribution and abundance, and it is therefore likely that multiple abiotic and biotic mechanisms are contributing to the changing community structure within the River Endrick.

Table 6.45: Species which have maintained a similar distribution in 1960 and 2010 but have significantly increased or decreased in absolute abundance between the two study periods.

Abundance Increases	**Abundance Decreases**
TRICLADIDA	EPHEMEROPTERA
Polycelis tenuis	*Ameletus inopinatus*
Polycelis felina	*Baetis muticus*
	Centroptilum luteolum
CRUSTACEA	*Ecdyonurus venosus*
Gammarus pulex	*Leptophlebia marginata*
	Paraleptophlebia cincta
EPHEMEROPTERA	*Habrophlebia fusca*
Siphlonurus lacustris	
Baetis rhodani	PLECTOPTERA
Rhithrogena semicolorata	*Amphinemura sulcicollis*
Ecdyonurus torrentis/insignis[*]	*Leutra inermis*
Serratella ignita	*Isoperla grammatica*
Caenis rivulorum	*Dinocras cephalotes*
	Siphonoperla torrentium
PLECOPTERA	
Brachyptera risi	TRICHOPTERA
Nemoura avicularis	*Polycentropus flavomaculatus*
Euleuctra geniculata	
Leuctra hippopus	COLEOPTERA
Leuctra nigra	*Esolus parallelopipedus*
Capnia bifrons	
HEMIPTERA	
Notonecta glauca	
Sigara falleni	
TRICHOPTERA	
Hydropsyche siltalai	
Plectrocnemia conspersa	
COLEOPTERA	
Hydraena gracilis	
Elmis aenea	
Oulimnius tuberculatus	
Limnius volkmari	

[*] These species have been analysed together due to identification issues.

CHAPTER 7 Diversity and community function change in a river with a legacy of minimal human influence

7.1 Introduction

Biological communities are flexible entities. Variations in the biotic and abiotic environment can lead to changes in community structure through changes in species distribution and abundance. The degree to which these changes influence community function is the basis of much recent research, most often associated with human induced modifications to the environment and the resultant effects on ecosystem function (Chapin et al., 2000; Schmitz et al., 2003; Arthrington et al., 2010).

Freshwater ecosystems are losing biodiversity faster than terrestrial and marine systems (Dudgeon et al., 2006) and rivers particularly have been highlighted recently as under the greatest threat from pervasive human activity (Vörösmarty et al., 2010). Human activity has been shown to influence riverine community structure through myriad routes. Changes to hydrological flow through water impoundment have been shown to influence community structure and function (Armitage, 2006; Kanno & Vokoun, 2010). Inputs of pollutants to rivers have affected riverine community structure for centuries (Hynes, 1966; Friberg et al., 2010) and, more recently, the influences of invasive species and global climate change have been shown to have a significant effect on the species composition in river systems (Woodward et al., 2002; Devin et al., 2005; Durance & Ormerod, 2007).

There is generally a good understanding of the mechanisms controlling the distribution of species in river systems, but how changes in community structure are manifest in river systems are not so well understood. Structural change in communities can result in changes in the functional groups present within the community, ultimately affecting how the community functions. Community function corresponds to the biological and ecological response of the community to the environment and can be measured by general biological and ecological traits of community members. Changes in community function may provide an indication of possible mechanisms which facilitated the original change. For example, impoundment of a watercourse affects flow and temperature of the watercourse downstream, this in turn influences the communities downstream to those tolerating decreased flows and increased temperatures (Spence & Hynes, 1971; Lessard & Hayes, 2003)

The previous chapter highlighted significant changes in the distribution and abundance of macroinvertebrate species in the River Endrick. Using simple measures of community structure and derived measures of community function, I analyse how species changes have affected the structure and function of the macroinvertebrate community in the River Endrick after 50 years.

7.2 Methods

7.2.1 Study area

The River Endrick is located in West Central Scotland, between Lat: 56^o 06' N & 55^o 58' N and Long: 004^o 07' W & 004^o 31' W (Figure 7.1). The watershed of the river lies entirely in the midland valley of Scotland which is dominated by soft (old red sandstone) solid geology. The river rises at a height of 495m and flows in a generally westerly direction for 49 km where it enters Loch Lomond (a large (71 km^2) lake). Landuse within the catchment is dominated by agriculture but four settlements are also likely to influence the river (Maitland, 1966) (Figure 7.1).

7.2.3 River Endrick community structure

Collections of the macroinvertebrate fauna of the River Endrick were made in 1960 and 2010 at seven sites along the main channel of the river (Figure 7.1) using the same sample collection method in each study period (Maitland, 1966). Samples collected in October 1959, February 1960 and June 1961 will be referred to as the 1960 study period. Samples collected in February/March 2010, June 2010, October 2010 and February 2011, will be referred to as the 2010 study period. Collected samples were identified to species and the number of each species recorded. Samples collected in February, June and October were combined to provide an annual measure of the macroinvertebrate community at each of the 7 sites in each study period. As sampling effort at each site differed due to habitat differences, samples were standardised to a constant sampling effort of number of individuals of each species collected per one hour sampling at a site. For each site in each study period a standard measure of the macroinvertebrate community was available for 7 sites in each study period. (For a full description of collection methods please refer to chapter 6).

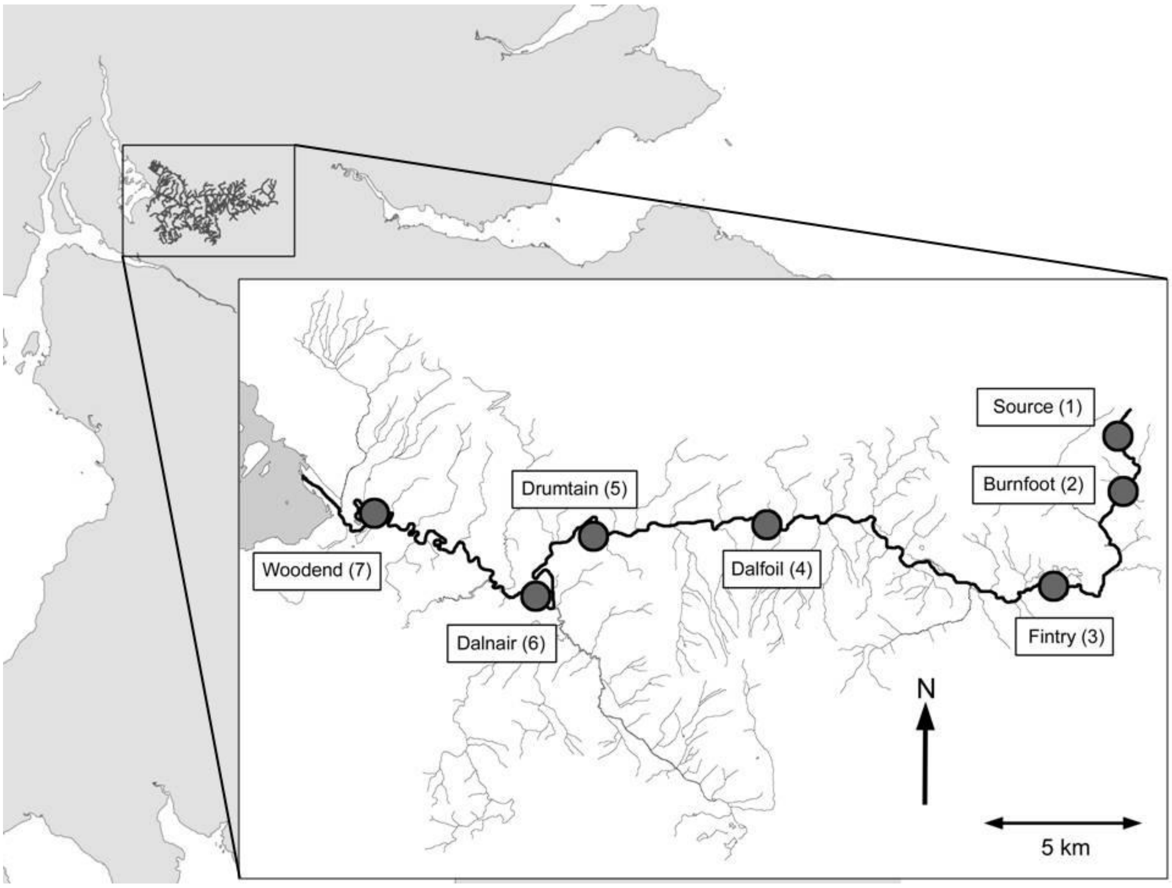


Figure 7.1: Location of the 7 sampling sites on the main channel of the River Endrick.

7.2.4 Changes in community structure

Measures of community richness (total number of recorded species), abundance (total number of recorded individuals) and diversity (Shannon-Weiner index of diversity), were calculated for each site. To assess any change in simple community structure between the study periods, differences between site community richness, community abundance and community diversity were compared between years. The significance of any differences were tested using chi-squared, for the richness and abundance measures, and for differences in Shannon-Weiner diversity, the method in Waite (2000) was applied.

To determine the degree to which the structure of the community had changed between and within study periods, Bray-Curtis similarities were calculated. Firstly, to determine the degree to which the species abundance of the river community as a whole had changed between the two study periods, the similarity between study periods was calculated for the whole river (i.e. all sites combined). Secondly, to determine the degree to which the species abundance of the community changed along the length of the river, from source to mouth, the similarity in adjacent sites species abundance was calculated for each study period separately. Thirdly, to determine the degree to which the sites had changed between study periods, the similarity between species abundance at the same site in each study period (i.e. the similarity between site 1 in 1960 and site 1 in 2010) was calculated. Finally, to determine overall change in species abundance patterns for both study periods, a complete linkage dendrogram was produced to assess the degree of clustering between sites. Complete linkage clustering was used in preference to a simple linkage clustering as single linkage clustering can be sensitive to noise in the data (Milligan, 1996) and complete linkage clustering delineates clusters with clear discontinuities (Legender & Legendre, 1998).

7.2.5 River Endrick community function

Changes to community function arising through any changes to species composition between the two study periods were investigated using three separate measures of community function. Functional feeding abundance, saprobic abundance and flow preference were defined using data available in Moog (2002). Functional feeding abundance provided an insight into community structure changes associated with changes in available food resources. Saprobic abundance provided insight into the effects changes in the water chemistry within the river had on macroinvertebrate community structure. Differences in flow preference of the macroinvertebrate community between the two study periods provided insight into changes to the flow characteristics of the watercourse and the resultant effects on community structure.

7.2.5.1 Functional feeding abundance

At each site, in each study period separately, the functional feeding abundance of the macroinvertebrate community was calculated based on the species recorded, including abundance, and the functional feeding groups of the species as defined by Moog (2002). Moog (2002) defines the functional feeding group of each species into 10 categories (shredders, grazers, active filter feeders, passive filter feeders, detritus feeders, leaf borers/miners, xylophagous, predators, parasites and other feeding types). These 10 categories are then ranked for each species from, 0 indicating no use of that feeding mechanism to a 10 indicating a unique feeding mechanism (e.g. the functional feeding group of *Leuctra fusca* has been defined as; shredder – 3, grazer – 3, and detritus feeder – 4). Functional feeding groups for the Tricladida were derived from Reynoldson (1978), (because there are no published data), *Rhyacophila munda* was assigned the same functional feeding categories as *R. dorsalis*, and *Crangonyx pseudogracilis* was assigned the same functional feeding categories as *Gammarus pulex*.

In each study period separately, functional abundance was calculated on a site by site basis. For each species, at each site, the recorded abundance of that species was proportionally divided according to the 10 functional feeding categories of that species as defined by Moog (2002). For example, if 120 *Leuctra fusca* were collected at a site, the functional feeding abundance contributed by *L. fusca* to the macroinvertebrate community would be 36 shredders, 36 grazers and 48 detritus feeders. Using these calculated species functional feeding abundances, for each site, in each study period, total functional feeding abundance was calculated for the macroinvertebrate community, by summing the number of each of the 10 functional feeding categories. Thus, for each site, in each study period, the abundance of each of the 10 categories provided a measurement of community functional feeding abundance.

7.2.5.2 Saprobic abundance

At each site, in each study period separately, the saprobic abundance of the macroinvertebrate community was calculated based on the species recorded, including abundance, and the saprobic group of the species as defined by Moog (2002). Moog (2002) defines the saprobic group of each species into 5 categories (xenosaprobic – fully clean water; oligosaprobic – little or no influence; beta-mesosaprobic – moderately influenced; alpha-mesosaprobic – heavily polluted; and polysaprobic – extremely polluted). These 5 categories are then ranked for each species from, 0 indicating no association with that water type, to a 10 indicating a unique association with that water type (e.g. the saprobic association of *Leuctra fusca* has been defined as; oligosaprobic – 2, beta-mesosaprobic – 6, and alpha-mesosaprobic – 2). Saprobic ranks were not available for Tricladida, Hemiptera, 1 species of Malacostraca (*Crangonyx pseudogracilis*), 3 species of Plecoptera (*Dinocras cephalotes*, *Nemurella pictetii*, and *Protonemura meyeri*) and 1 species of Trichoptera (*Rhyacophila munda*). These species were thus not included in this part of analysis. The measure of saprobic abundance used here would provide an indication of any changes to the macroinvertebrate community which may have arisen as a result of changes to the water physio-chemistry within the River Endrick.

In each study period separately, saprobic abundance was calculated on a site by site basis. For each species, at each site, the recorded abundance of that species was proportionally divided according to the 5 saprobic categories of that species as defined by Moog (2002). For example, if 120 *Leuctra fusca* were collected at a site, the saprobic abundance contributed by *L. fusca* would be 24 oligosaprobic, 72 beta-mesosaprobic and 24 alpha-mesosaprobic. Using these calculated species saprobic abundances, for each site, in each study period, total saprobic abundance was calculated for the macroinvertebrate community, by summing the number of each of the 5 saprobic categories. Thus, for each site, in each study period, the abundance of each of the 5 categories provided a measurement of community saprobic abundance.

7.2.5.3 Flow and temperature preference

At each site, in each study period separately, the flow preference of the macroinvertebrate community was calculated based on the species recorded, including abundance, and the flow preference of the species as defined by Moog (2002). Moog (2002) defines the flow and temperature preference of each species into 10 categories (eucrenal – mountain string, maximum temperature <9^{o}C; hypocrenal – mountain stream, maximum temperature <9^{o}C; epirhithral – upper-trout region, maximum temperature <9^{o}C; metarhithral – lower-trout region, maximum temperature <13^{o}C; hyporhithral – grayling region, maximum temperature <18^{o}C; epipotamal – brabel region, maximum temperature ≥20^{o}C; metapotamal – bream region, maximum temperature >20^{o}C; hypopotamal – brackish-water region, maximum temperature >20^{o}C; littoral zone – lentic sites; profundal zone – lake bottom). These 10 categories are then ranked for each species from, 0 indicating no association with that flow type, to a 10 indicating a unique association with that flow type (e.g. the flow preference of *Leuctra fusca* has been defined as; epirhithral – 1, metarhithral – 2; hyporhithral – 3 (2.9); epipotamal – 2; metapotamal – 2; littoral zone – + (0.1); the ‘+’ associated with the littoral zone here is given a 0.1 rank and the largest associated rank (hyporhithral) is reduced by 0.1, this method is applied throughout). Flow preferences were not available for Tricladida, Hemiptera, 1 species of Malacostraca (*Crangonyx pseudogracilis*), and 1 species of Trichoptera (*Rhyacophila munda*). These species were thus not included in this part of analysis.

In each study period separately, flow preference was calculated on a site by site basis. For each species, at each site, the recorded abundance of that species was proportionally divided according to the 10 flow categories of that species as defined by Moog (2002). For example, if 120 *Leuctra fusca* were collected at a site, the flow preference of *L. fusca* would be epirhithral – 12, metarhithral – 24, hyporhithral – 34.8, epipotamal – 24, metapotamal – 24 and littoral zone – 1. Using these calculated species flow preferences, for each site, in each study period, total flow and temperature preference was calculated for the macroinvertebrate community, by summing the number of each of the 10 flow categories. Thus, for each site, in each study period, the abundance of each of the 10 categories provided a measurement of community flow preference.

7.2.6 Changes in community function

To determine the degree to which the function of the community had changed between and within study periods, Bray-Curtis similarities were calculated separately for the three measures of community function (i.e. functional feeding abundance, saprobic abundance and flow preference) derived from the species community structure data and the information on species functional feeding groups provided by Moog (2002) (see above).

For each of the three measures of community function, a complete linkage dendrogram was produced to assess the degree of clustering between sites. To standardise the clustering for each of the 3 community function measures, sites were clustered based on an 80% or greater Bray-Curtis similarity linkage. For each of the 3 measures of community function, the pattern of site clustering was investigated further to determine possible mechanisms underlying the clustering. This was done by combining all sites within each cluster and calculating relative abundance for each category associated with the community function measure being investigated (e.g. for saprobic abundance there are 5 categories). For each community function, the combined abundance for each of the cluster groups was then plotted as a histogram of relative cluster abundance on the categories of community function. The three histogram plots were then used to determine possible underlying mechanisms which resulted in community clustering patterns.

7.2.7 Statistical analysis

Chi-squared statistic for differences in richness and abundance and t-statistic calculation for Shannon-Weiner differences were calculated using Microsoft Office Excel 2007 (Microsoft, 2007). Bray-Curtis similarities and cluster dendrograms were produced using Primer version 6.1.5 (Clarke & Gourley, 2006) on log (x+1) transformed abundance data.

7.3 Results

7.3.1 Community structure changes

Differences in the richness, abundance and diversity of the communities on the River Endrick varied between years (Table 7.1). Richness in terms of number of species recorded remained similar between sites over the 50 years, except for the community at site 4 which has significantly increased in the number of recorded species. Abundance at all sites had increased significantly and diversity (measured as Shannon-Weiner index) had decreased significantly at all sites (Table 7.1)

Between 1960 and 2010, for the whole river system (i.e. all sites combined), the species structure of the River Endrick (of those species examined) was 79% similar. The similarity in species abundance between adjacent sites in each study period separately ranged from 46% to 79% in the 1960 study period and ranged from 35% to 86% in the 2010 study period (Table 7.2). The similarity in site species abundance between the two study periods ranged from 41% to 64% (Table 7.3). The dendrogram of species abundance similarities revealed 4 distinct site clusters (upper reaches, middle reaches, lower reaches and site 1 in 2010) and highlighted low similarity between site 1 in 2010 and other sites in the two study periods (Figure 7.2). Except for Site 1 in 2010, the clustering of sites fitted well with a general downstream pattern from the source of the river, which is likely linked to longitudinal changes to physical (e.g. slope, altitude, substrate) and chemical (e.g. nutrients, suspended solids) characteristics (Vannote et al., 1980).

Table 7.1: Measures of community structure from 1960 and 2010 and significance of difference: species richness is the total number of species recorded; number of individuals is the total number of individuals recorded; diversity is the Shannon-Weiner index of diversity; Sig. is the significance of the difference between the two measures between study years at each site.

	Species Richness			**Number of Individuals**			**Diversity**		
	1960	**2010**	**Sig.**	**1960**	**2010**	**Sig.**	**1960**	**2010**	**Sig.**
Site 1	27	20	0.211	1859	1811	0.271	2.591	2.242	<0.01
Site 2	34	39	0.440	1586	3571	<0.001	2.900	2.422	<0.003
Site 3	41	40	0.938	3489	5693	<0.001	2.879	2.620	<0.003
Site 4	36	49	0.037	3185	10292	<0.001	2.924	2.126	<0.003
Site 5	35	42	0.272	2765	16364	<0.001	2.458	2.197	<0.01
Site 6	38	50	0.062	1668	4140	<0.001	2.577	1.993	<0.005
Site 7	26	29	0.624	530	1533	<0.001	2.502	2.255	<0.01

Table 7.2: Bray-Curtis similarity measures for adjacent sites in both study periods for measurements of species abundance.

	Species Abundance (% similarity)	
	1960	**2010**
Site 1 & Site 2	74	35
Site 2 & Site 3	71	71
Site 3 & Site 4	75	70
Site 4 & Site 5	79	87
Site 5 & Site 6	74	71
Site 6 & Site 7	46	37

Table 7.3: Bray-Curtis similarity measures for sites in both study periods (e.g. similarity between site 1 in 1960 and site 1 in 2010) for measurements of species abundance (species), functional feeding abundance (feeding), saprobic abundance (saprobic), and flow preference (flow).

	Species (% similarity)	**Feeding (% similarity)**	**Saprobic (% similarity)**	**Flow (% similarity)**
Site 1	41	95	98	85
Site 2	72	95	94	93
Site 3	71	96	95	93
Site 4	70	92	89	90
Site 5	69	83	83	84
Site 6	66	90	91	91
Site 7	64	83	86	88

7.3.2 Community function changes

7.3.2.1 Functional feeding abundance

Six (shredder, grazer, passive filter feeder, detritus feeders, xylophagous and predators) of the original 10 functional feeding categories were associated with the species recorded from the River Endrick in the 1960 and 2010 study period (Figure 7.2). Between 1960 and 2010, for the whole river system (i.e. all sites combined), the functional feeding abundance of the River Endrick (of those species examined) was 94% similar. The similarity in site functional feeding abundance between study periods ranged from 83% to 96% (Table 7.4). The dendrogram of functional feeding abundance revealed three distinct cluster groups (Figure 7.4). A histogram of relative functional feeding abundance in each of the three cluster groups revealed the relative influence of the difference feeding mechanisms had in clustering sites (Figure 7.5). Cluster group 1 (Site 7 in 1960) was associated with a high relative abundance of individuals with shredding and predatory feeding mechanisms. Cluster group 2 contained 5 communities collected from sites 3 and 4 in both 1960 and 2010, and site 5 in 2010, and was associated with a high relative abundance of individuals with detrivorous and passive filter feeding mechanisms. Cluster group 3 contained 8 communities collected from sites 1, 2 and 6 in 1960 and 2010, site 5 in 1960 and site 7 in 2010, and was associated with a high relative abundance of individuals using a grazing feeding mechanism. Further separation of group 2 and group 3 clusters may have been accentuated by the relative abundance ratio of individuals with grazing feeding mechanisms (GRA) to individuals with detritus feeding mechanism (DET), which is lower in group 2 cluster when compared with group 3 cluster (Figure 7.5).

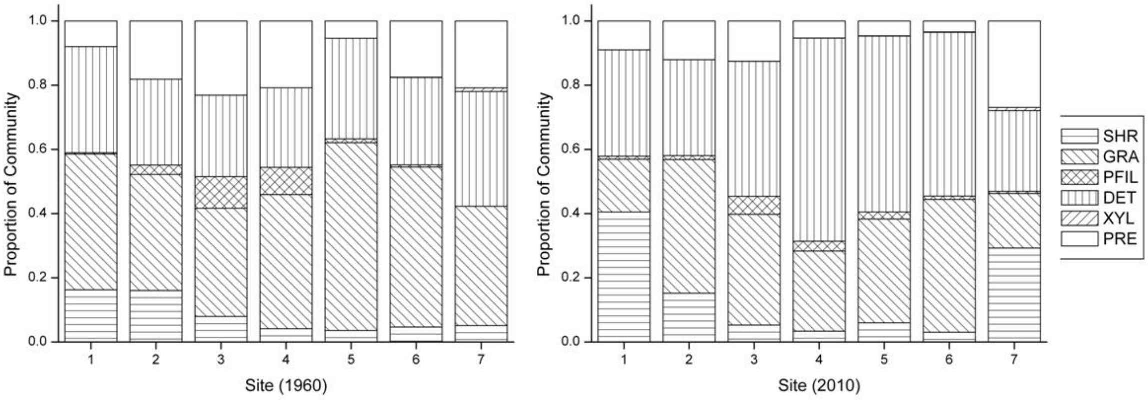


Figure 7.2: Functional feeding composition of the River Endrick community in 1960 and 2010 (SHR – shredder, GRA – grazer, PFIL – passive filter feeder, DET – detritus feeders, XYL – xylophagous, PRE – predator).

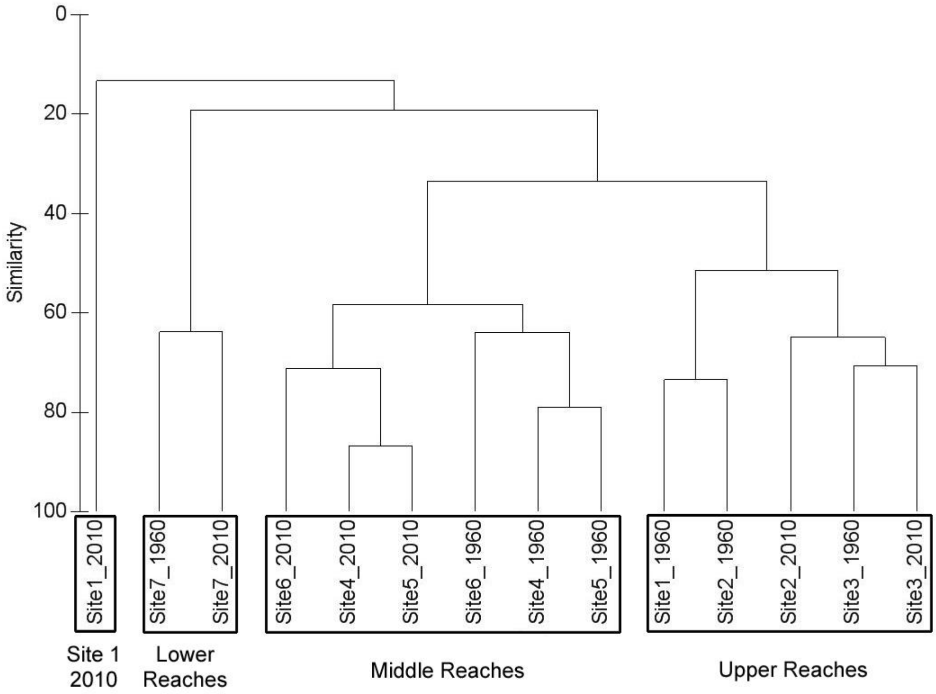


Figure 7.3: Complete linkage dendrogram of species abundance at each of the 7 sites in both study periods. Clustering has been made manually into 4 distinct groups (lower, middle, upper reaches, and site 1 in 2010).

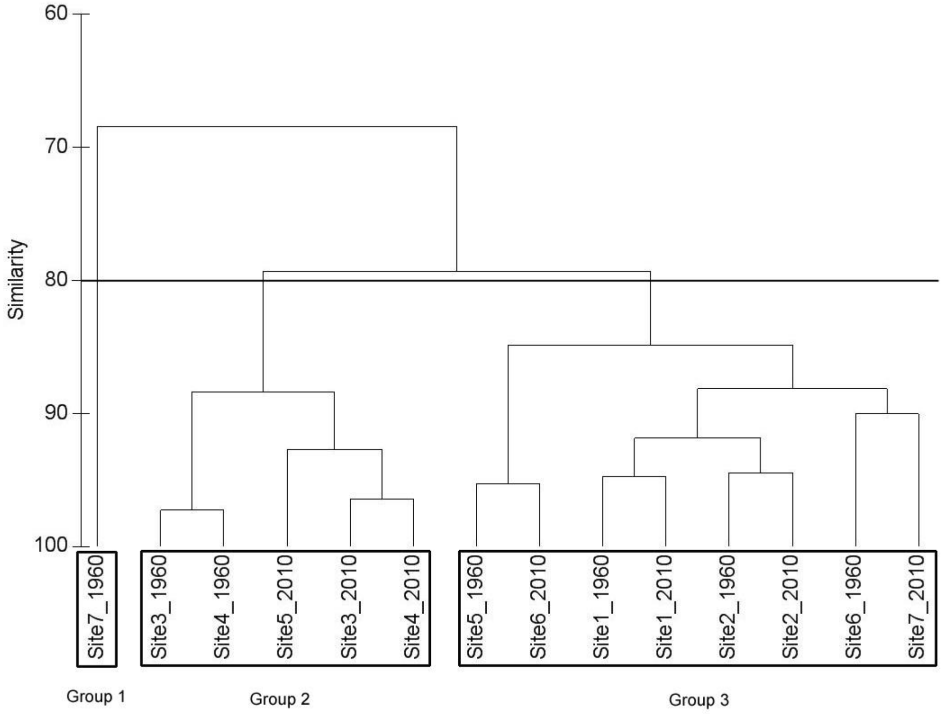


Figure 7.4: Complete linkage dendrogram of functional feeding abundance at each of the 7 sites in both study periods. Clustering has been made at 80% similarity into 3 distinct cluster groups.

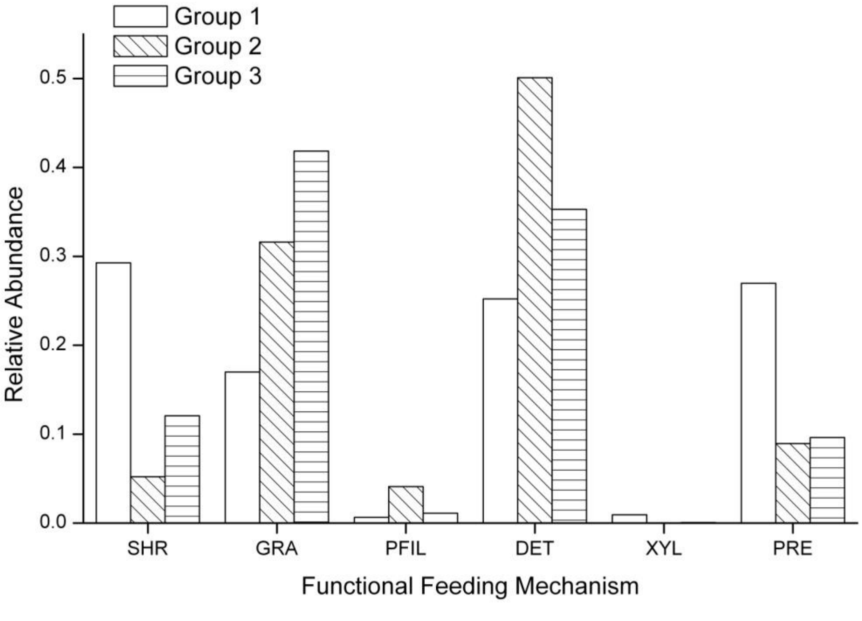


Figure 7.5: Relative abundance of the different feeding mechanisms in the 3 groups highlighted from the functional abundance dendrogram. (SHR – shredder, GRA – grazer, PFIL – passive filter feeder, DET – detritus feeders, XYL – xylophagous, PRE – predator).

7.3.2.2 Saprobic abundance

Between 1960 and 2010, for the whole river system, the saprobic abundance of the River Endrick was 94% similar (Figure 7.6). The similarity in site saprobic abundance between study periods ranged from 83% to 98% (Table 7.3). The dendrogram of saprobic abundance revealed four distinct groups (Figure 7.7). A histogram of relative saprobic abundance in each of the four groups revealed the relative importance of the different saprobic tolerance in each of the cluster groups (Figure 7.8). Cluster group 1 contained 3 communities from sites 4, 5 and 6 collected in 2010, and was associated with a high relative abundance of beta-mesosaprobic individuals (i.e. species with a high tolerance of water degraded by human activities). Cluster group 2 contained 3 communities collected from site 7 in 1960 and 2010 and site 6 in 1960, and was associated with a high relative abundance of alpha-mesosaprobic and polysaprobic individuals (i.e. species with an ability to tolerate heavily/extremely polluted water conditions). Cluster group 3 contained 2 communities both collected at site 2 in 1960 and 2010, and was associated with a high relative abundance of individuals with oligosaprobic tolerance (i.e. species with little or no tolerance of human influenced water conditions). Cluster group 4 contained 6 communities collected from site 1 and 3 in 1960 and 2010 and site 4 and 5 in 1960, and was associated with a high relative abundance of individuals with xenosaprobic tolerance (i.e. species showing a propensity for water conditions that have not been influenced by human activities).

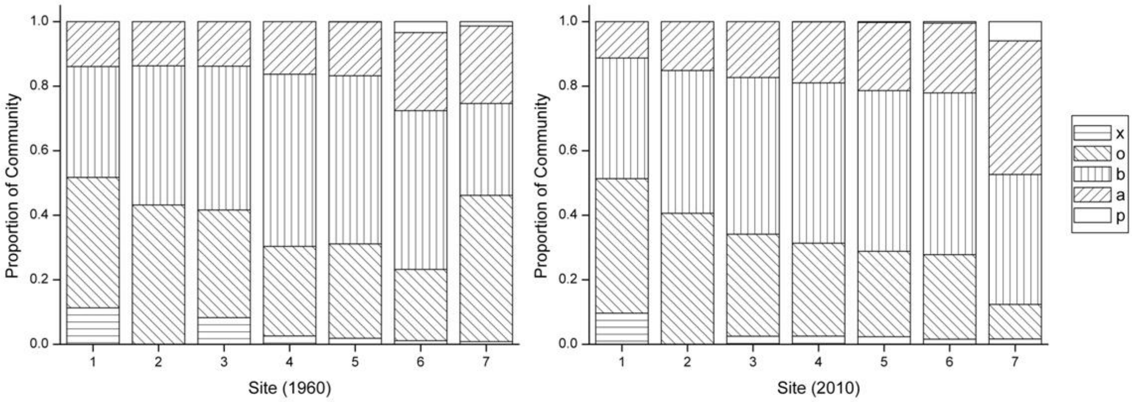


Figure 7.6: Saprobic composition of the River Endrick community in 1960 and 2010 (x – xenosaprobic; o – oligosaprobic; b – beta-mesosaprobic; a – alpha-mesosaprobic; p – polysaprobic).

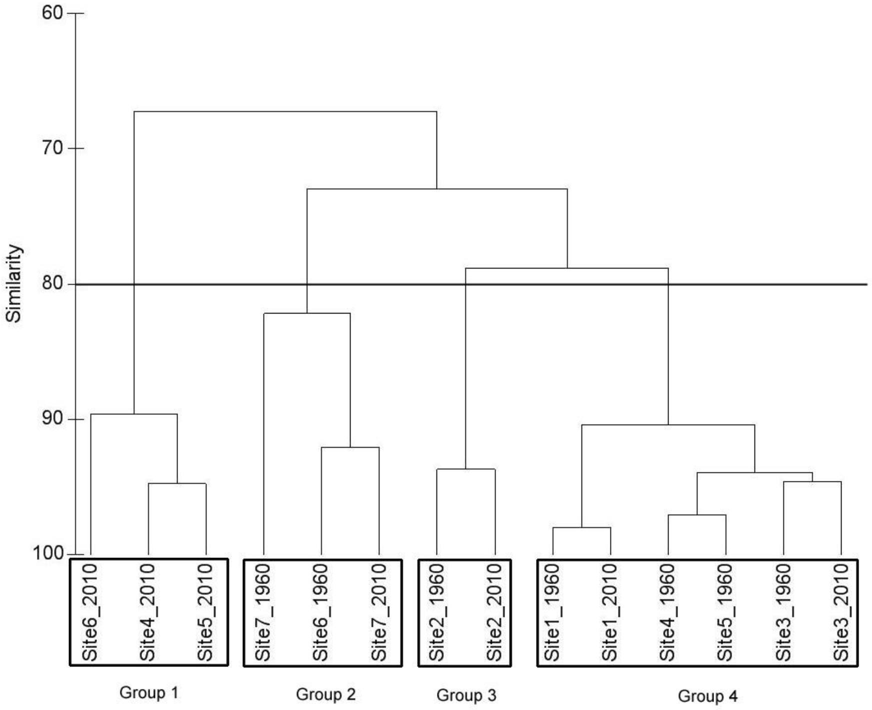


Figure 7.7: Complete linkage dendrogram of saprobic abundance at each of the 7 sites in both study periods. Clustering has been made at 80% similarity into 4 distinct cluster groups.

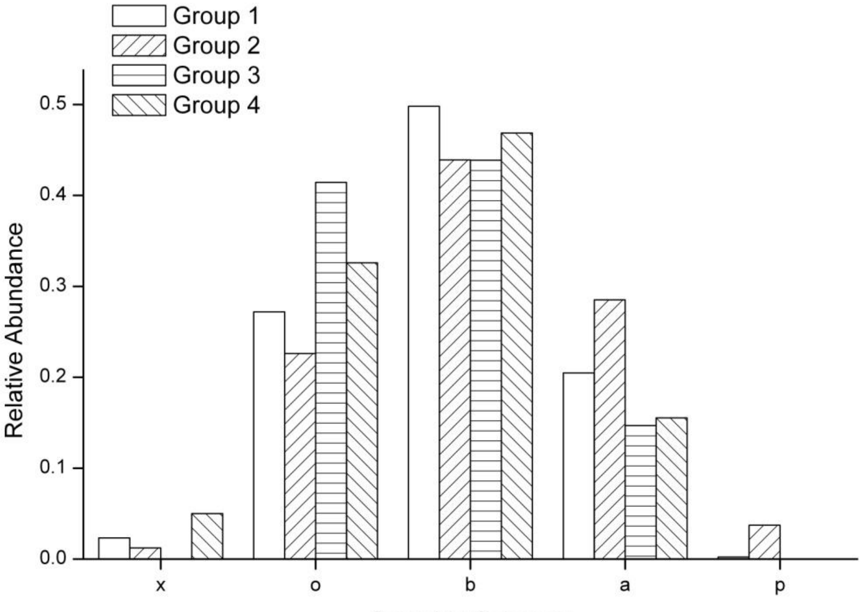


Figure 7.8: Relative abundance of the different saprobic tolerance in the 4 groups highlighted from the saprobic abundance dendrogram. (x – xenosaprobic; o – oligosaprobic; b – beta-mesosaprobic; a – alpha-mesosaprobic; p – polysaprobic).

7.3.2.3 Flow and temperature preference

Between 1960 and 2010, for the whole river system, the flow preference of the River Endrick was 94% similar (Figure 7.9). The similarity in site flow and temperature preference between study periods ranged from 84% to 93% (Table 7.3). The dendrogram of flow and temperature preference revealed three distinct cluster groups (Figure 7.10). A histogram of the relative abundance in each of the three cluster groups revealed the relative importance of the different flow and temperature preference in each of the three cluster groups (Figure 7.11). Cluster group 1 was associated with a high relative abundance of individuals with a preference for slow flow conditions and higher maximum temperature (i.e. littoral, epipotamal and metapotamal). Cluster group 1 contained only communities collected from site 7 which is the site in the lower reaches of the river. Cluster group 2 was associated with a high relative abundance of individuals with a preference for high flow conditions (i.e. eucrenal, hypocrenal, and epirhithral). Cluster group 2 contained only the 2010 site 1 community. Cluster group 3 was associated with a high relative abundance of individuals with a preference for moderate flow and temperature conditions (i.e. metarhithral and hyporhithral). Cluster group 3 contained 11 communities collected from sites 2 to 6 in both study periods and the community collected at site 1 in 1960.

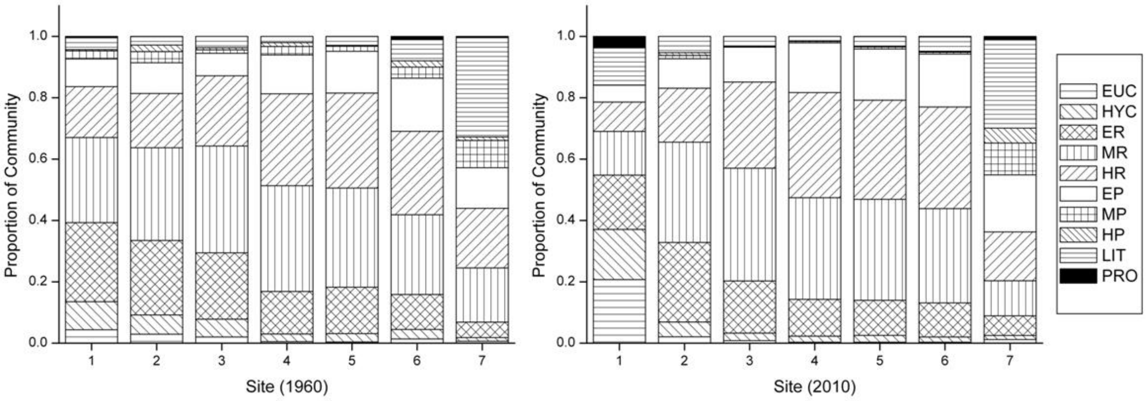


Figure 7.9: Flow and temperature composition of the River Endrick community in 1960 and 2010 (EUC – eucrenal; HYC – hypocrenal; ER – epirhithral; MR – metarhithral; HR – hyporhithral; EP – epipotamal; MP – metapotamal; HP – hypopotamal; LIT – littoral zone; PRO – profundal zone).

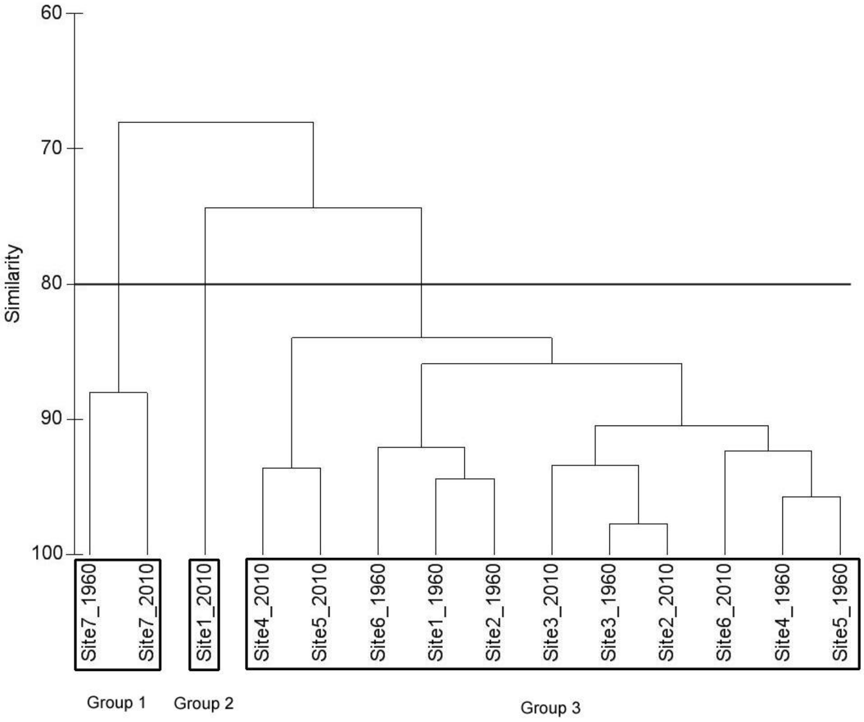


Figure 7.10: Complete linkage dendrogram of flow and temperature preference at each of the 7 sites in both study periods. Clustering has been made at 80% similarity into 3 distinct cluster groups.

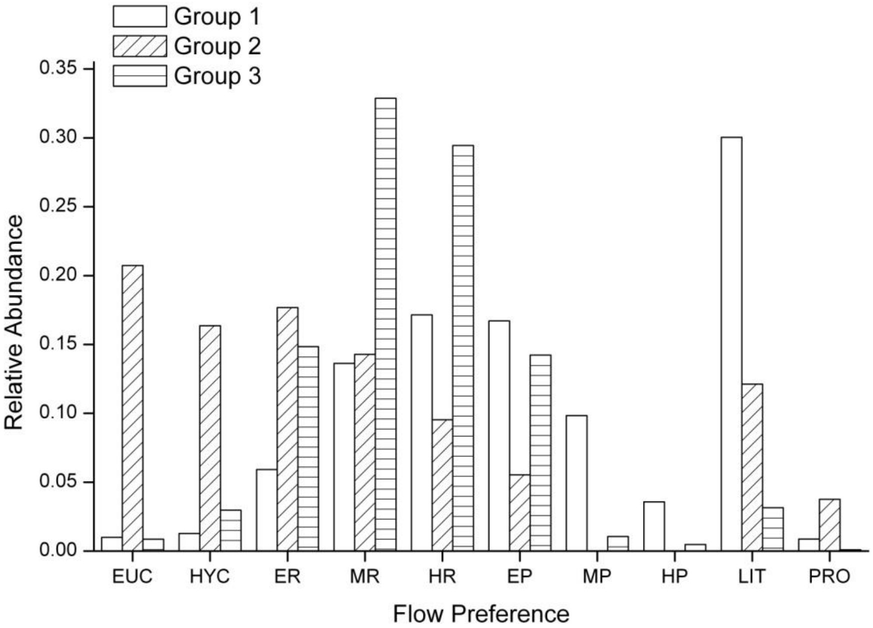


Figure 7.11: Relative abundance of the different flow preferences in the 3 groups highlighted from the flow preference dendrogram. (EUC – eucrenal; HYC – hypocrenal; ER – epirhithral; MR – metarhithral; HR – hyporhithral; EP – epipotamal; MP – metapotamal; HP – hypopotamal; LIT – littoral zone; PRO – profundal zone).

7.4 Discussion

The biodiversity of the macroinvertebrate community in the River Endrick has reduced significantly since 1960. The macroinvertebrate community within the river has shown differential change in structure and function between the two study periods. Some communities have remained consistent in terms of structure and function while others have shown distinct differences between study periods.

Generally, community structure fits well with the longitudinal gradient of changing physical and chemical factors associated with river systems (Vannote et al., 1980). Communities in both study periods clustered well into upper, middle and lower reaches, but within study period clustering was evident. This is clearly evident in the middle reaches of the river where the communities at sites 4, 5 and 6 clustered into study periods (Figure 7.3).

7.4.1 Headwaters

Notwithstanding the general consistency in community structure patterns within the catchment over 50 years, the structure of the headwater community was distinctly different in 2010 from all other communities collected from the River Endrick. Further investigation of community function changes has highlighted some broad mechanisms which may be driving this change. In terms of both functional feeding and water chemistry tolerance the headwater community in the River Endrick has remained highly similar between study periods, indicating that available food resources and the chemical characteristics of the water in the headwaters has remained similar over the 50 year period. The separation of the 2010 headwater community in terms of flow preferences however, indicated a broad driver of change associated with flow rates and temperature tolerances, resulting in the separation of this community.

Changes to the flow and temperature preference of the headwater community in 2010 has resulted in a community dominated to a greater degree by species showing a preference for high altitude flow conditions and low ($< 9^{o}C$) maximum temperatures (Moog, 2002). In addition to these changes, there was also some indication of a high abundance of species associated with littoral and profundal ‘flow’ preferences (i.e. very slow flow and $> 20^{o}C$ temperatures), only the communities located in the lower reaches of the river had a higher relative abundance of these species types. The contrasting nature of flow preferences of the species comprising the headwater community of the River Endrick in 2010 highlights the complex nature of changing conditions and the resultant effects on community structure.

7.4.2 Upper reaches

Communities in the upper reaches of the catchment (i.e. communities at sites 1, 2 and 3, not including the community at site 1 in 2010) were grouped together in terms of species composition. Within the upper reaches cluster, the communities at site 1 and site 2 in 1960 were more similar than communities at site 2 in 2010 and site 3 in both study periods. This indicates shift in the community site 2 in 2010 to a composition more similar to that at site 3, further downstream.

Functional feeding composition of communities at site 1 and 2 showed relatively high abundances of species using a grazing feeding mechanism. The community at site 3 was, to a greater degree, dominated by species showing detrivorous feeding mechanisms. This pattern of feeding function was consistent in both study periods. Community water chemistry preference in the upper reaches of the river was consistent at a site level in both study periods, although distinctions were apparent between different sites. Water chemistry preference of the communities at sites 1 and 3 were influenced by a relatively high abundance of species showing a complete intolerance of water conditions affected by human activities (i.e. xenosaprobic). At site 2, relatively high abundance of species with a general intolerance of water conditions affected by human activities (i.e. oligosaprobic), separated site 2 communities from the others in the River Endrick. Generally, community function in the upper reaches of the river was dominated by species with a requirement for very clean water. In terms of flow preference, community function in the upper reaches of the river remained similar at sites 1 (in 1960), 2 and 3 in both study periods, although complex mechanisms appear to be separating sites and study periods within this large general group.

7.4.3 Middle reaches

Communities in the middles reaches of the River Endrick (i.e. communities at sites, 4, 5 and 6) were grouped together in terms of species composition, but there was a distinct separation of these sites between study periods. Functional feeding composition of the communities in the middle reaches of the river has remained broadly consistent. Functional feeding composition of the community at site 4 has maintained a relatively high abundance of species using detrivorous and passive filter feeding mechanisms in both study periods. The community at site 6 has maintained a relatively high abundance of species using grazing feeding mechanisms. The community at site 5 has changed between study periods. Functional feeding composition of this community in 1960 was more similar to that of the community at site 6, and by 2010 functional feeding composition of the community at site 5 was more similar to site 4.

Community function, in terms of water chemistry tolerance, in 1960, was similar at sites 4 and 5 which had relatively high abundances of species with no tolerance of water conditions influenced by human activities. The community at site 6 in 1960 has a relatively high abundance of species associated with mildly (i.e. alpha-mesosaprobic) to grossly (i.e. polysapribic) human impacted water conditions. In 2010, community function was similar for sites 4, 5 and 6 in 2010, with a high abundance of mildly pollution tolerant species in these communities. The move in community function at site 6 from one with a high tolerance of human influenced water chemistry to a community with a lower tolerance of human influenced water conditions has likely arisen as a result of improvements to the water quality of a tributary inflowing just upstream of site 6 (Doughty & Maitland, 1994). As the water quality in the River Endrick has remained at a generally high standard throughout the study period (Doughty & Maitland, 1994), it is surprising that the sites 4 and 5 are clustered differently than their 1960 analogues. The samples collected from these sites (i.e. sites 4 and 5) in 1960 clustered with sites 1 and 3 from both study periods. The communities at sites 4, 5 and 6 in 2010 were also less similar to other communities in the study in terms of water chemistry tolerance. Against the background of consistently clean water, this suggests more subtle mechanisms controlling community structure that cannot be predicted by the simple measure of biological water quality detailed in Doughty & Maitland (1994).

Structuring of the community in terms of species preference for flow conditions in the middle reaches was broadly similar at sites 4, 5 and 6 in both study periods, although high similarity existed between sites 4 and 5 in 2010 and sites 4 and 5 in 1960 . Community structure determined by flow characteristics in the middle reaches was dominated by a high relative abundance of species with a preference for moderate flow types (i.e. metarhithral and hyporhithral) associated with a temperature range from 5 ^{o}C to 14 ^{o}C and not more than 18 ^{o}C (Moog 2002) which fits well with these communities position within the River Enrdick.

7.4.4 Lower reaches

The macroinvertebrate community in the lower reaches of the river (i.e. communities collected at site 7) was highly similar in terms of species composition in both study periods. Functional feeding composition of the community in the lower reaches was distinctly different in the two study periods. Specifically, the functional feeding composition of the community in the lower reaches of the river in 1960 was distinctly different from all other communities in the river system due to a relatively higher abundance of predatory species and species using a shredding feeding mechanism. In contrast, the community at site 7 in 2010 had a relatively high abundance of species using grazing feeding mechanisms. Reasons for the changes to the feeding function of the community between the two study periods are not clear. A comparison of photographs taken of the lower reaches of the river does not reveal any obvious change in the vegetation cover present; in fact this section of the river appears to have remained remarkably similar. The high relative abundance of predatory invertebrates in 1960 is indicative of a low abundance of fish predators. Since the 1960 study, Loch Lomond has seen an large increase in non-native fish species (Adams, 1994) some of which are present in the lower reaches of the river (pers. obs.). The changing fish fauna of the lower reaches of the river may be influencing the change in feeding function of the macroinvertebrate community in the lower reaches of the river. The invasion of the non-native, *Crangonyx pseudogracilis*, may also be influencing community structure in the lower reaches of the river.

Structuring of community function in terms of water chemistry and flow conditions was similar in both study periods, with the community in the lower reaches of the river dominated by a relatively high abundance of species with an ability to tolerate highly influenced water conditions, highly reduced flows and high maximum temperatures. As the water quality in the River Endrick is high (Doughty & Maitland, 1994), the high saprobic tolerance of the lower reaches community is not indicative of poor water quality, but a reflection of species within the community being able to tolerate the lower oxygen conditions associated with reduced flow in the lower parts of the river.

7.5 Conclusions

The macroinvertebrate community of the River Endrick has shown a significant decline in biodiversity in the last 50 years. Changes, in terms of structure and function of the macroinvertebrate community, have shown some general trends (i.e. the longitudinal distribution of communities with distance downstream) but also some counterintuitive change (i.e. the increase in both cold and warm water adapted species in the headwaters of the river). The distinct difference in community structure in the headwaters of the catchment in 2010 is not surprising, but the mechanisms underlying the change are. River headwaters are likely to be subjected to the greatest change as a result of global climate change. Warming is predicted to be especially pronounced in high altitude systems (IPCC, 2007), and it is expected that these effects will have a marked effect on the biota (Wrona. et al., 2006; Heino et al., 2009). The small nature of headwaters (i.e. shallow, narrow and often exposed with no large vegetation cover) means the effects of increasing temperatures and changes to hydrology are likely to affect the communities in these areas to the greatest extent, mostly with an associated loss of cold water adapted species at high altitudes (Durance & Ormerod, 2007). The results here do not completely reflect this general trend as there has been an increase in both the relative abundance of species with a requirement of cold fast flows and an increase in the relative abundance of species with a requirement for warmer slow flows. The contrasting nature of community change in the headwaters o the River Endrick clearly requires further investigation. Changes in the community structure in the middle reaches of the river in terms of saprobic tolerance cannot be simply explained in terms of change to the level of human influence on the water conditions within the River Endrick and also requires further investigation.

CHAPTER 8 General Discussion

In this thesis six studies have investigated long-term change in aquatic macroinvertebrate communities in two river systems with contrasting legacies from human activity. As freshwater ecosystems are losing biodiversity faster than terrestrial and marine systems (Dudgeon et al., 2006) and rivers particularly have been highlighted recently as under the greatest threat from pervasive human activity (Vörösmarty et al., 2010), finding mechanisms that drive change and how change is manifest in river systems is imperative.

The short-term response of the macroinvertebrate community to changes in water physio-chemistry are well known (Hynes, 1966), and have formed the basis of biological monitoring of waterways worldwide. The long-term response of the macroinvertebrate community to changing water physio-chemistry is less well understood (Jackson & Füreder, 2006). In chapter 2, long-term change in the spatial and temporal distribution of common macroinvertebrate Families revealed complex colonisation patterns which were not explained by simple measures of life-history (flight capability) or pollution tolerance. Although the majority of macroinvertebrate Families in the River Clyde have increased their occurrence over the 32 year study period, against the background of improving water physio-chemistry, two Families have shown a significant decline and another has shown counter intuitive spatial change. Chapter 3 investigated relative influence of the local environment in structuring the richness of the macroinvertebrate community. Variation in water physio-chemistry was identified as the strongest driver of change in macroinvertebrate community richness, but the intimate link between land use and water physio-chemistry was also important.

Results from chapter 2 and chapter 3 highlighted the important role water physio-chemistry has in structuring macroinvertebrate communities, but also that recolonisation and establishment within a community following changes to water physio-chemistry is not a purely physiological (i.e. pollution tolerance) response. These chapters indicate that interactions between community members within a reforming community are also important structuring forces.

Finding assembly rules in community ecology is key to providing insight into the mechanisms underpinning changes in ecosystems arising as a result of a response to environmental fluctuation, restoration and non-native species introduction. The degree to which existing community structure influences community formation was investigated in chapter 4.

The differential response of macroinvertebrate Families in communities reforming following improvements to previously impacted river systems (chapter 2 and chapter 3) presents a challenge for the accurate assessment of biotic condition. One commonly employed method of biotic assessment in river systems is the reference condition approach, where impacted communities are compared with analogous pristine communities. In chapter 4 the suitability of this reference condition method was tested with a commonly used software programme, RIVPACS (River InVertebrate Prediction and Classification System; Wright et al., 1984). RIVPACS is used to predict the structure of communities in the absence of human influence, using a small suite of measured environmental variables. Comparisons of predicted ‘pristine’ community composition with the composition of communities reforming in the River Clyde revealed significant differences between idealised community composition and extant community composition. These significant differences were attributed to the influence of founding community composition on the composition of the contemporary community (Ledger et al., 2006).

Some of the possible mechanisms driving differences in the community structure following colonisation and establishment of individuals in a reforming community were investigated in chapter 5. Resource use by a colonising predator was shown to be influenced significantly by competition and colonisation patterns. Colonisation and establishment within an already diverse community significantly reduced the trophic position occupied by the coloniser, which was linked to increased competition with already established predatory species. The effect of these differences in resourse use as a result of colonisation patterns may have serious consequences for future functionality of the community as resource use has been shown to influence future generations. The results from this chapter are important, not only in the context of community reformation but also in furthering our understanding of the mechanisms involved in community assembly.

Insights gained from the analysis of the long-term data collected from the River Clyde has provided an interesting insight into some of the mechanisms involved in community reformation following disturbance. Communities also alter as a result of ‘natural’ changes to their environment.

In spite of the geographic proximity, the River Endrick has not been influenced, to the same degree as the River Clyde, by human activities. Despite this lack of obviously direct influence, results from chapter 6 and chapter 7 have highlighted significant changes in the macroinvertebrate community of this river over a 50 year period.

In chapter 6, changes in the distribution and abundance of 78 species were investigated. The local extinction of three species and the possible extinction of three additional species represent a major loss for this river system. One of these, the loss of *Crenobia alpina*, is not a phenomenon unique to the River Endrick as the loss of this species has been noted from another British west coast river system (Durance & Ormerod, 2010). Distribution changes of some species may have arisen through alterations to the availability of food resources, and prevailing flow and/or temperature conditions. There is also some evidence of life history changes in some species, but this requires further investigation.

The primary causes of species distribution and abundance changes in the River Endrick are unclear. No specific mechanism could account for the mosaic of shifting species distribution and abundance patterns, and it is therefore likely that multiple abiotic and biotic mechanisms are contributing to the changing community structure within the River Endrick.

Possible changes to the diversity and functionality of communities in the River Endrick arising as a result of the changes in species distribution and abundance were investigated in chapter 7. The significant loss in community diversity at all study sites since 1960 fits with global trends but presents a bleak view of the macroinvertebrate community in this river system. While community function fitted generally well with the longitudinal environmental gradient associated with river systems (Vannote et al., 1980) there have been changes in community function over the 50 year study period. Significant changes in community structure and function at the headwaters of the catchment complimented and contrasted findings from other river systems (Durance & Ormerod, 2007. Superficially the change in the headwaters was not related to a change in the available food resources or to changes in the water saprobity. The change in the headwater community was linked to the increased relative abundance of both cold water adapted and warm water adapted species. This apparently contradictory finding requires further investigation.

The results of this study present some interesting perspectives on contingent long-term change in river communities. The River Clyde macroinvertebrate community has increased in richness over the 32 year study period, which contrasts the long-term trends from the River Endrick. Differences in the taxonomic resolution of the two river studies likely account for some of this contradiction, but the overwhelming response of the macroinvertebrate community to improvements in water physio-chemistry in the River Clyde would almost certainly mask any subtle change in species distribution, like those illustrated from the River Endrick.

8.1 Future work

The results from this thesis have highlighted the differential response of macroinvertebrate communities to long-term change in river systems.

The River Endrick and the Loch Lomond area are of national and international importance for biodiversity. Within the Loch Lomond catchment there 3 protected sites (2 of international importance) which are directly associated with the River Endrick. The significant loss in biodiversity in the River Endrick may have serious consequences for both the river and the lake, after all invertebrates are the primary food resource for the majority of fish species some of which have a commercial value to the area (i.e. Atlantic salmon, *Salmo salar*, and brown/sea trout, *S. trutta*). Thus, the mechanistic functions driving biodiversity loss and species distribution change on the River Endrick need to be investigated and identified. Initial findings of the work presented here should provide a springboard for small scale studies targeting specific species. For example, investigation of the possible life history changes in S*eratella ignita*, and *Anphinemura sulcicollis;* the effects of competitive interaction between the invasive *Crangonyx pseudogracilis* and its native analogue *Gammarus pulex*; the effects of the counter intuitive range expansion of *Asellus aquaticus* and *Erpobdella octoculata*. Results from these small scale studies should provide an insight into the relative magnitude of influence these changes may have in the future, in addition to providing information on possible remediation routes.

River biomonitoring must evolve with the changing nature of river communities. Intrinsic changes to assembly mechanisms of community reformation following remediation efforts must be accounted for in an accurate assessment of biological condition. The innovative methods developed by the Institute of Freshwater Ecology through the use of reference sites for river bioassessment (i.e. RIVPACS software) need updating. The majority (1,842) of the total (2,175) samples which comprise the reference site data set for Great Britian were collected pre mid 1990's (Figure 8.1) and 'natural' changes to these reference sites must be considered to provide an accurate assessment of contemporary river condition, if this methodology is not to become outdated.

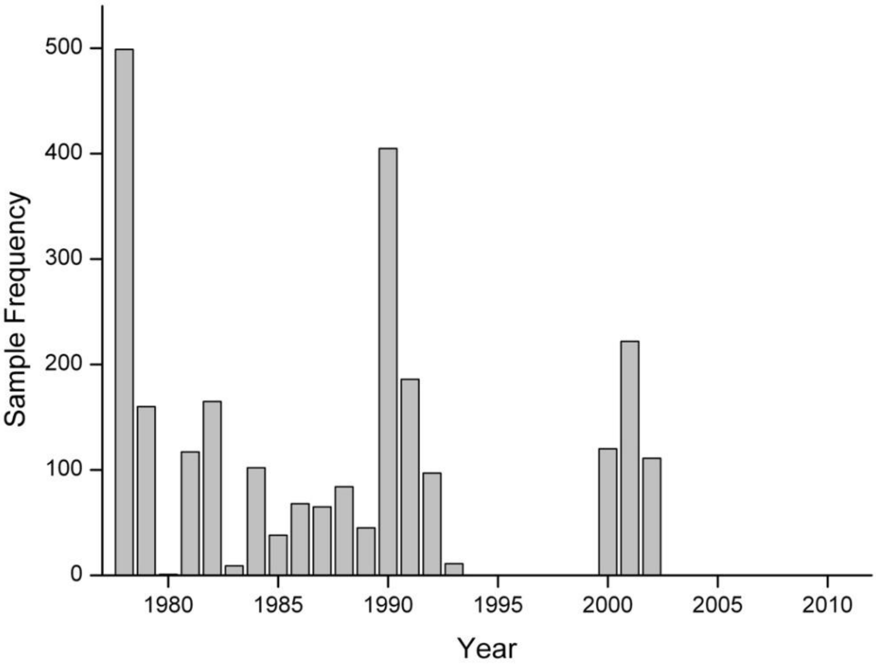


Figure 8.1: Annual frequency of samples collected for RIVPACS reference database for Great Britain (CEH, 2010).

APPENDIX A Overview of the land use and solid geology of the two river systems (River Clyde and River Endrick) and the location of the sampling sites used in this study.

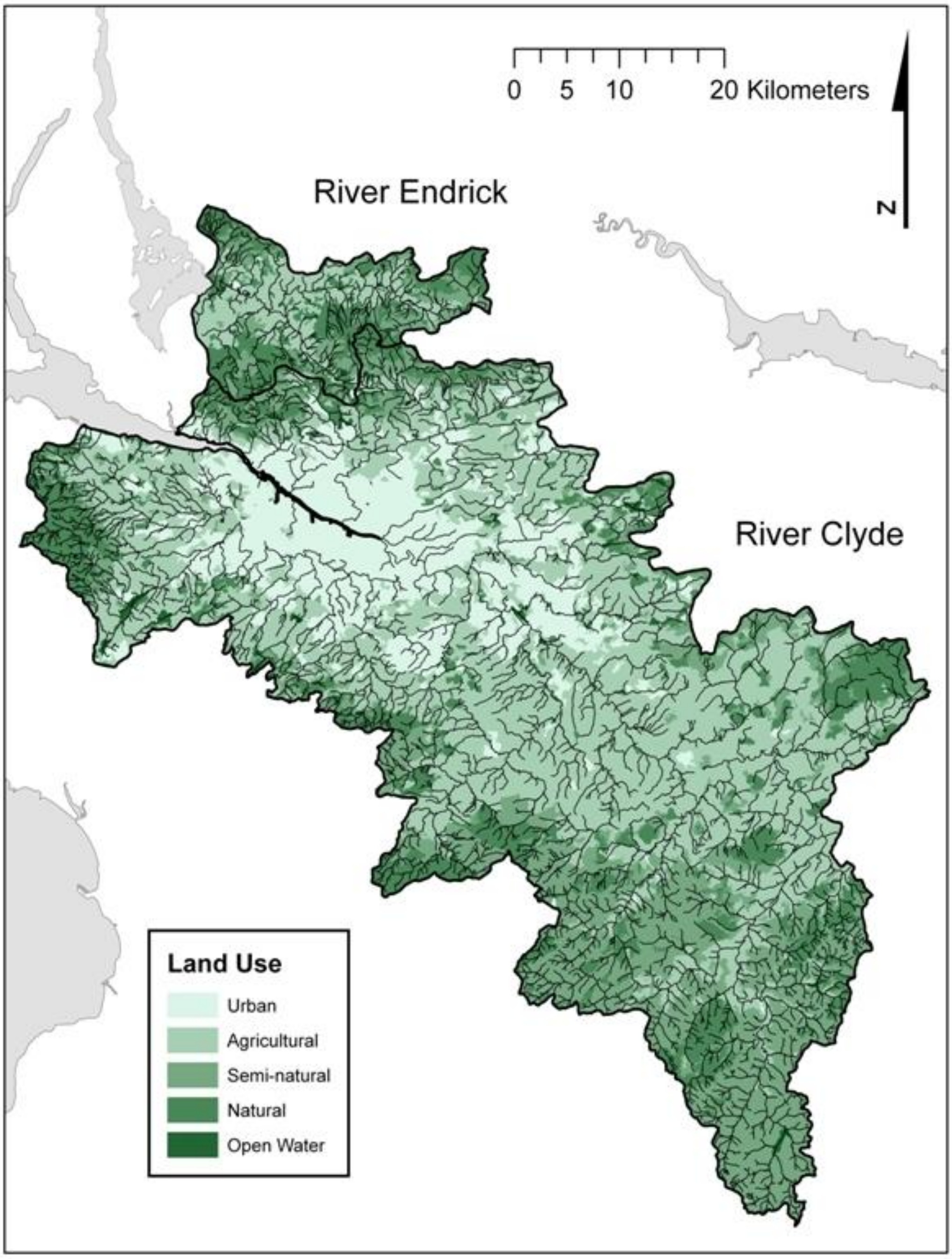


Figure A.1: General land use within the River Clyde and the River Endrick. Land use types have been derived from the CORINE landcover dataset (EEA, 1990).

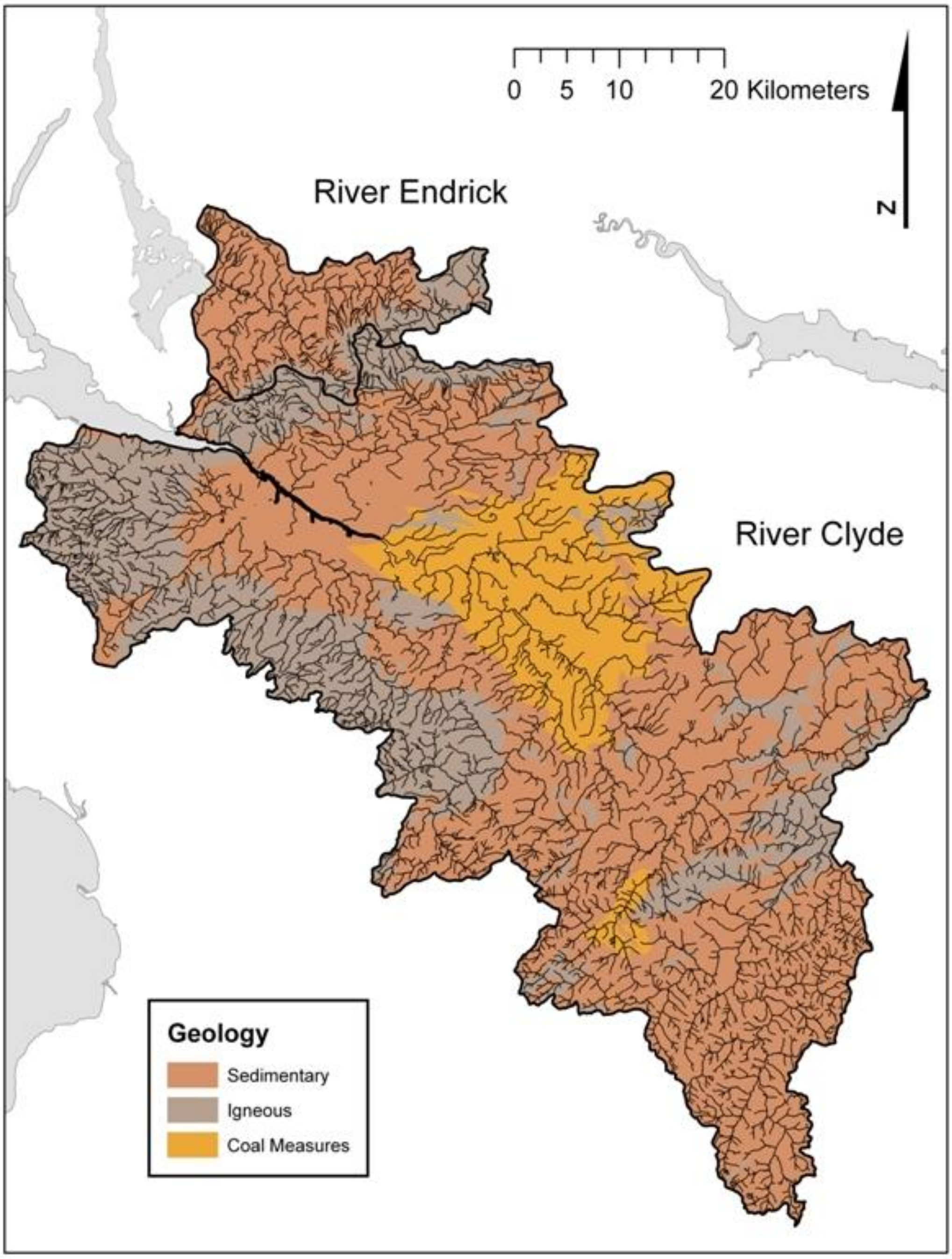


Figure A.2: General solid geology within the River Clyde and the River Endrick. Solid geology has been derived from the British Geological Survey dataset DiGMapGB-625. Reproduced with the permission of the British Geological Survey ©NERC. All rights Reserved.

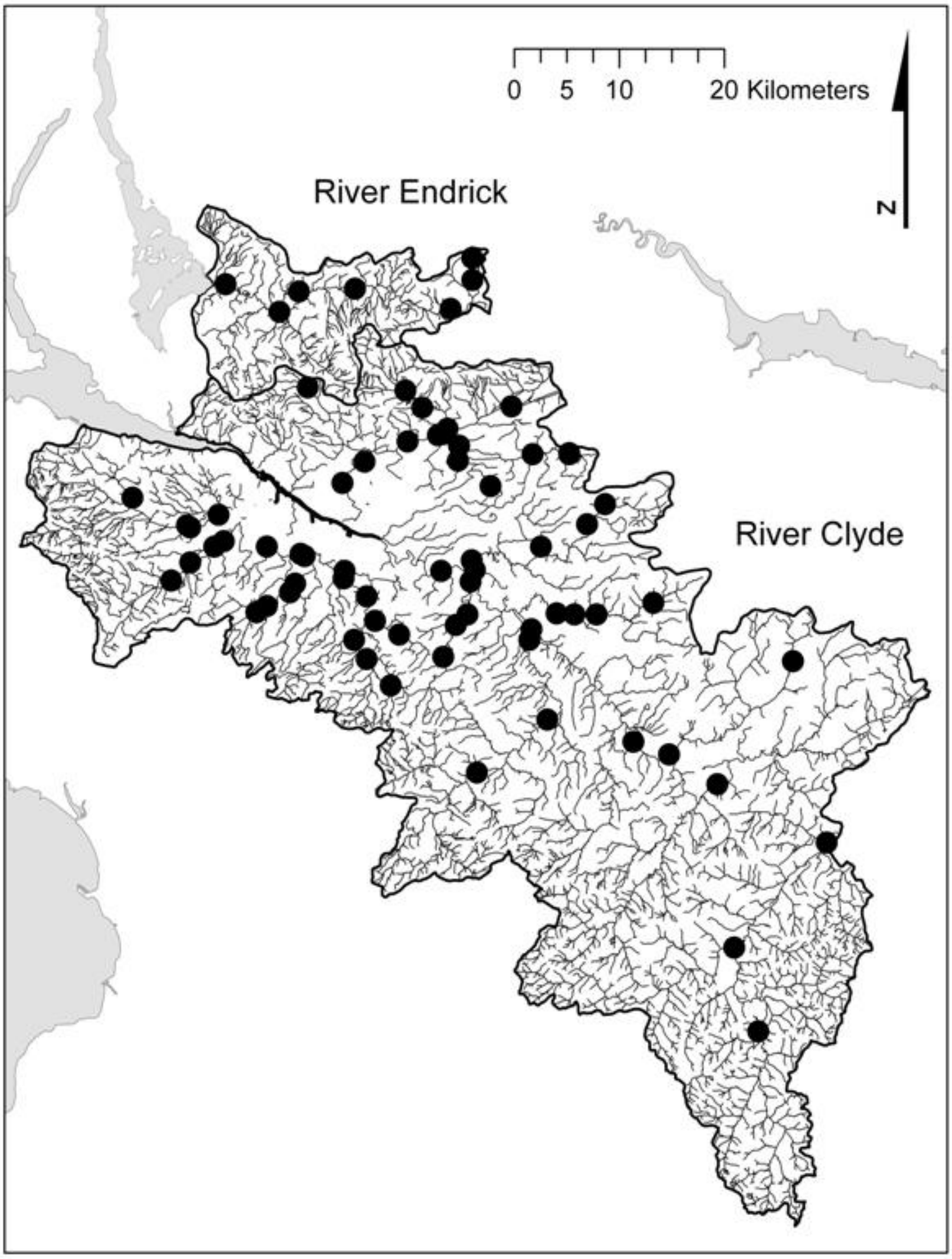


Figure A.3: Location of the sampling sites used in this study.

APPENDIX B Species of Tricladida, Hirudinea, Megaloptera, Ephemeroptera, Plecoptera, Hemiptera, Neuroptera, Trichoptera, Lepidoptera and Coleoptera recorded in the 1960 and 2010 study periods

Table B.1: List of species recorded in the 1960 and 2010 study periods. Numbers indicate the number of sites from which the spices was recorded; + indicates the detection at one of the original 5 sites not included in the 2010 study

	1960	**2010**
TRICLADIDA		
Crenobia alpina	2	0
Dendroceolum lacteum	2	1
Dugesia lugubris	2	1
Polycelis felina	1	3
Polycelis nigra	2	2
Polycelis tenuis	2	1
HIRUDINEA		
Batracobdella paludosa	1	1
Dina lineata	1	0
Erpobdella octoculata	2	4
Erpobdella testacea	0	1
Glossiphonia complata	3	3
Glossiphonia heteroclita	2	1
Helobdella stagnalis	4	6
Hemiclepsis marginata	1	0
Theromyzon tessulatum	1	0
MEGALOPTERA		
Asellus aquaticus	2	4
Crangonxy pseudogracilis	0	2
Gammarus pulex	5	6
EPHEMEROPTERA		
Ameletus inopinatus	1	1
Baetis muticus	5	3
Baetis niger	0	1
Baetis rhodani	6	5
Baetis scambus	0	4
Caenis rivulorum	5	6
Centroptilium luteolum	3	1
Ecdyonurus torrentis/insignis	6	6
Ecdyonurus venosus	5	5
Electrogena lateralis	2	4

Table B.1: continued

	1960	**2010**
EPHEMEROPTERA contd.		
Habrophlebia fusca	3	4
Leptophlebia marginata	4	4
Leptophlebia vespertina	0	3
Paraleptophlebia cincta	1	2
Paraleptophlebia submarginata	3	6
Procloeon pennulatum	2	3
Rhithrogena semicolorata	5	5
Serratella ignita	7	6
Siphlonurus lacustris	1	4
PLECOPTERA		
Amphinemoura standfussi	1	0
Amphinemoura sulcicollis	7	5
Brachyptera risi	4	3
Capnia bifrons	4	4
Chloroperla tripunctata	2	0
Dinocras cephalotes	3	2
Diurna bicaudata	0	1
Euleuctra geniculata	2	3
Isoperla grammatica	6	5
Leuctra hippopus	7	7
Leuctra inermis	6	7
Leuctra fusca	6	2
Leuctra moselyi	2	4
Leuctra nigra	1	2
Nemoura avicularis	4	5
Nemoura cambrica	1	6
Nemoura cinerea	0	1
Nemurella pictetii	0	2
Perla bipunctata	2	2
Perlodes microcephala	2	4
Protonemura meyeri	3	6
Siphonoperla torrentium	6	5
Taeniopteryx nebulosa	3	0
HEMIPTERA		
Gerris costai	1	1
Gerris lacustris	1	1
Hesperocorxia sahlbergi	+	0
Nepa cinerea	1	0
Notonecta glauca	1	2
Paracorixia concinna	0	1
Sigara distincta	1	0
Sigara dorsalis	1	2

Table B.1: continued

	1960	**2010**
HEMIPTERA contd.		
Sigara falleni	1	1
Sigara fossarum	+	1
Velia caprai	6	0
NEUROPTERA		
Sialis lutaria	1	1
Sialis fuliginosa	1	4
TRICHOPTERA		
Adicella reducta	0	1
Agapetus fuscipes	3	1
Agraylea multipunctata	1	0
Anabolia nervosa	1	0
Athripsodes aterrimus	0	2
Athripsodes cinereus	0	1
Beracodes minutus		1
Berae pullata	0	1
Brachycentrus subnubilus	0	1
Chaetopteryx villosa	0	1
Cyrnus trimaculatus	1	2
Drusus annulatus	+	2
Glossosoma boltoni	1	3
Halesus digitatus	0	3
Halesus radiatus	0	4
Hydropsyche pelluidula	4	4
Hydropsyche siltalai	5	5
Hydroptilia sp.	+	6
Ithytrichia sp.	0	1
Lepidostoma hirtum		
Limniphilis lunatus	0	1
Linmiphilus fuscicornis	0	1
Lype phaeopa	1	1
Lype phaeopa	0	1
Mystacides azuna	0	1
Mystacides longicornis	0	1
Odontocerum albicore	0	3
Philopotamus montanus	+	2
Plectrocnemia conspersa	2	4
Polycentropus flavomaculatus	6	6
Polycentropus irroratus	1	1
Polycentropus irroratus	0	1
Potamophylax cingulatus	0	4
Potamophylax latipennis	0	3
Psychomyia pusilla	5	4

Table B.1: continued

	1960	**2010**
TRICHOPTERA contd.		
Rhyacophila dorsalis	6	5
Rhyacophila munda	2	2
Sericostoma personatum	1	5
Silo pallipes	0	1
Tinodes waeneri	2	1
Wormaidia occipitalis	0	1
LEPIDOPTERA		
Nymphula nymphaeata	1	1
COLEOPTERA		
Agabus bipustulatus	+	0
Agabus guttatus	+	2
Anacaena globulus	0	1
Brychis elevatus	1	0
Coelostoma orbiculare	0	1
Deronectes elegans	3	0
Donacia versicolorea	+	0
Dytiscus marginata	0	1
Elmis aenea	7	7
Esolus parallelpipedus	6	4
Gyrinus aeratus	0	1
Gyrinus substriatus	1	0
Haliplus confinis	0	
Haliplus lineatocollis	+	0
Haliplus wehnckei	1	4
Helodes marginata	3	0
Helophorus aquaticus	1	0
Helophorus brevipalipis	0	3
Helophorus granularis	1	0
Helophorus. dorsalis	+	0
Hydraena gracilis	6	5
Hydraena nigrita	+	0
Hydrobius fuscipes	0	1
Hydrocyphon deflexicollis	+	0
Hydroporus ferrugineus	1	0
Hydroporus melanarius	1	0
Hydroporus memnonius	0	1
Hydroporus rufifrons	1	0
Hygrotus inaequalis	+	0
Ilybuis fuliginosus	0	1
Laccobius biguttatus	1	0
Laccophilus minutus	1	0
Limnebius papposus	1	0

Table B.1: continued

	1960	**2010**
COLEOPTERA contd.		
Limnius volkmari	7	5
Orectochilus villosus	3	0
Oreodytes sanmarki	3	5
Oreodytes septentrionalis	3	0
Oulimnius tuberculatus	7	7
Platambus maculatus	+	2
Riolus cupreus	+	0
Riolus subviolaceus	0	3
Stictotarsus duodecimpustulatus	0	2

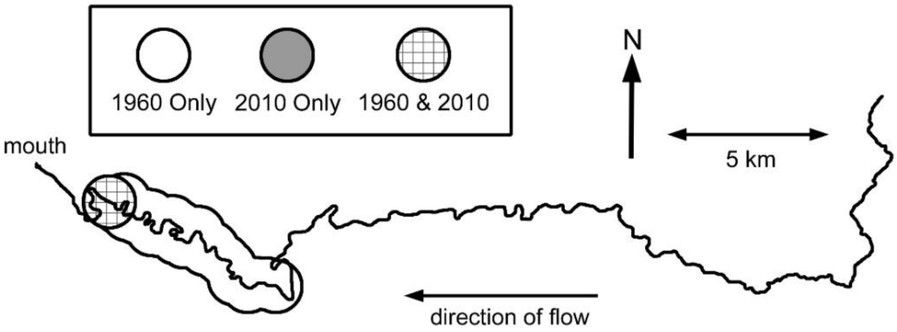
APPENDIX C Species with similar distribution on the River Endrick in the 1960 and 2010 study periods

C.1 Tricladida

Dugesia lugubris was relatively uncommon in both 1960 and 2010 (Table C.1). *D. lugubris* is found exclusively in the lower reaches of the River Endrick (Figure C.1a). Site occupancy and distribution of abundance appear similar in both study periods (Figure C.1b). *(a) Similar distribution in 1960 and 2010.*

Table C.1: Numerical summary of *D. lugubris* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	18	2.42 (± 5.59)	2
2010	11	1.57 (± 4.16)	1



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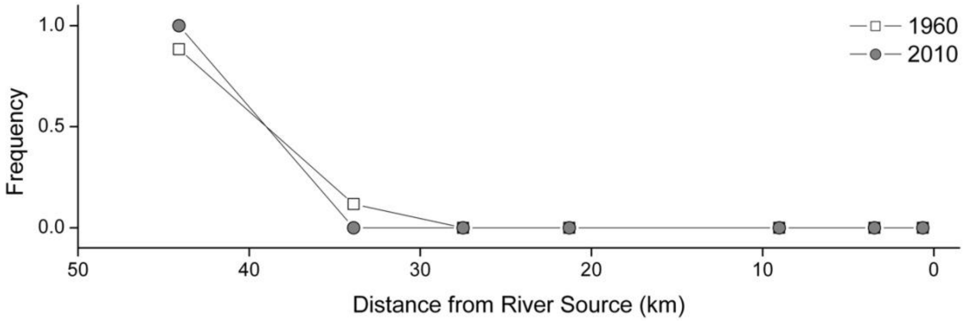


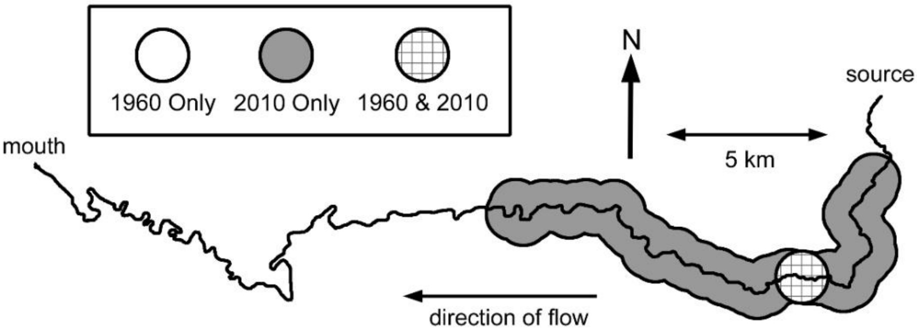
(b)

Figure C.1: Distribution of *D. lugubris* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *D. lugubris* in each study period.

Polycelis felina was relatively common in both 1960 and 2010 (Table C.2). *P. felina* is found exclusively in the upper reaches of the River Endrick (Figure C.2a). Site occupancy and distribution of abundance appear similar in both study periods (Figure C.2b). Absolute abundance as increased significantly ($\chi^2_c = 4.9e^3$, $p < 0.0001$) between 1960 and 2010 (Table C.2). *(a) Similar distribution in 1960 and 2010.*

Table C.2: Numerical summary of *P. felina* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	29	2.71 (± 7.18)	1
2010	490	46.86 (± 105.65)	3



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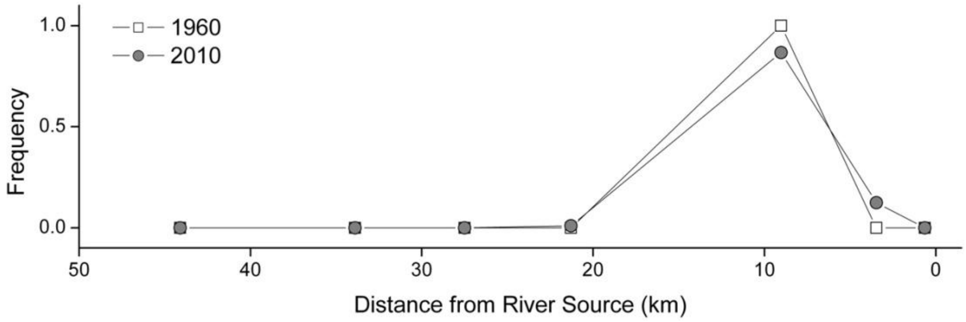


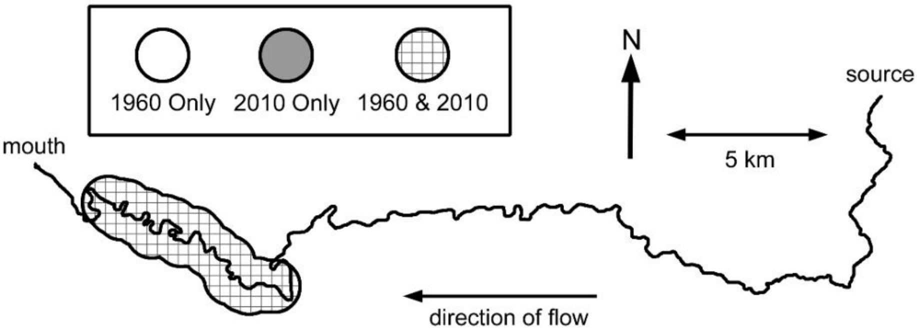
(b)

Figure C.2: Distribution of *P. felina* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *P. felina* in each study period.

Polycelis nigra was relatively common in both 1960 and 2010 (Table C.3). *P. nigra* is found exclusively in the lower reaches of the River Endrick (Figure C.3a). Site occupancy and distribution of abundance appear similar in both study periods (Figure C.3b). *(a) Similar distribution in 1960 and 2010.*

Table C.3: Numerical summary of *P. nigra* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	21	2.86 (± 6.72)	2
2010	36	5.28 (± 13.55)	2



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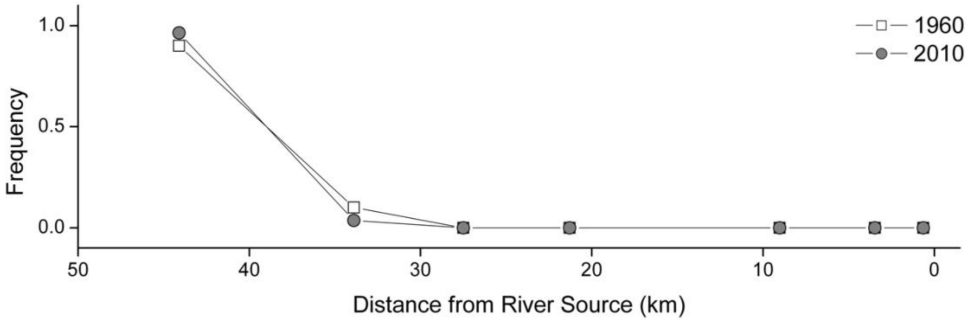


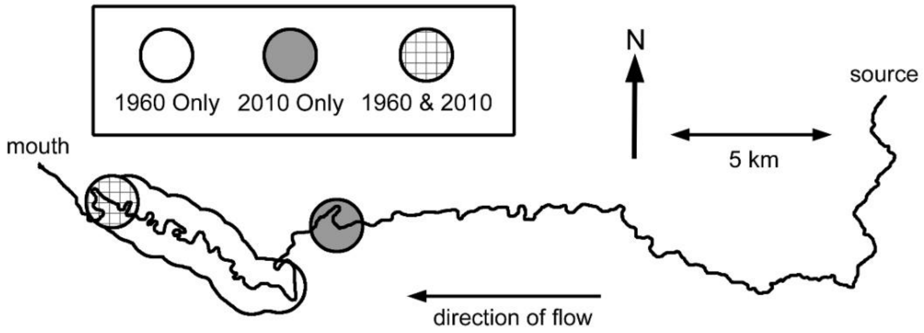
(b)

Figure C.3: Distribution of *P. nigra* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *P. nigra* in each study period.

Polycelis tenuis was relatively common in both 1960 and 2010 (Table C.4). *P. tenuis* is found exclusively in the lower reaches of the River Endrick (Figure C.4a). Site occupancy and distribution of abundance appear similar in both study periods (Figure C.4b). Absolute abundance as increased significantly ($\chi^2_c = 70.389$, $p < 0.0001$) between 1960 and 2010 (Table C.4). *(a) Similar distribution in 1960 and 2010.*

Table C.4: Numerical summary of *P. tenuis* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	52	7.14 (± 17.61)	2
2010	113	19.43 (± 50.53)	2



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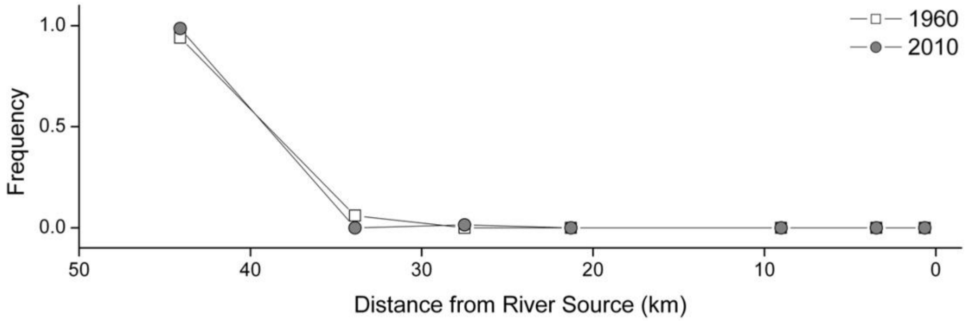


(b)

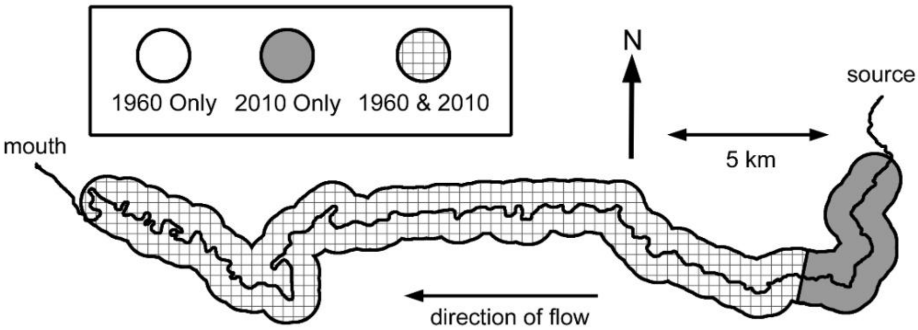
Figure C.4: Distribution of *P. tenuis* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *P. tenuis* in each study period.

C.2 Crustacea

Gammarus pulex was relatively common in both 1960 and 2010 (Table C.5). *G. pulex* is found along almost all of the River Endrick (excluding the extreme upper reaches; Figure C.5a). Site occupancy and distribution of abundance appear similar in both study periods (Figure C.5b). Absolute abundance as increased significantly ($\chi^2_c = 3.9e^3$, $p < 0.0001$) between 1960 and 2010 (Table C.5). *(a) Similar distribution in 1960 and 2010.*

Table C.5: Numerical summary of *G. pulex* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	185	24.00 (± 23.14)	5
2010	1034	212.42 (± 367.42)	6



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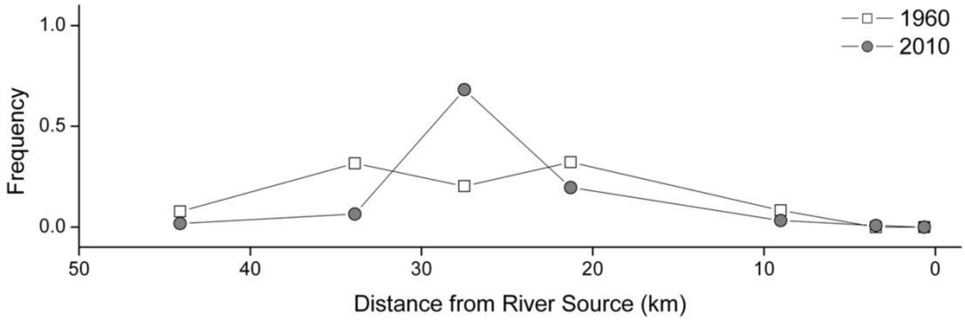


(b)

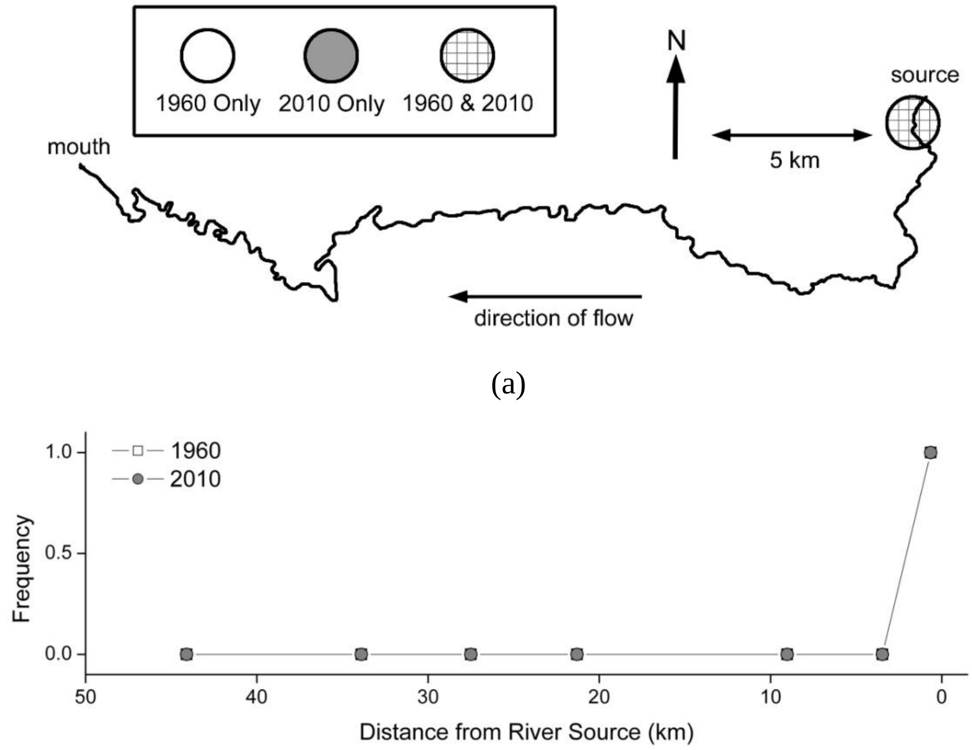
Figure C.5: Distribution of *G. pulex* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *G. pulex* in each study period.

C.3 Ephemeroptera

Ameletus inopinatus is found only at the source of the River Endrick (Figure C.6a). Site occupancy and distribution of abundance are identical in both study periods (Table C.6; Figure C.6a). Absolute abundance has decreased significantly ($\chi^2_c = 9.59$, $p = 0.0020$) between 1960 and 2010 (Table C.6). *(a) Similar distribution in 1960 and 2010.*

Table C.6: Numerical summary of *A. inopinatus* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	1	2.71 (± 7.18)	1
2010	19	0.14 (± 0.38)	1



(a)

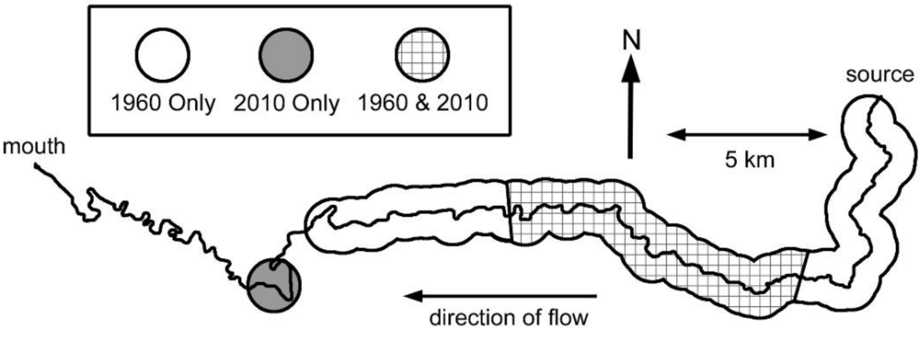
(b)

Figure C.6: Distribution of *A. inopinatus* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *A. inopinatus* in each study period.

Baetis muticus was common in both 1960 and 2010 (Table C.7). *B. muticus* is found along the middle reaches of the River Endrick (Figure C.7a). Site occupancy and distribution of abundance appear similar in both study periods (Figure C.7b). Absolute abundance has decreased significantly ($\chi^2_c = 224.232$, $p < 0.0001$) between 1960 and 2010 (Table C.7). *(a) Similar distribution in 1960 and 2010.*

Table C.7: Numerical summary of *B. muticus* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	312	43.14 (± 45.35)	5
2010	47	5.43 (± 7.91)	3



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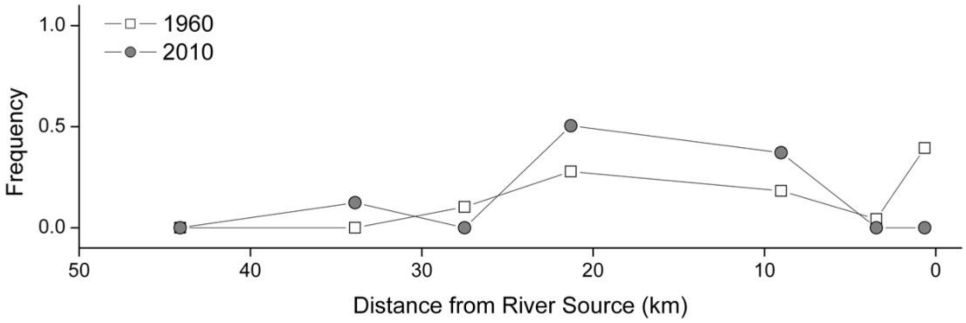


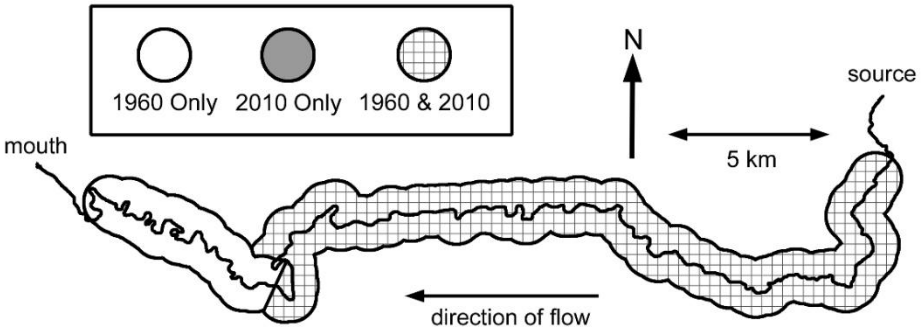
(b)

Figure C.7: Distribution of *B. muticus* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *B. muticus* in each study period.

Baetis rhodani was extremely abundant in both 1960 and 2010 (Table C.8). *B. rhodani* is found along almost all of the River Endrick (Figure C.8a) and was collected in all seasons and in all habitat types. Site occupancy and distribution of abundance appear similar in both study periods (Figure C.8b). Absolute abundance has increased significantly (χ^2_c = 210.859, $p < 0.0001$) between 1960 and 2010 (Table C.8). *(a) Similar distribution in 1960 and 2010.*

Table C.8: Numerical summary of *B. rhodani* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	1474	209.71 (± 212.98)	6
2010	2032	439.81 (± 657.56)	5



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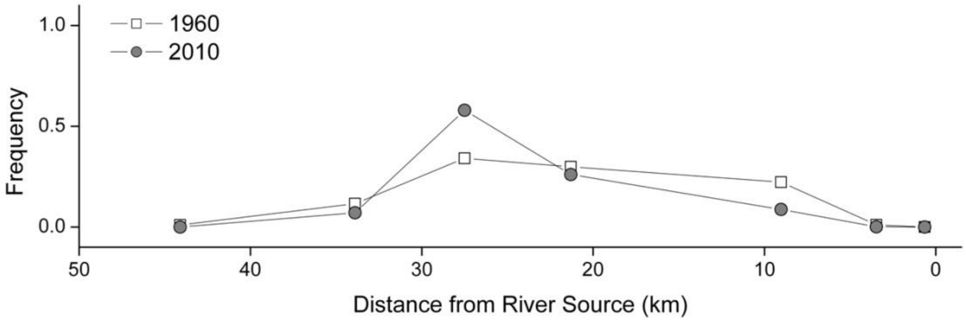


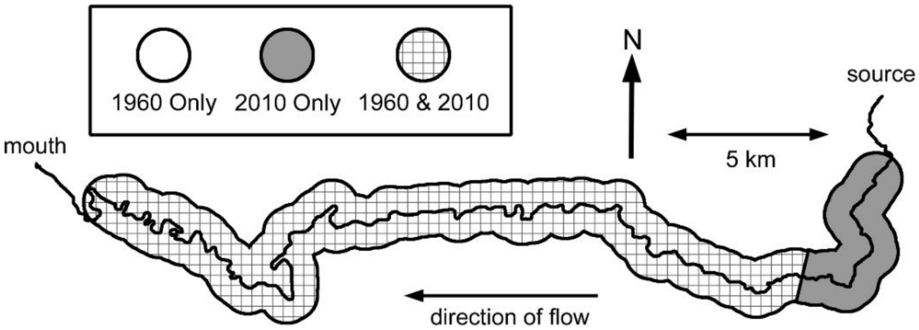
(b)

Figure C.8: Distribution of *B. rhodani* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *B. rhodani* in each study period.

Caenis rivulorum was abundance in both study periods (Table C.9). Site occupancy and distribution of abundance appear similar in both study periods (Figure C.9). Absolute abundance has increased significantly ($\chi^2_c = 1.2e^3$, $p < 0.0001$) between 1960 and 2010 (Table C.9). *(a) Similar distribution in 1960 and 2010.*

Table C.9: Numerical summary of *C. rivulorum* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	200	30.29 (± 35.71)	5
2010	1550	164.14 (± 339.63)	6



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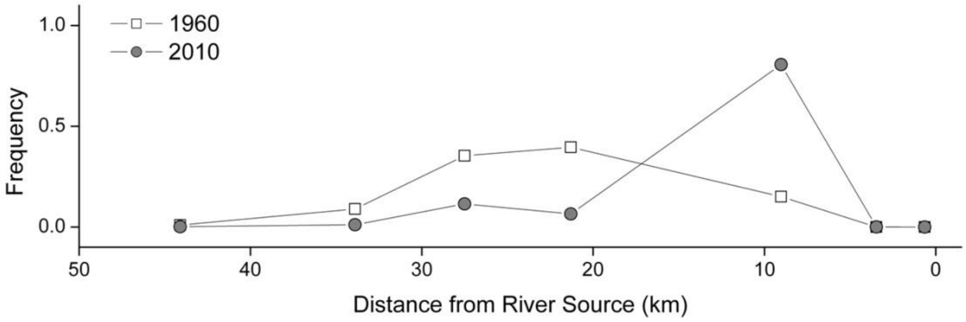


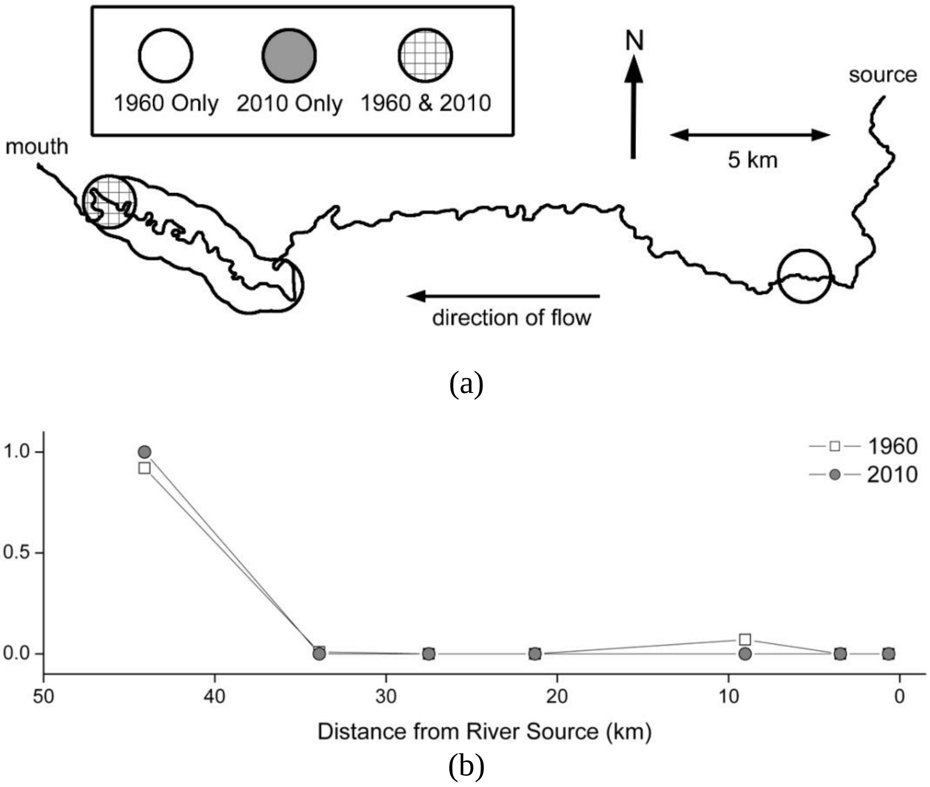
(b)

Figure C.9: Distribution of *C. rivulorum* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *C. rivulorum* in each study period.

Centroptilum luteolum was collected in both 1960 and 2010 (Table C.10). *C. luteolum* was found along the middle reaches of the River Endrick in 1960 but was only recorded from the lower reaches of the River in 2010 (Figure C.10a). Site occupancy and distribution of abundance appear similar in both study periods (Figure C.10b). Site occupancy has not changed significantly between 1960 and 2010 (Fisher's exact test; p = 0.615). Absolute abundance has decreased significantly ($\chi^2_c = 224.232$, $p < 0.0001$) between 1960 and 2010 (Table C.10). *(a) Similar distribution in 1960 and 2010.*

Table C.10: Numerical summary of *C. luteolum* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	223	30.57 (± 73.59)	3
2010	16	2.29 (± 6.05)	1



(a)

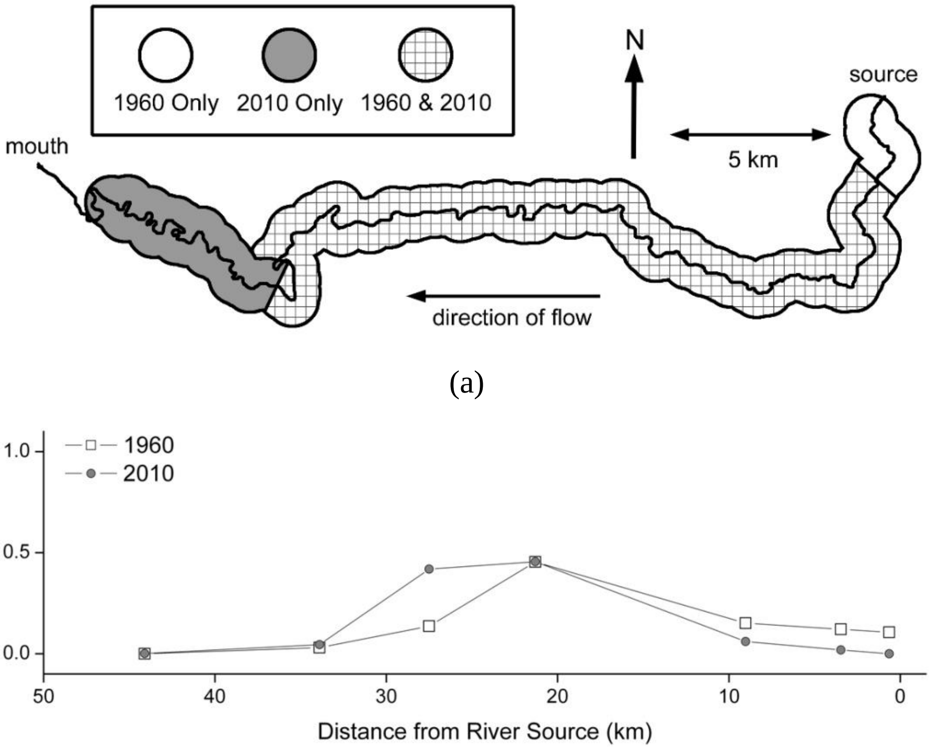
(b)

Figure C.10: Distribution of *C. luteolum* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *C. luteolum* in each study period.

Ecdyonurus torrentis/insignis[*] was abundant in both 1960 and 2010 (Table C.11). *E. torrentis/insignis* is found along almost all of the River Endrick (Figure C.11a). Site occupancy and distribution of abundance appear similar in both study periods (Figure C.11b). Absolute abundance has decreased significantly ($\chi^2_c = 8.5e^3$, $p < 0.0001$) between 1960 and 2010 (Table C.11). *(a) Similar distribution in 1960 and 2010.*

Table C.11: Numerical summary of *E. torrentis/insignis* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	140	9.43 (± 9.80)	6
2010	1234	127.29 (± 180.44)	6



(a)

(b)

Figure C.11: Distribution of *E. torrentis/insignis* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *E torrentis/insignis* in each study period.

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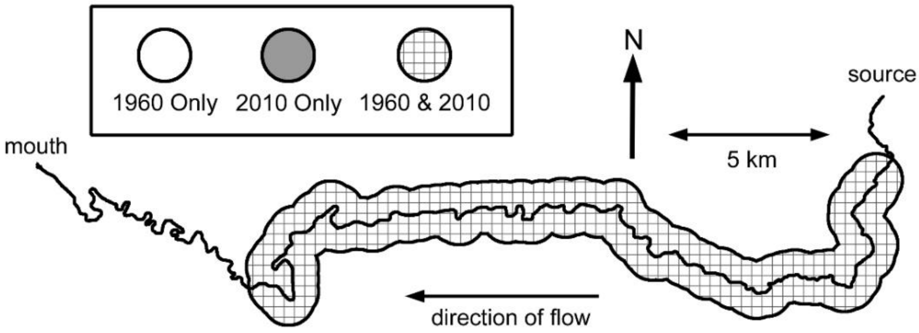
[*] These species have been analysed together due to identification issues.

Ecdyonurus venosus was abundant in both 1960 and 2010 (Table C.12). *E. venosus* is found along almost all of the River Endrick (excluding the lower reaches and extreme upper reaches; Figure C.12a). Site occupancy and distribution of abundance appear similar in both study periods (Figure C.12b). Absolute abundance has decreased significantly ($\chi^2_c = 13.389$, $p = 0.0003$) between 1960 and 2010 (Table C.12). *(a) Similar distribution in 1960 and 2010.*

Table C.12: Numerical summary of *E. venosus* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	183	30.00 (± 37.90)	5
2010	133	31.57 (± 46.85)	5



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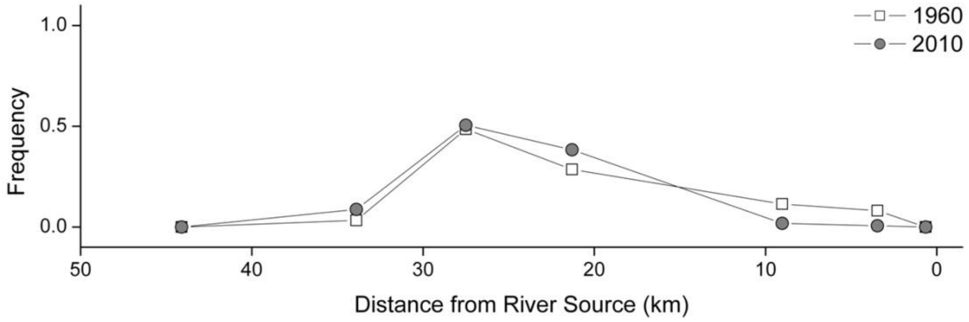


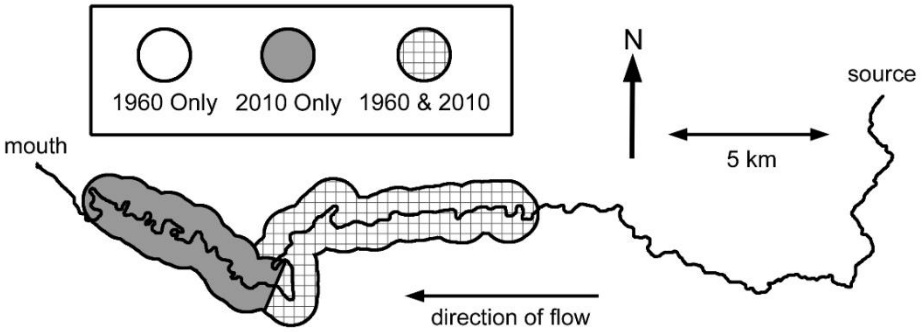
(b)

Figure C.12: Distribution of *E. venosus* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *E. venosus* in each study period.

Habrophlebia fusca was collected in both 1960 and 2010 (Table C.13). *H. fusca* was found along the lower middle reaches of the River Endrick (Figure C.13a). Site occupancy and distribution of abundance appear similar in both study periods (Figure C.13b). Site occupancy has not changed significantly between 1960 and 2010 (Fisher's exact test; p = 0.102). Absolute abundance has decreased significantly (χ^2_c = 11.358, p = 0.0008) between 1960 and 2010 (Table C.13). *(a) Similar distribution in 1960 and 2010.*

Table C.13: Numerical summary of *H. fusca* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	37	4.71 (± 6.63)	3
2010	16	2.29 (± 2.43)	4



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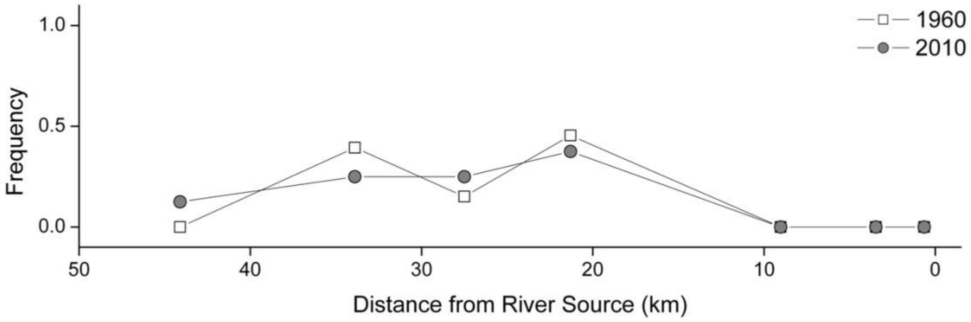


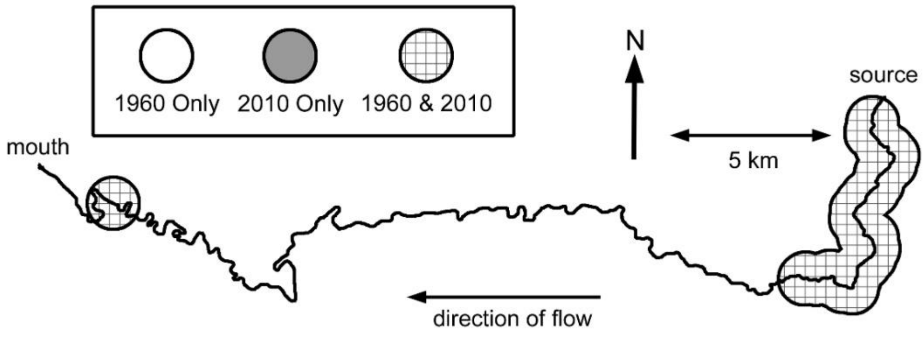
(b)

Figure C.13: Distribution of *H. fusca* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *H. fusca* in each study period.

Leptophlebia marginata was common in both 1960 and 2010 (Table C.14). *L. marginata* was found in the extreme lower reaches and the upper reaches of the River Endrick in both 1960 and 2010 (Figure C.14a). Site occupancy and distribution of abundance appear similar in both study periods (Figure C.14b). Absolute abundance has decreased significantly ($\chi^2_c = 5.879$, p = 0.015) between 1960 and 2010 (Table C.14). *(a) Similar distribution in 1960 and 2010.*

Table C.14: Numerical summary of *L. marginata* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	31	3.14 (± 5.37)	4
2010	17	2.00 (± 3.00)	4



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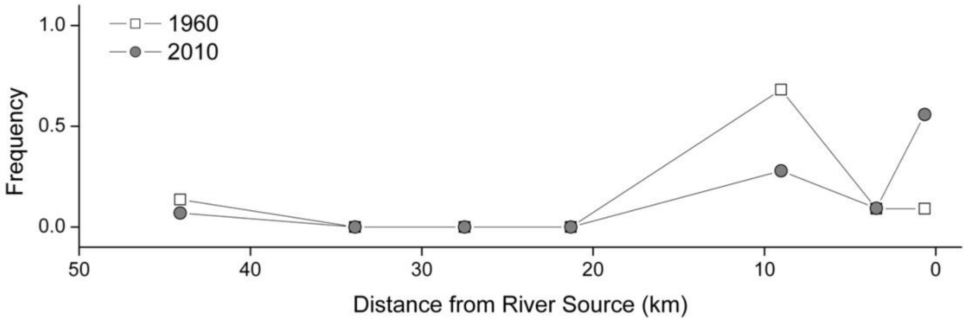


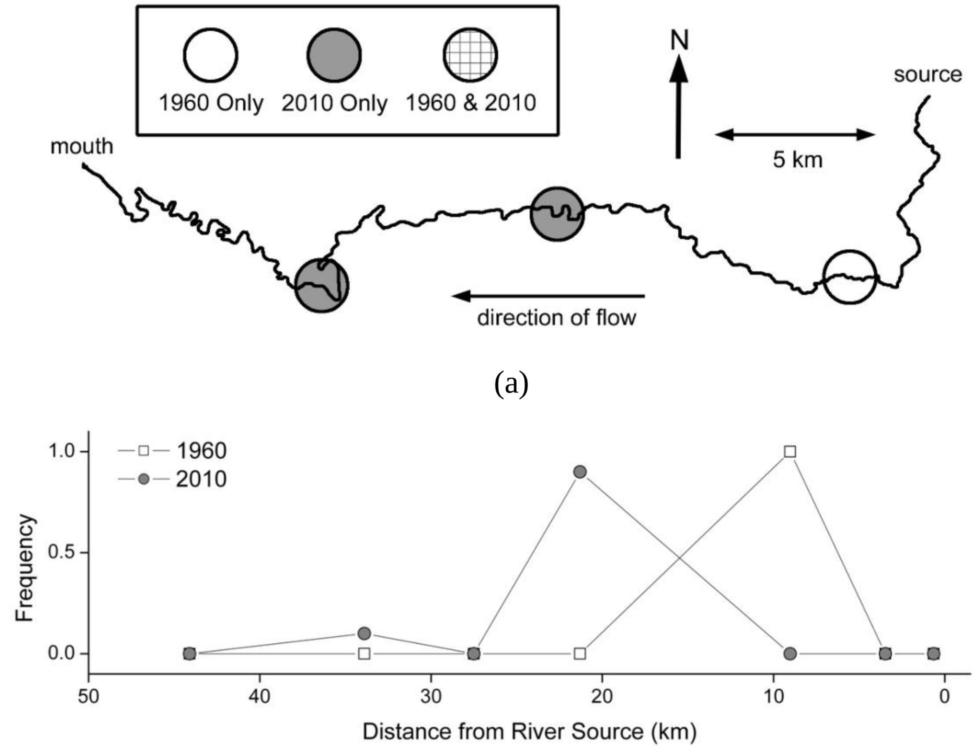
(b)

Figure C.14: Distribution of *L. marginata* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *L. marginata* in each study period.

Paraleptophlebia cincta occurred sporadically in the River Endrick in both 1960 and 2010 (Figure C.15, Table C.15). Absolute abundance has decreased significantly ($\chi^2_c = 8.679$, p = 0.0032) between 1960 and 2010 (Table C.15). *(a) Similar distribution in 1960 and 2010.*

Table C.15: Numerical summary of *P. cincta* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	21	2.00 (± 5.29)	1
2010	7	1.00 (± 2.23)	2



(a)

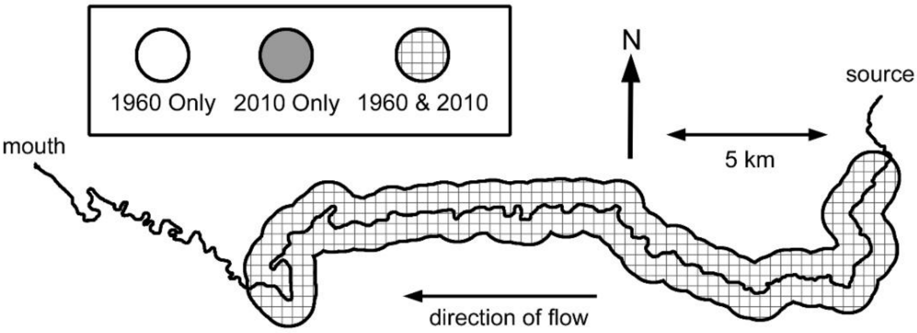
(b)

Figure C.15: Distribution of *P. cincta* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *P. cincta* in each study period.

Rhithrogena semicolorata was abundant in both 1960 and 2010 (Table C.16). *R. semicolorata* is found along almost all of the River Endrick (excluding the lower reaches and extreme upper reaches; Figure C.16a). Site occupancy and distribution of abundance appear similar in both study periods (Figure C.16b). Absolute abundance has increased significantly ($\chi^2_c = 1.5e^5$, $p < 0.0001$) between 1960 and 2010 (Table C.16). *(a) Similar distribution in 1960 and 2010.*

Table C.16: Numerical summary of *R. semicolorata* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	237	29.71 (± 39.31)	5
2010	6173	1473.86 (± 2143.03)	5



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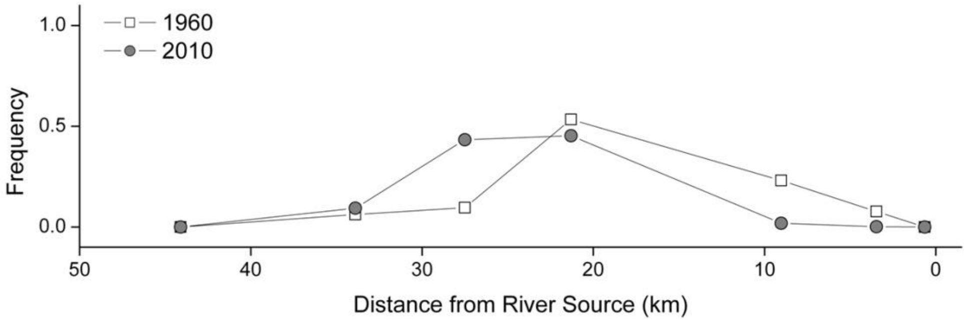


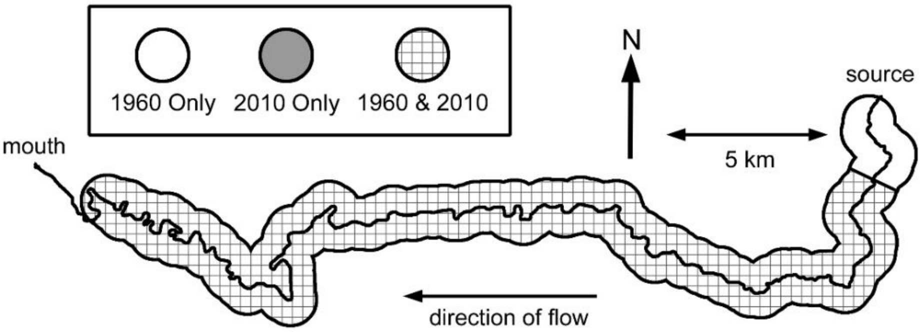
(b)

Figure C.16: Distribution of *R. semicolorata* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *R. semicolorata* in each study period.

Serratella ignita was extremely abundance in both study periods (Table C.17). All individuals of this species were collected only in the summer months in 1960 (Maitland, 1965). While the majority of individuals were collected in the summer samples in 2010, 11 individuals were collected in autumn samples from site 5 and site 6. Absolute abundance has increased significantly ($\chi^2_c = 3.0e^4$, $p < 0.0001$) between 1960 and 2010 (Table C.17). *(a) Similar distribution in 1960 and 2010.*

Table C.17: Numerical summary of *S. ignita* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	1989	264.57 (± 252.58)	7
2010	9728	1434.49 (± 1568.19)	6



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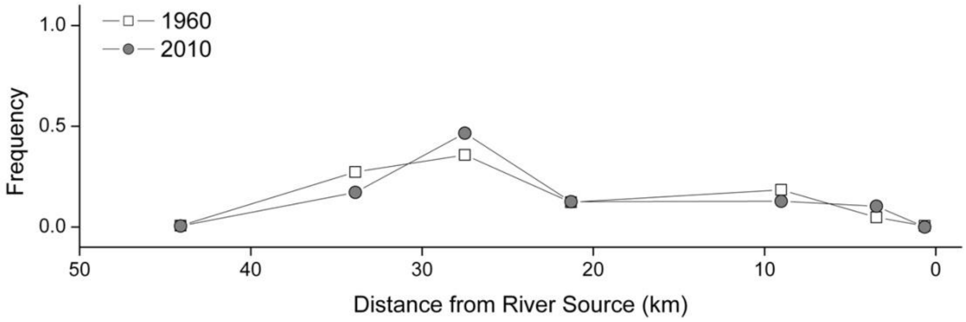

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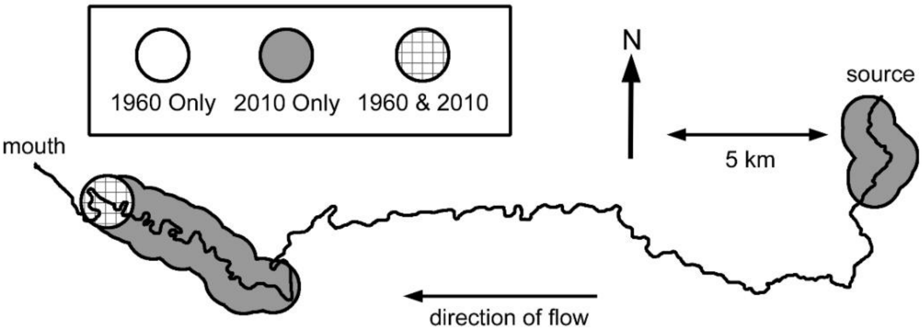
Figure C.17: Distribution of *S. ignita* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *S. ignita* in each study period.

Siphlonurus lacustris found exclusively in the lowers reaches in 1960, this species was recorded from the site at the source of the river in 2010 (Figure C.18a). 33 individuals were collected from the river in 2010; 22 were collected from the lower reaches compared to 11 from the upper reaches (Figure C.18b). Those specimens collected in the lower reaches were found exclusively in habitats with slow flow (i.e. pool and emergent macrophyte), while the specimens collected from the upper reaches were predominantly found in faster flowing conditions (i.e. in riffle and moss covered rock). The detection of this species in 2010 outwith the historic range in 1960 was not significant (Fisher's exact test; $p = 0.224$). Absolute abundance has increased significantly ($\chi^2_c = 151.250$, $p = 0.0020$) between 1960 and 2010 (Table C.18). *(a) Similar distribution in 1960 and 2010.*

Table C.18: Numerical summary of *S. lacustris* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	3	0.43 (± 1.13)	1
2010	33	3.86 (± 4.52)	4



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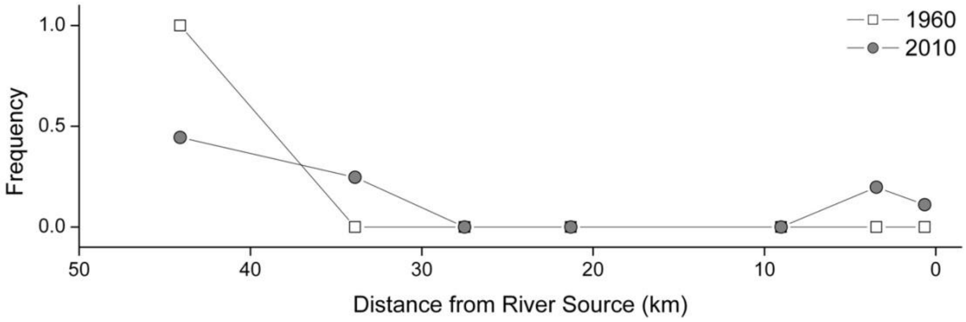


(b)

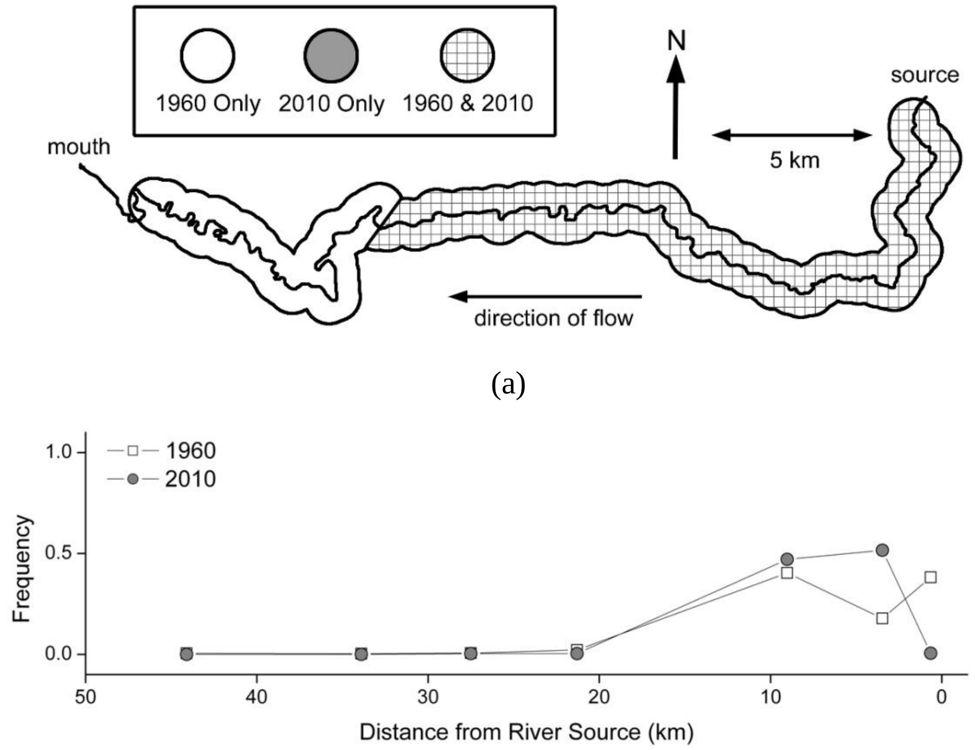
Figure C.18: Distribution of *S. lacustris* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *S. lacustris* in each study period.

C.4 Plecoptera

Amphinemura sulcicollis was abundance in both study periods (Table C.19). Site occupancy and distribution of abundance appear similar in both study periods (Figure C.19). Absolute abundance has decreased significantly ($\chi^2_c = 285.387$, $p < 0.0001$) between 1960 and 2010 (Table C.19). *(a) Similar distribution in 1960 and 2010.*

Table C.19: Numerical summary of *A. sulcicollis* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	1433	158.71 (± 201.67)	7
2010	793	76.05 (± 127.84)	5



(a)

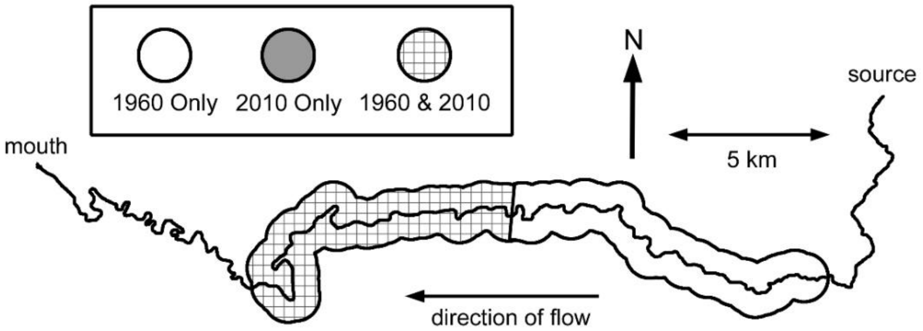
(b)

Figure C.19: Distribution of *A. sulcicollis* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *A. sulcicollis* in each study period.

Brachyptera risi was collected in both 1960 and 2010 (Table C.20). *B. risi* was found along the lower middle reaches of the River Endrick (Figure C.20a). Site occupancy and distribution of abundance appear similar in both study periods (Figure C.20b). Absolute abundance has increased significantly ($\chi^2_c = 190.571$, $p < 0.0001$) between 1960 and 2010 (Table C.20). *(a) Similar distribution in 1960 and 2010.*

Table C.20: Numerical summary of *B.risi* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	53	7.57 (± 8.40)	4
2010	154	41.71 (± 66.03)	3



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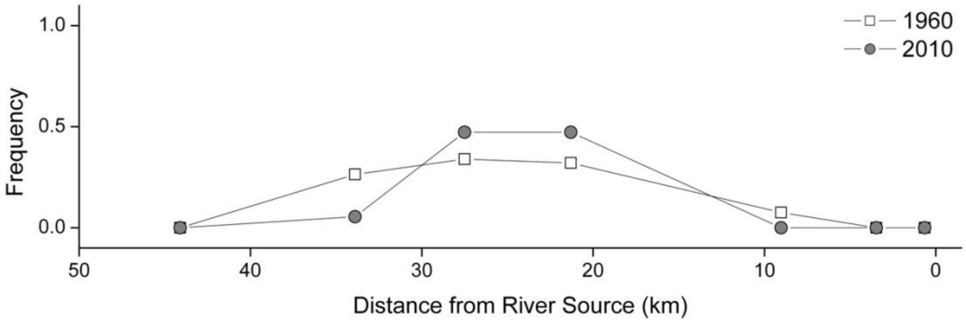


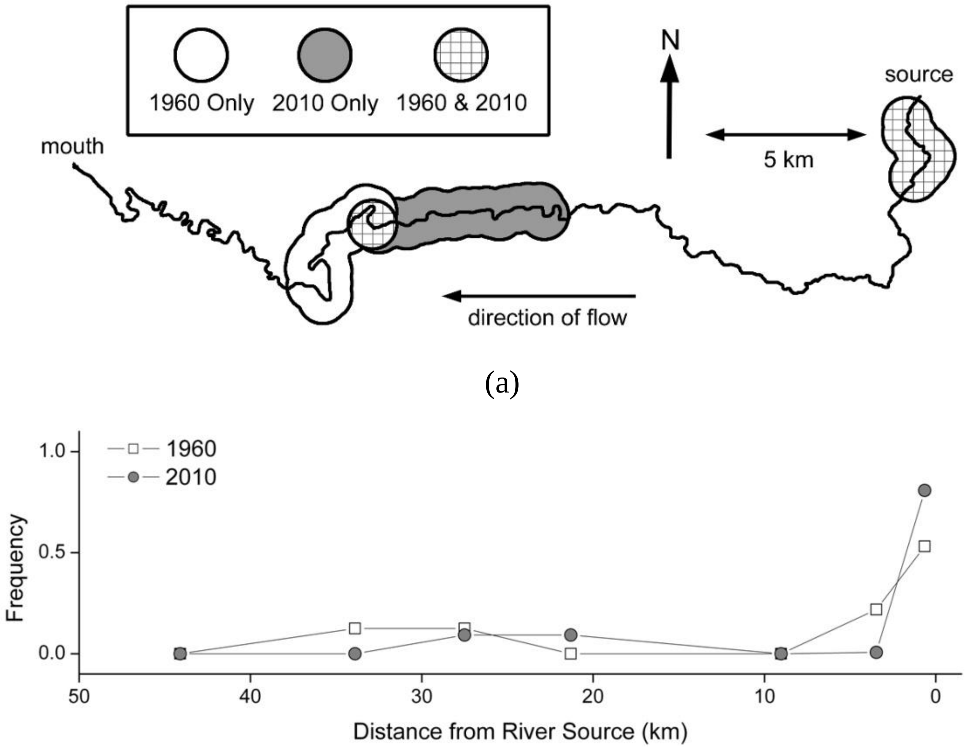
(b)

Figure C.20: Distribution of *B. risi* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *B.risi* in each study period.

Capnia bifrons distribution of this species in the two study periods remains broadly similar, with two populations present on the River Endrick (Figure C.21). The large of the two populations was found in the upper reaches in 1960 and 2010 (Figure C.21b). Absolute increased has increased significantly ($\chi^2_c = 548.350$, $p < 0.00001$) between 1960 and 2010 (Table C.21). *(a) Similar distribution in 1960 and 2010.*

Table C.21: Numerical summary of *C. bifrons* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	**Total Number**	**River Mean**	**Number of Sites**
1960	36	4.57 (± 6.11)	4
2010	177	27.71 (± 57.62)	4



(a)

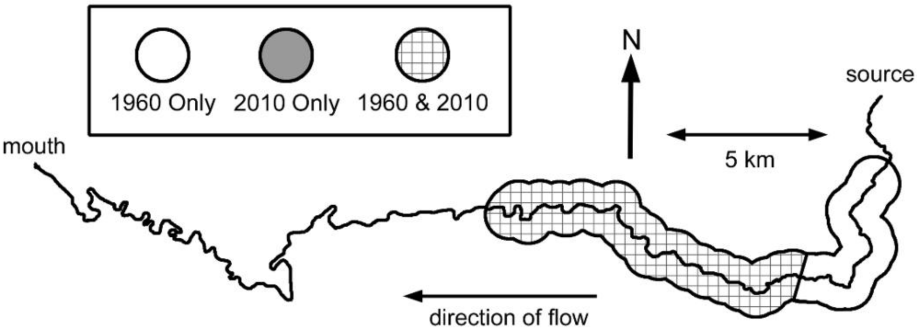
(b)

Figure C.21: Distribution of *C. bifrons* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *C. bifrons* in each study period.

Dinocras cephalotes was common in both study periods (Table C.22). Site occupancy and distribution of abundance appear similar in both study periods (Figure C.22). Absolute abundance has decreased significantly ($\chi^2_c = 62.095$, $p = 0.0002$) between 1960 and 2010 (Table C.22). *(a) Similar distribution in both study periods*.

Table C.22: Numerical summary of *D. cephalotes* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	87	8.43 (± 18.46)	3
2010	13	1.29 (± 2.63)	2



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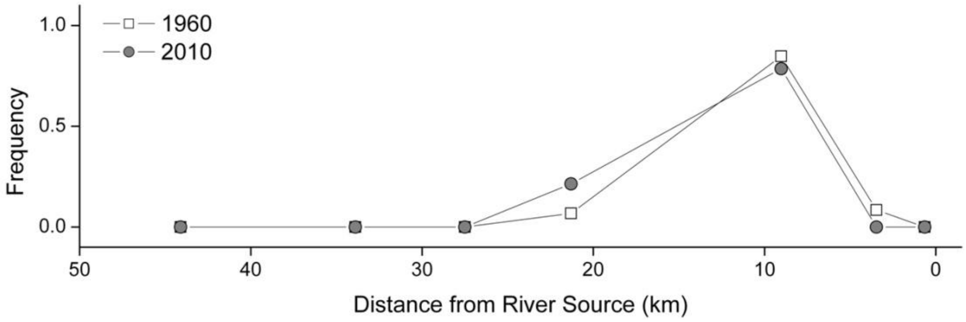


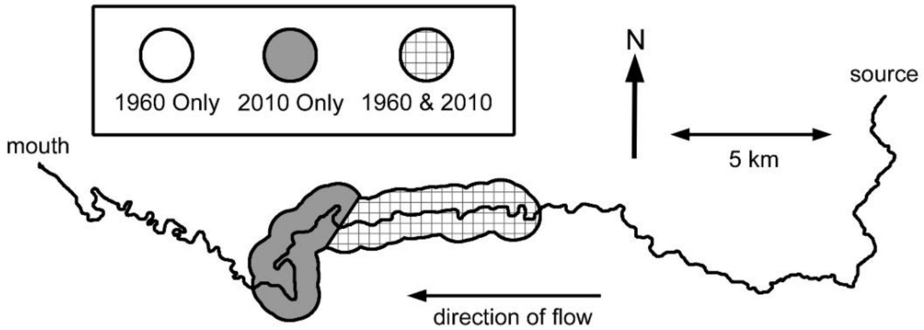
(b)

Figure C.22: Distribution of *D. cephalotes* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *D. cephalotes* in each study period.

Euleuctra geniculata was recorded in both study periods in the middle reaches of the river (Table C.23; Figure C.23). Site occupancy and distribution of abundance appear similar in both study periods (Figure C.23). Absolute abundance has increased significantly (χ^2_c = 1.7e^3, $p < 0.0001$) between 1960 and 2010 (Table C.23). *(a) Similar distribution in both study periods*.

Table C.23: Numerical summary of *E. geniculata* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	22	5.43 (± 12.30)	2
2010	214	46.29 (± 92.30)	3



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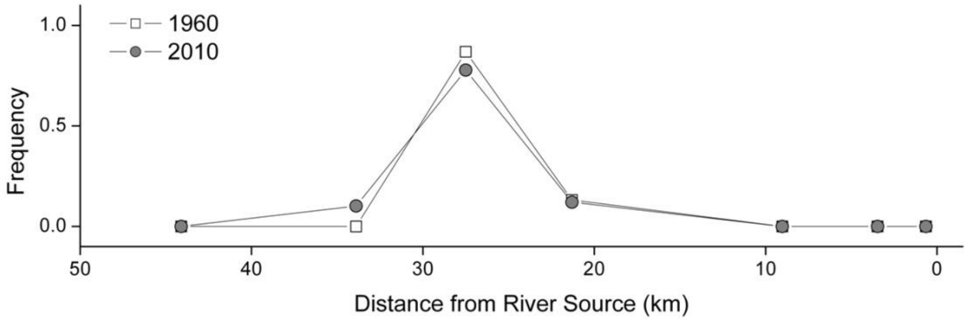


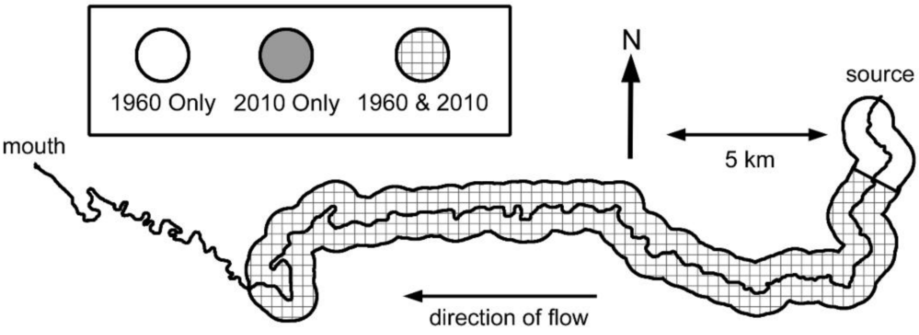
(b)

Figure C.23: Distribution of *E. geniculata* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *E. geniculata* in each study period.

Isoperla grammatica was abundant in both study periods (Table C.24). Site occupancy and distribution of abundance appear similar in both study periods (Figure C.24). Absolute abundance has decreased significantly (χ^2_c = 138.743, p = 0.0002) between 1960 and 2010 (Table C.24). *(a) Similar distribution in both study periods*.

Table C.24: Numerical summary of *I. grammatica* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	722	78.57 (± 117.22)	6
2010	405	40.86 (± 61.06)	5



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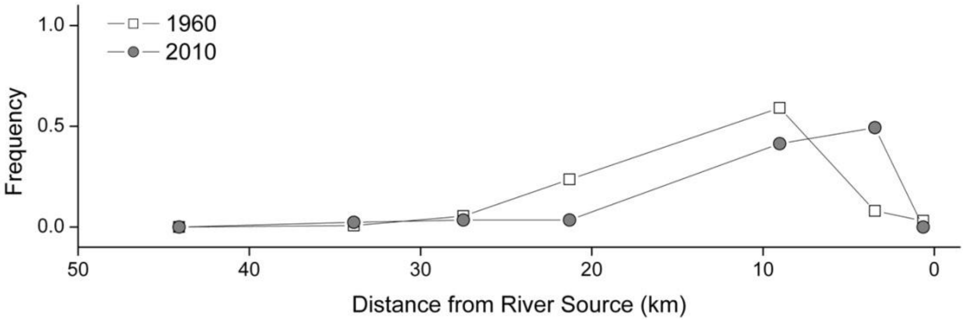

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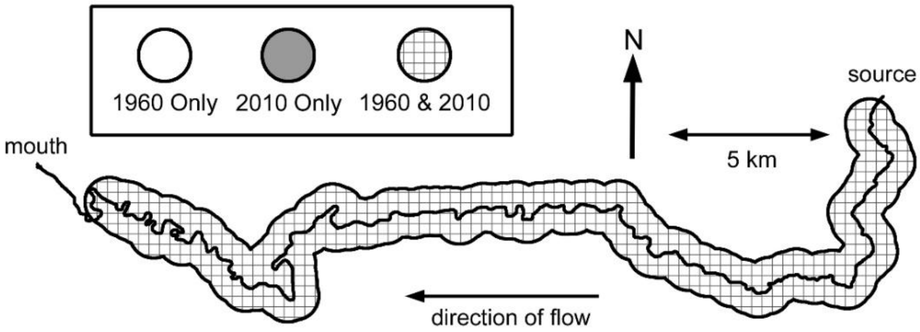
Figure C.24: Distribution of *I. grammatica* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *I. grammatica* in each study period.

Leuctra hippopus was highly abundant in both study periods (Table C.25). Site occupancy and distribution of abundance appear similar in both study periods (Figure C.25). Absolute abundance has increased significantly (χ^2_c = 291.424, p = 0.0002) between 1960 and 2010 (Table C.25). *(a) Similar distribution in both study periods*.

Table C.25: Numerical summary of *L. hippopus* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	489	52.86 (± 69.91)	7
2010	867	100.43 (± 110.09)	7



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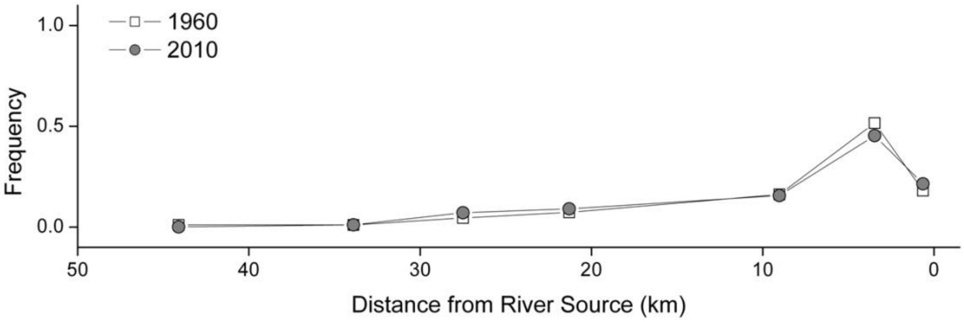

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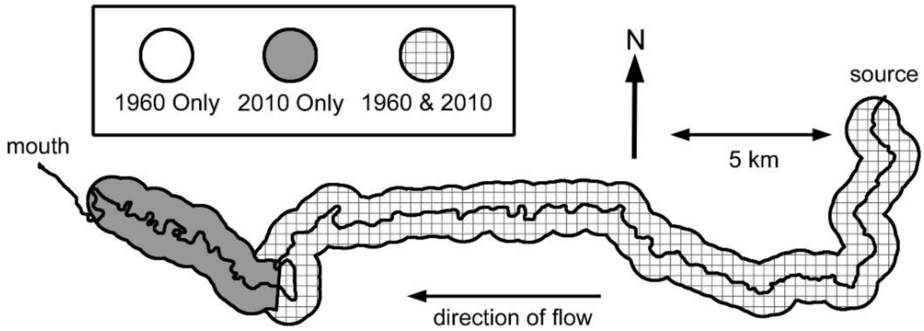
Figure C.25: Distribution of *L. hippopus* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *L. hippopus* in each study period.

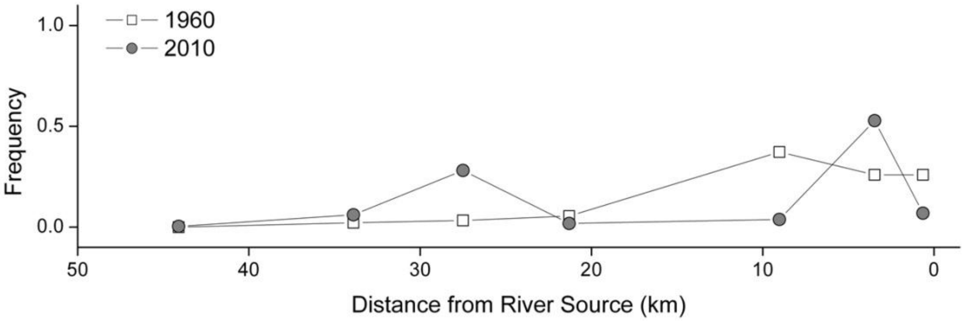
Leutra inermis was highly abundant in both study periods (Table C.26). Site occupancy and distribution of abundance appear similar in both study periods (Figure C.26). Absolute abundance has decreased significantly ($\chi^2_c = 13.572$, $p = 0.0002$) between 1960 and 2010 (Table C.26). *(a) Similar distribution in 1960 and 2010.*

Table C.26: Numerical summary of *L. inermis* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	672	73.29 (± 76.82)	6
2010	576	70.14 (± 95.03)	7



(a)



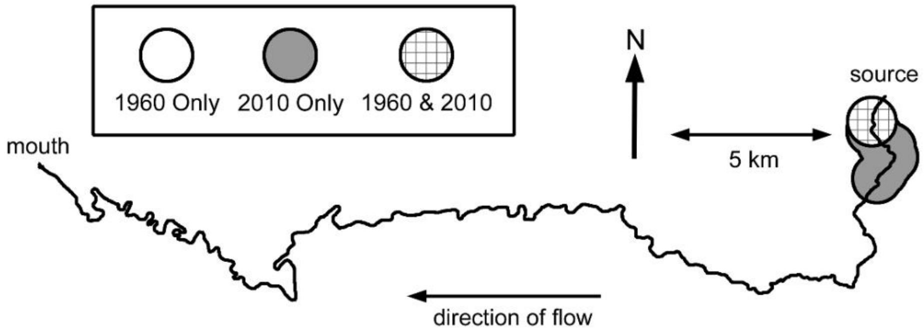
(b)

Figure C.26: Distribution of *L. inermis* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *L. inermis* in each study period.

Leuctra nigra was only recorded from the extreme upper reaches of the River Endrick in both 1960 and 2010 (Figure C.27). Site occupancy and distribution of abundance are similar in both study periods (Table C.27; Figure C.27a). Absolute increased has increased significantly ($\chi^2_c = 232.408$, $p < 0.00001$) between 1960 and 2010 (Table C.27). *(a) Similar distribution in 1960 and 2010.*

Table C.27: Numerical summary of *L. nigra* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	30	4.29 (± 11.34)	1
2010	114	16.14 (± 42.27)	2



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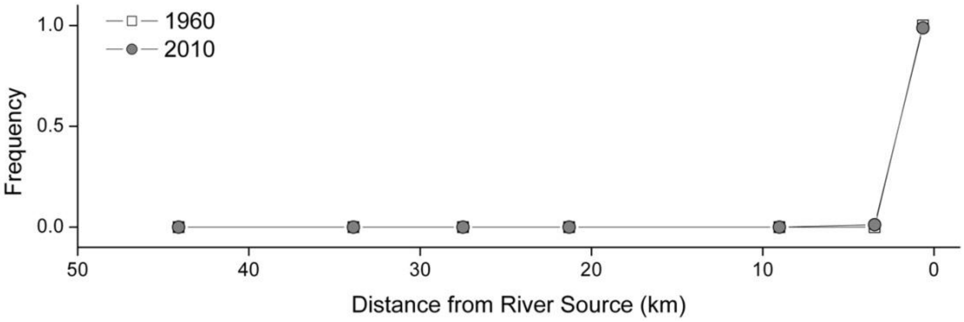


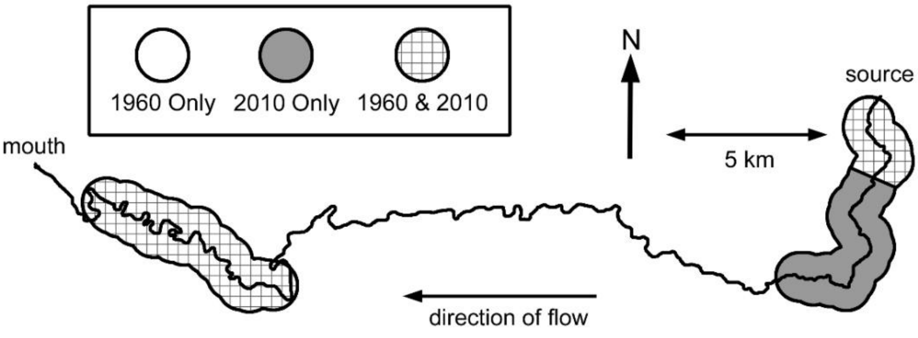
(b)

Figure C.27: Distribution of *L. nigra* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *L. nigra* in each study period.

Nemoura avicularis was recorded in both study periods in the extreme upper and lower reaches of the river (Table C.28; Figure C.28). Site occupancy and distribution of abundance appear similar in both study periods (Figure C.28). Absolute abundance has increased significantly ($\chi^2_c = 1.6e^3$, $p < 0.0001$) between 1960 and 2010 (Table C.28). *(a) Similar distribution in both study periods*.

Table C.28: Numerical summary of *N. avicularis* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	65	8.43 (± 14.71)	4
2010	384	54.57 (± 126.45)	5



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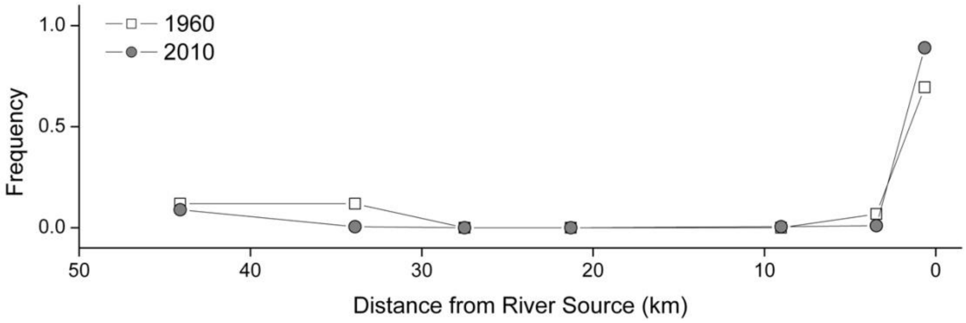

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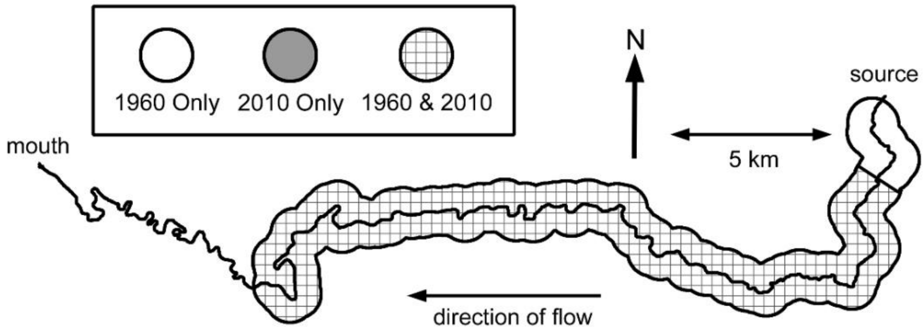
Figure C.28: Distribution of *N. avicularis* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *N. avicularis* in each study period.

Siphonoperla torrentium was common in both study periods (Table C.29). Site occupancy and distribution of abundance appear similar in both study periods (Figure C.29). Absolute abundance has decreased significantly (χ^2_c = 110.068, p = 0.0002) between 1960 and 2010 (Table C.29). *(a) Similar distribution in both study periods*.

Table C.29: Numerical summary of *S. torrentium* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	296	32.29 (± 43.29)	6
2010	115	12.57 (± 17.00)	5



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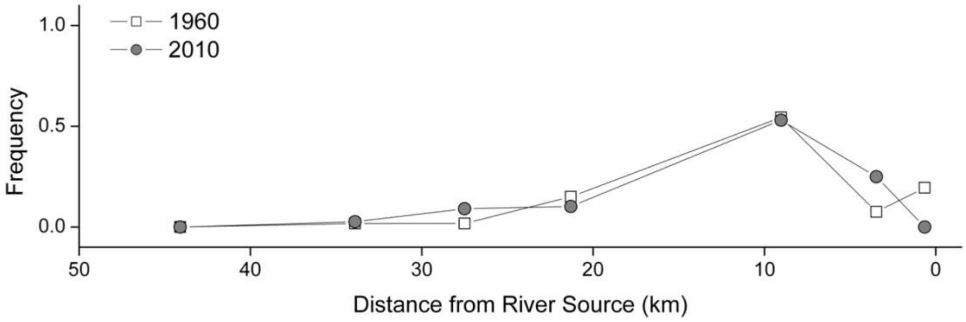

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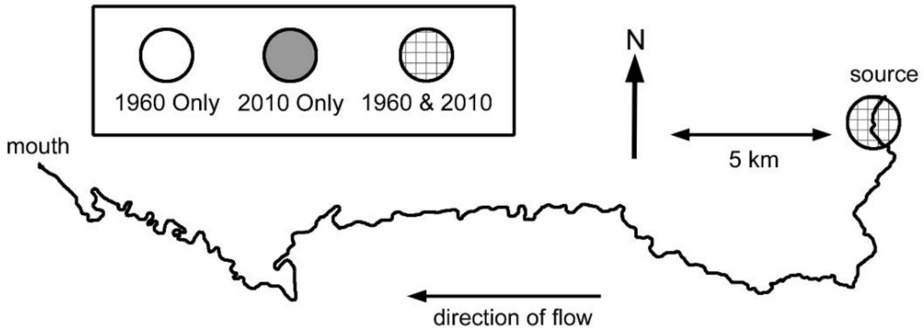
Figure C.29: Distribution of *S. torrentium* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *S. torrentium* in each study period.

C.5 Hemiptera

Gerris costai was only collected at the site located close to the source of the river in both study periods (Table C.30; Figure C.30). *(a) Similar distribution in both study periods*.

Table C.30: Numerical summary of *G. costai* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	1	0.14 (± 0.38)	1
2010	1	0.14 (± 0.38)	1



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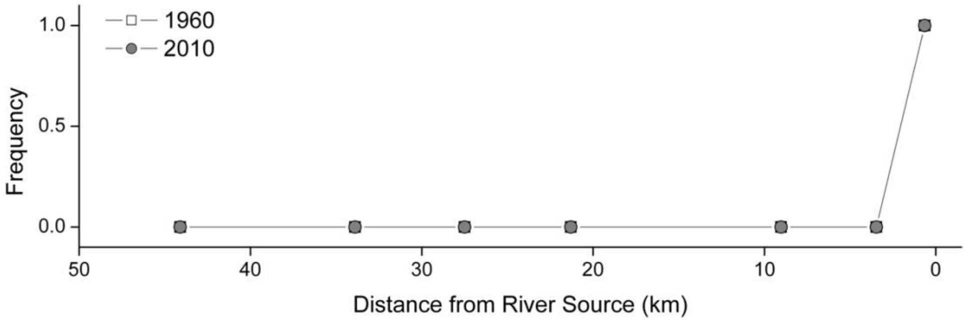

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Figure C.30: Distribution of *G. costai* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *G. costai* in each study period.

Gerris lacustris (L.) remains restricted to the lower reaches in both study periods (Figure C.31; Table C.31). No abundance data were available for *G. lacustris* in 1960, so only spatial distribution is presented for this species. *(a) Similar distribution in both study periods*.

Table C.31: Numerical summary of *G. lacustris* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	na	na	1
2010	2	0.57 (± 1.51)	1

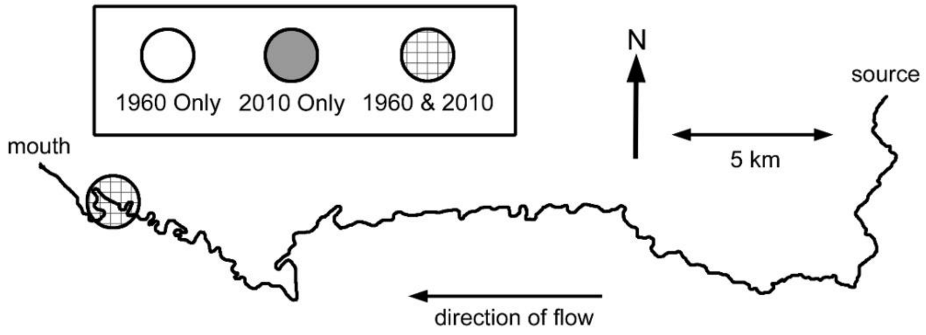
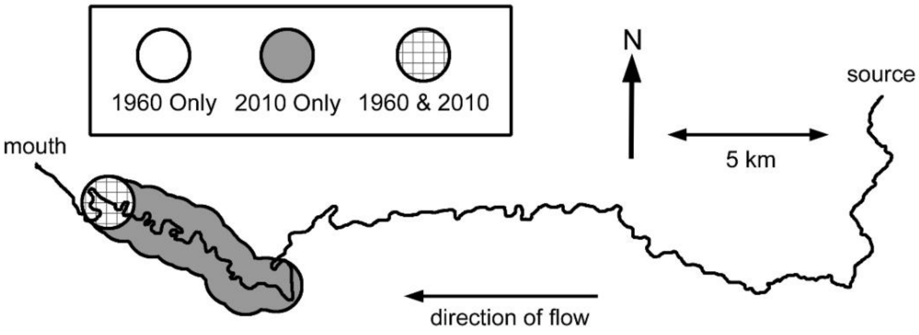


Figure C.31: Spatial distribution of *G. lacustris* in the river Endrick in 1960 and 2010.

Notonecta glauca was relatively common in both 1960 and 2010 (Table C.32). *N. glauca* is found exclusively in the lower reaches of the River Endrick (Figure C.32a). Site occupancy and distribution of abundance appear similar in both study periods (Figure C.32b). Absolute abundance has increased significantly (χ^2_c = 90.018, $p < 0.0001$) between 1960 and 2010 (Table C.32). *(a) Similar distribution in 1960 and 2010.*

Table C.32: Numerical summary of *N. glauca* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	14	2.00 (± 5.29)	1
2010	50	7.00 (± 18.08)	2



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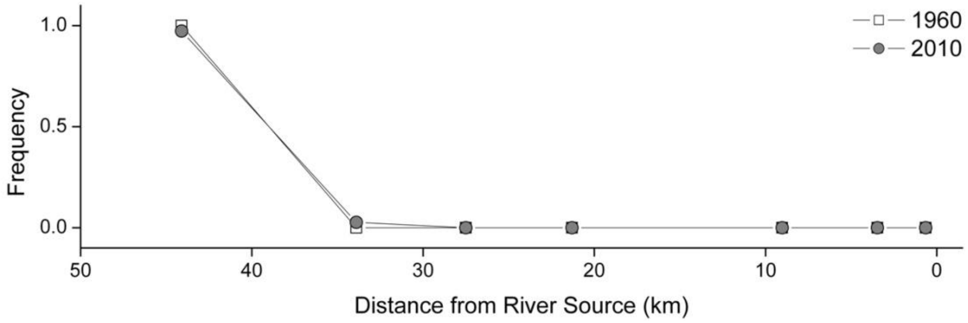


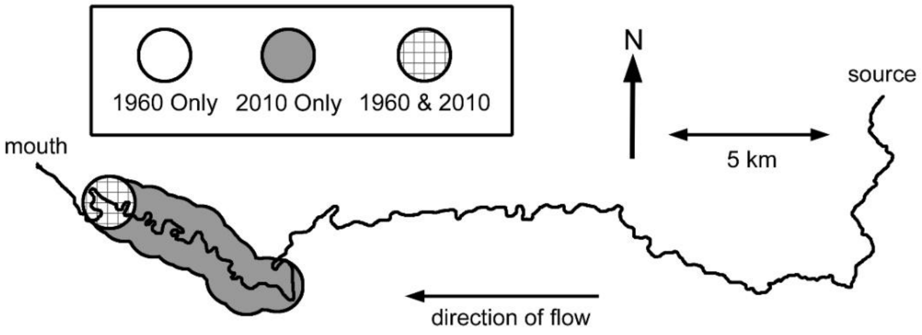
(b)

Figure C.32: Distribution of *N. glauca* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *N. glauca* in each study period.

Sigara dorsalis was relatively common in both 1960 and 2010 (Table C.33). *S. dorsalis* is found exclusively in the lower reaches of the River Endrick (Figure C.33a). Site occupancy and distribution of abundance appear similar in both study periods (Figure C.33b). *(a) Similar distribution in 1960 and 2010.*

Table C.33: Numerical summary of *S. dorsalis* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	13	1.86 (± 4.91)	1
2010	23	3.71 (± 9.39)	2



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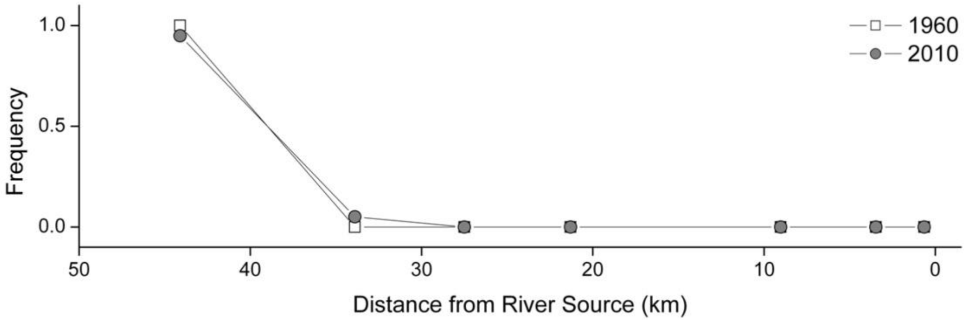


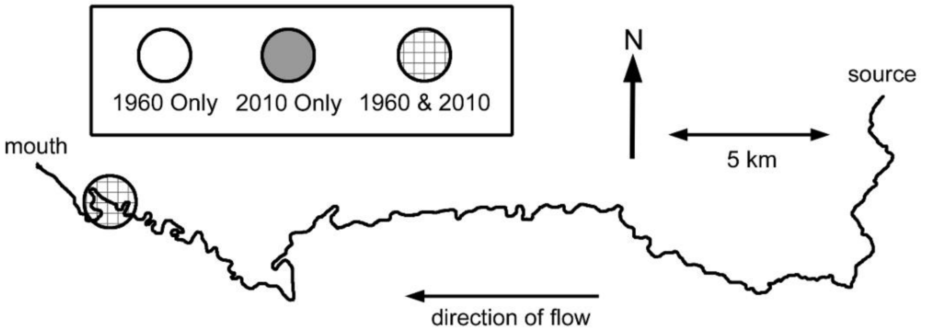
(b)

Figure C.33: Distribution of *S. dorsalis* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *S. dorsalis* in each study period.

Sigara falleni was relatively common in both 1960 and 2010 (Table C.34). *S. dorsalis* is found exclusively in the lower reaches of the River Endrick (Figure C.34a). Site occupancy and distribution of abundance appear similar in both study periods (Figure C.34b). Absolute abundance has increased significantly ($\chi^2_c = 42.284$, $p < 0.0001$) between 1960 and 2010 (Table C.34). *(a) Similar distribution in 1960 and 2010.*

Table C.34: Numerical summary of *S. falleni* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	22	3.14 (± 8.32)	1
2010	53	8.71 (± 23.06)	1



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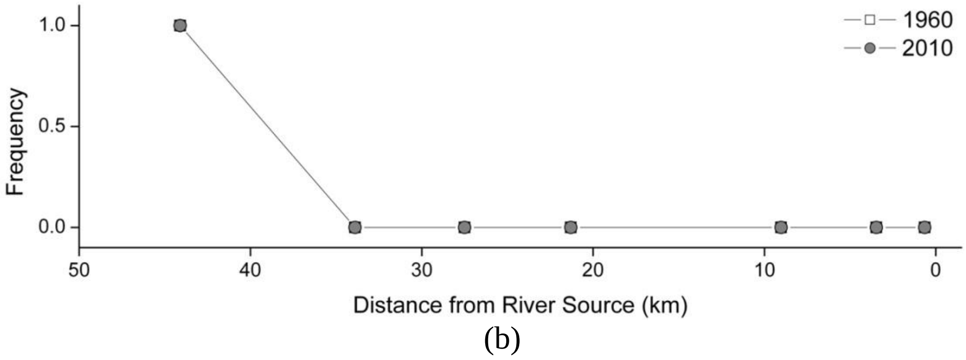


(b)

Figure C.34: Distribution of *S. falleni* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *S. falleni* in each study period.

Sigara fossarum was collected from the lower reaches of the river in both 1960 and 2010 from different sites. In 1960 this species was collected from the site at the mouth of the river. No abundance data were available for *S. fossarum* in 1960, so only spatial distribution is presented for this species. *(a) Similar distribution in both study periods*.

Table C.35: Numerical summary of *S. fossarum* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	na	na	na
2010	4	0.57 (± 1.51)	1

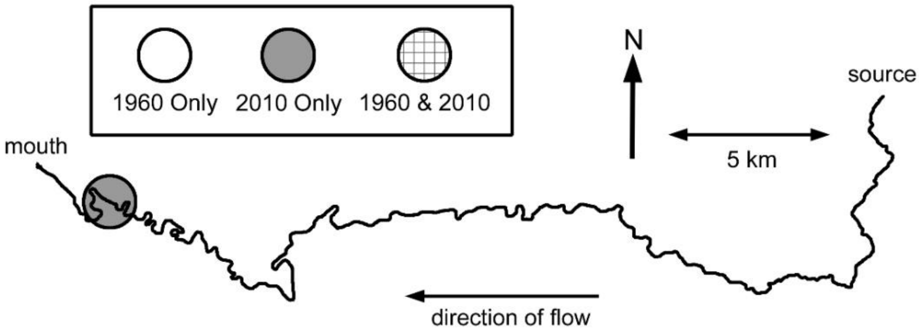


Figure C.35: Spatial distribution of *S. fossarum* in the river Endrick in 1960 and 2010.

C.6 Megaloptera

Sialis fuliginosa was collected sporadically throughout the length of the River Endrick in both study periods (Figure C.36). No abundance data were available for *S. fuliginosa* in 1960, so only spatial distribution is presented for this species. *(a) Similar distribution in both study periods*.

Table C.36: Numerical summary of *S. fuliginosa* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	na	na	1
2010	7	1 (± 1.52)	3

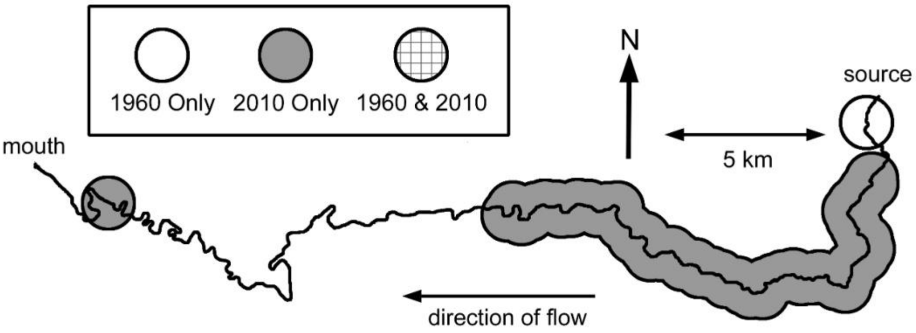


Figure C.36: Spatial distribution of *S. fuliginosa* in the river Endrick in 1960 and 2010.

Sialis lutaria was collected only in the lower reaches of the river in both study periods (Figure C.37). No abundance data were available for *S. lutaira* in 1960, so only spatial distribution is presented for this species. *(a) Similar distribution in both study periods*.

Table C.37: Numerical summary of *S. lutaira* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	na	na	1
2010	9	1.3 (± 4.03)	1

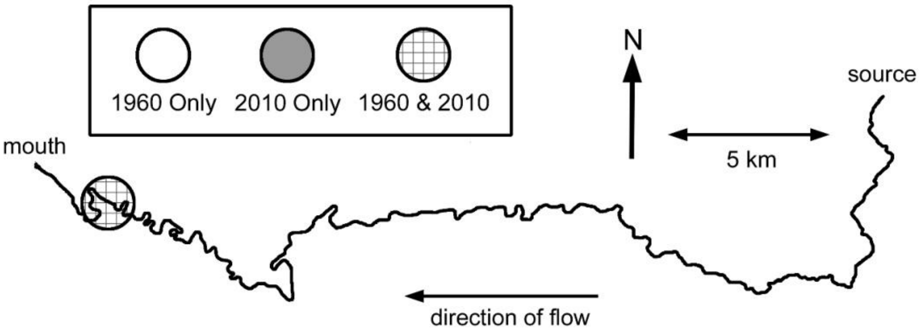


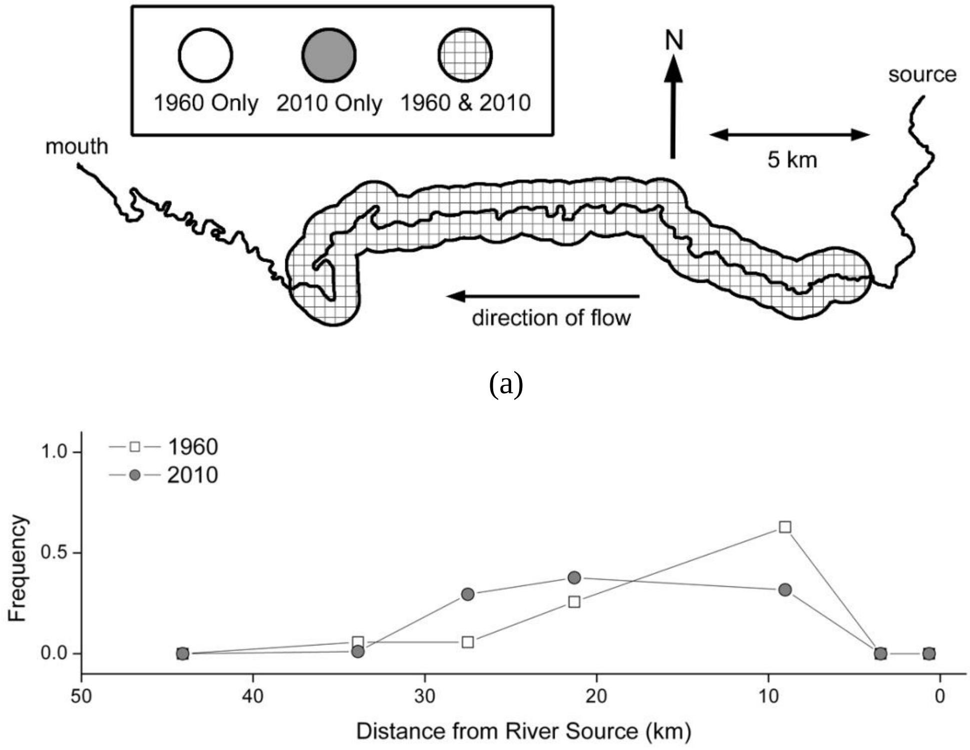
Figure C.37: Spatial distribution of *S. lutaira* in the river Endrick in 1960 and 2010.

C.7 Trichoptera

Hydropsyche pelluidula was common in both study periods (Table C.38). Site occupancy and distribution of abundance appear similar in both study periods (Figure C.38). Absolute abundance has remained similar (χ^2_c = 3.875, p = 0.050) between 1960 and 2010 (Table C.38). *(a) Similar distribution in both study periods*.

Table C.38: Numerical summary of *H. pelluidula* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	46	5.00 (± 8.14)	4
2010	62	8.71 (± 10.67)	4



(a)

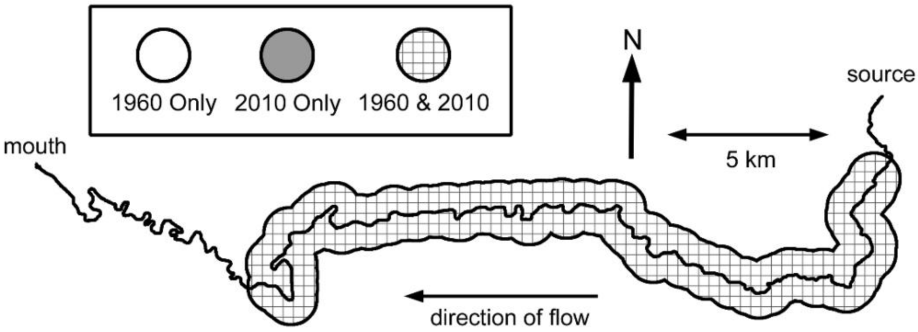
(b)

Figure C.38: Distribution of *H. pelluidula* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *H. pelluidula* in each study period.

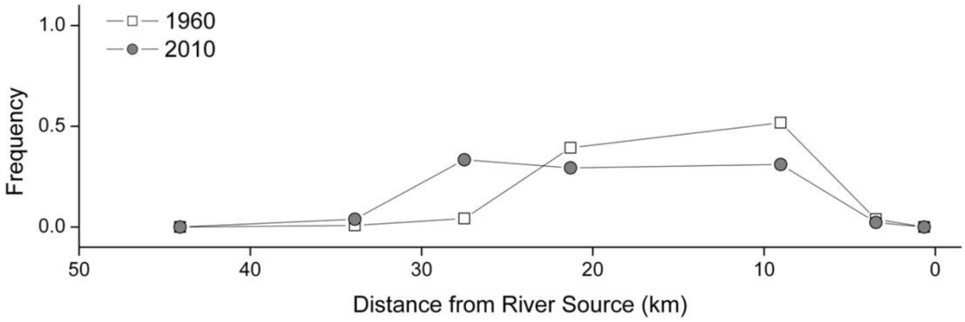
Hydropsyche siltalai was highly abundant in both study periods (Table C.39). Site occupancy and distribution of abundance appear similar in both study periods (Figure C.39). Absolute abundance has increased significantly ($\chi^2_c = 136.220$, $p < 0.0001$) between 1960 and 2010 (Table C.39). *(a) Similar distribution in both study periods*.

Table C.39: Numerical summary of *H. siltalai* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	1550	175.57 (± 266.81)	5
2010	2010	282.43 (± 316.16)	5



(a)



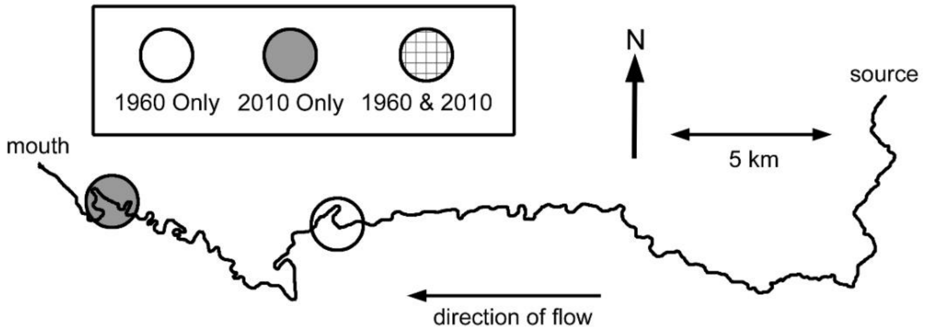
(b)

Figure C.39: Distribution of *H. siltalai* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *H. siltalai* in each study period.

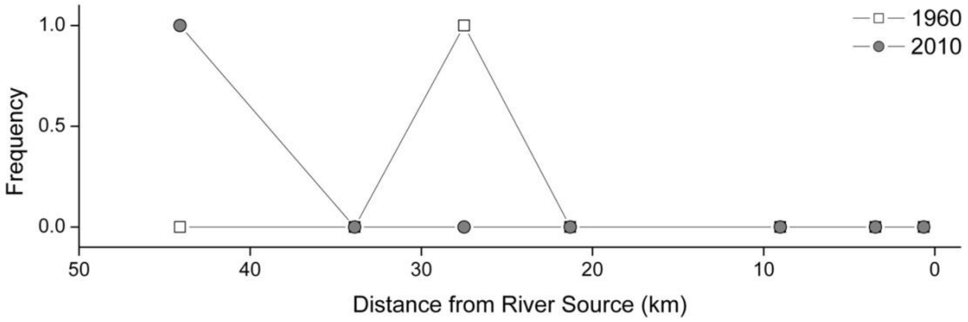
Lype phaeopa occurred sporadically in the River Endrick in both 1960 and 2010 (Figure C.40, Table C.40). *(a) Similar distribution in 1960 and 2010.*

Table C.40: Numerical summary of *L. phaeopa* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	1	0.14 (± 0.38)	1
2010	5	1.00 (± 2.65)	1



(a)



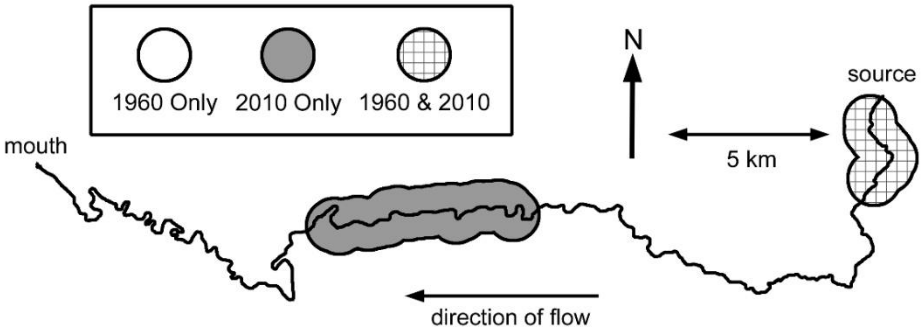
(b)

Figure C.40: Distribution of *L. phaeopa* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *L. phaeopa* in each study period.

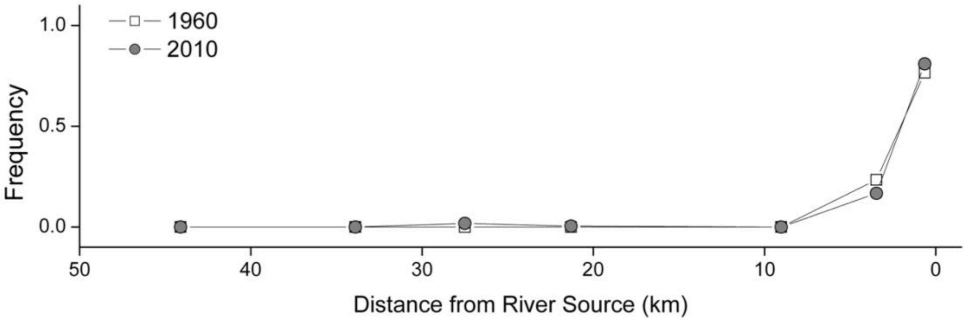
Plectrocnemia conspersa detected in 2010 in small numbers (1 and 3 individuals collected) at two additional sites downstream of the distribution detailed from the 1960 study (Figure C.41). The detection of this species in 2010 outwith the historic range in 1960 was not significant (Fisher's exact test; $p = 0.558$). Absolute abundance has increased significantly ($\chi^2_c = 750.948$, $p = 0.0020$) between 1960 and 2010 (Table C.41). *(a) Similar distribution in both study periods*.

Table C.41: Numerical summary of *P. conspersa* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	53	6.71 (± 13.55)	2
2010	235	31.28 (± 65.66)	4



(a)



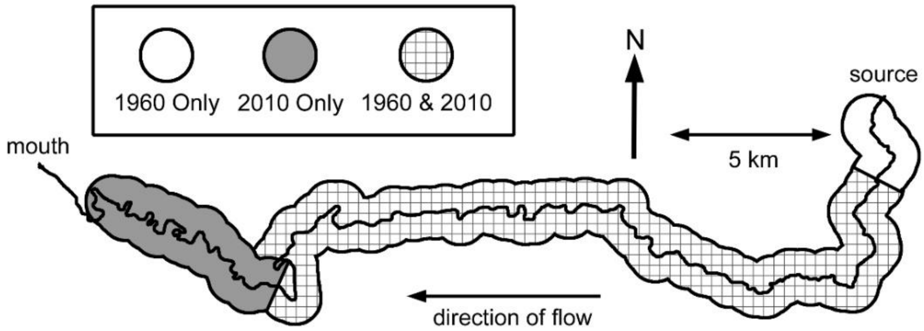
(b)

Figure C.41: Distribution of *P. conspersa* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *P. conspersa* in each study period.

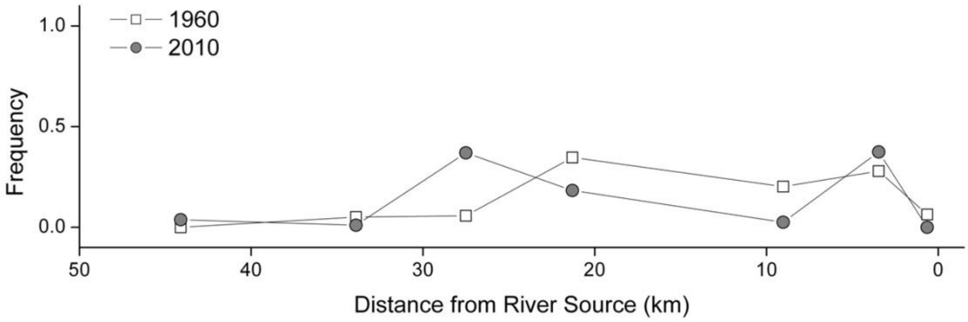
Polycentropus flavomaculatus was highly abundant in both study periods (Table C.42). Site occupancy and distribution of abundance appear similar in both study periods (Figure C.42). Absolute abundance has decreased significantly (χ^2_c = 130.556, $p < 0.0001$) between 1960 and 2010 (Table C.42). *(a) Similar distribution in both study periods*.

Table C.42: Numerical summary of *P. flavomaculatus* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	777	89.71 (± 83.52)	6
2010	458	64.14 (± 75.43)	6



(a)



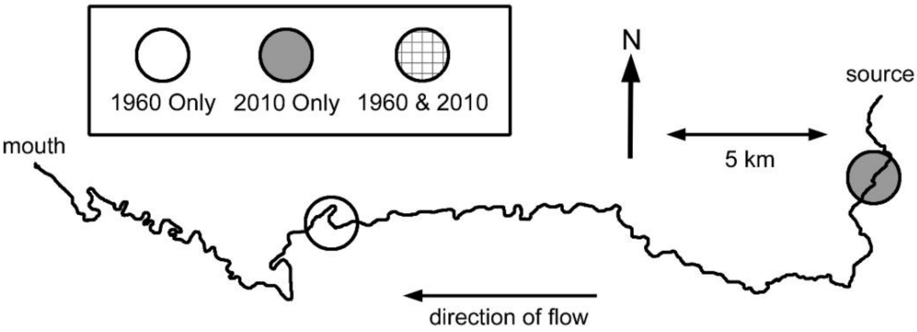
(b)

Figure C.42: Distribution of *P. flavomaculatus* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *P. flavomaculatus* in each study period.

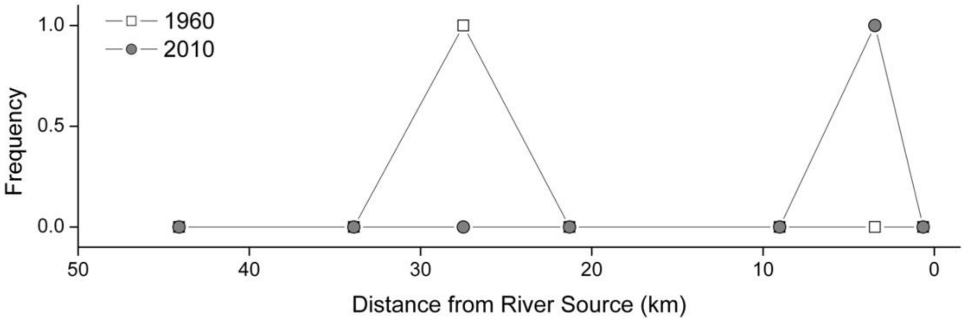
Polycentropus irroratus was recorded only once in each study period at two different sites (Table C.43; Figure C.43). *(a) Similar distribution in both study periods*.

Table C.43: Numerical summary of *P. irroratus* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	1	0.14 (± 0.38)	1
2010	1	0.14 (± 0.38)	1



(a)



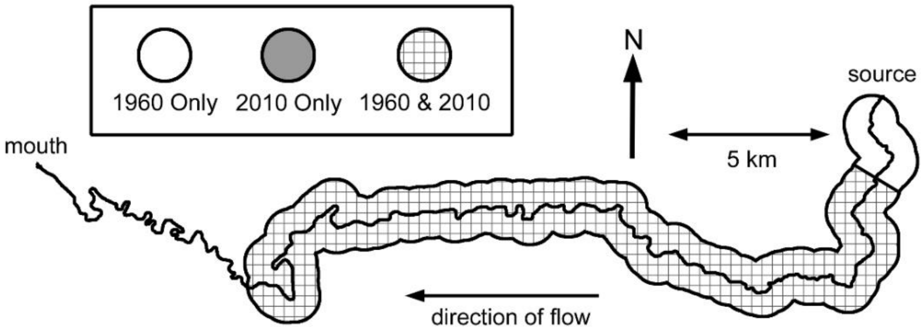
(b)

Figure C.43: Distribution of *P. irroratus* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *P. irroratus* in each study period.

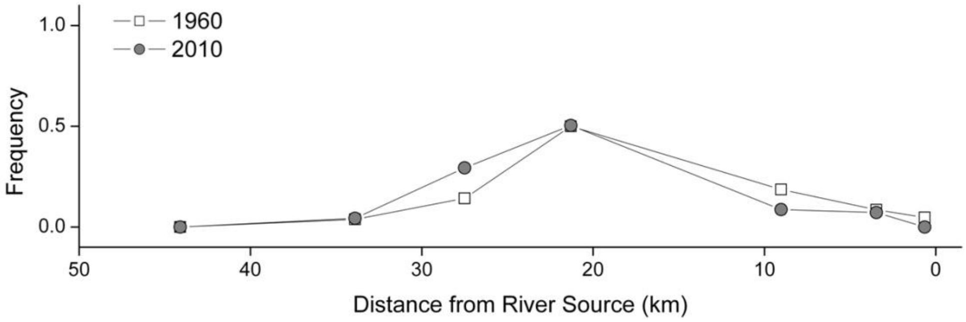
Rhyacophila dorsalis was abundant in both study periods (Table C.44). Site occupancy and distribution of abundance appear similar in both study periods (Figure C.44). Absolute abundance has not changed significantly ($\chi^2_c = 1.636$, $p = 0.201$) between 1960 and 2010 (Table C.44). *(a) Similar distribution in both study periods*.

Table C.44: Numerical summary of *R. dorsalis* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	**Total Number**	**River Mean**	**Number of Sites**
1960	367	48.29 (± 57.42)	6
2010	342	51.57 (± 67.87)	5



(a)



(b)

Figure C.44: Distribution of *R. dorsalis* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *R. dorsalis* in each study period.

C.8 Lepidoptera

Nymphula nymphaeta was collected from the lower reaches of the river in both study periods (Figure C.45). No abundance data were available for *N. nymphaeta* in 1960, so only spatial distribution is presented for this species. *(a) Similar distribution in both study periods*.

Table C.45: Numerical summary of *N. nymphaeta* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	na	na	1
2010	2	0.3 (± 0.91)	1

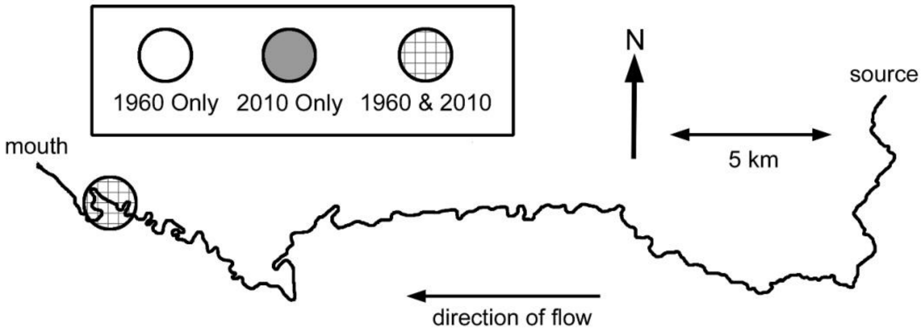


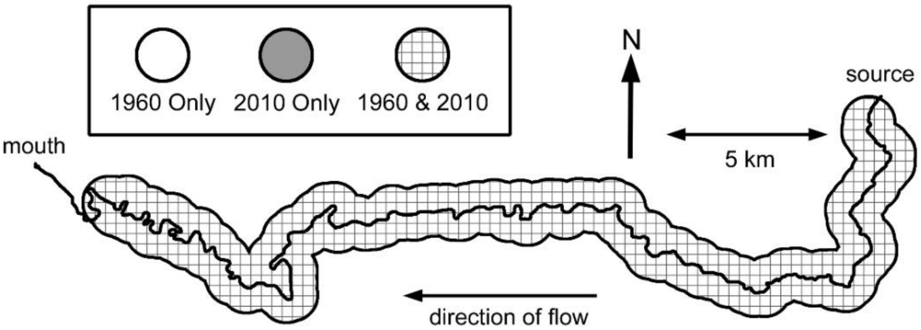
Figure C.45: Spatial distribution of *N. nymphaeta* in the river Endrick in 1960 and 2010.

C.9 Coleoptera

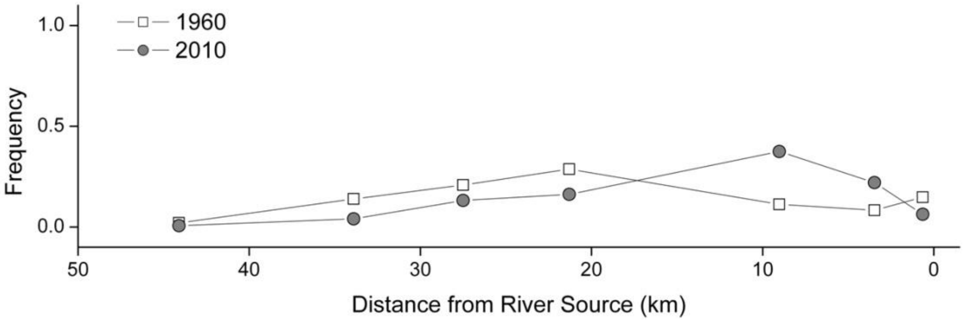
Elmis aenea was common in both study periods (Table C.46). Site occupancy and distribution of abundance appear similar in both study periods (Figure C.46). Absolute abundance has increased significantly ($\chi^2_c = 1.8e^3$ $p < 0.0001$) between 1960 and 2010 (Table C.46). *(a) Similar distribution in both study periods*.

Table C.46: Numerical summary of *E. aenea* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	511	68.57 (± 41.38)	7
2010	1479	169.14 (± 149.55)	7



(a)



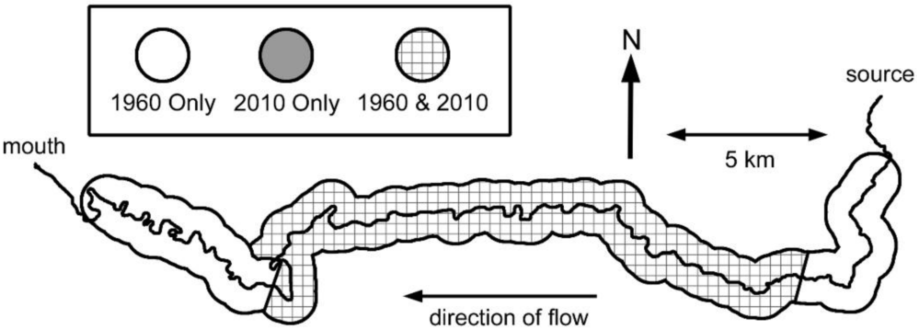
(b)

Figure C.46: Distribution of *E. aenea* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *E. aenea* in each study period.

Esolus parallelopipedus was common in both study periods (Table C.47). Site occupancy and distribution of abundance appear similar in both study periods (Figure C.47). Absolute abundance has decreased significantly ($\chi^2_c = 363.373$, $p < 0.0001$) between 1960 and 2010 (Table C.47). *(a) Similar distribution in both study periods*.

Table C.47: Numerical summary of *E. parallelopipedus* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	561	93.00 (± 122.61)	6
2010	109	15.71 (± 18.77)	4



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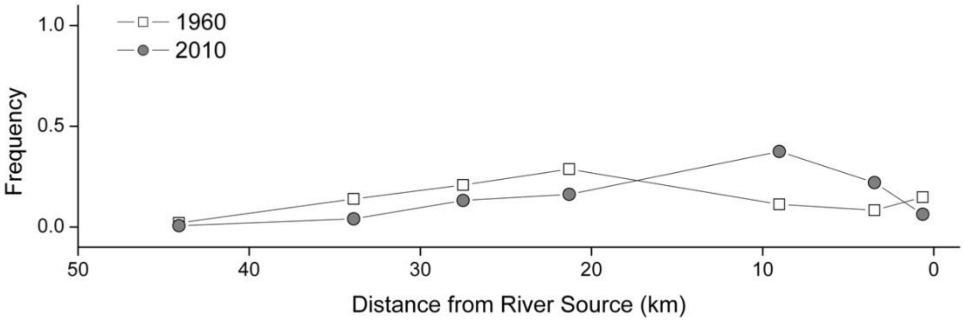


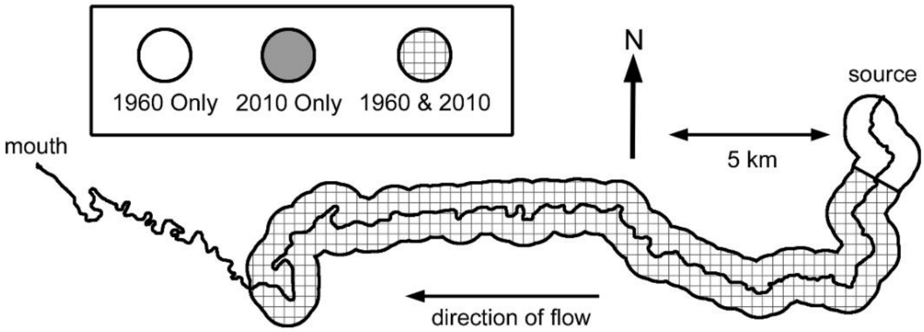
(b)

Figure C.47: Distribution of *E. parallelopipedus* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *E. parallelopipedus* in each study period.

Hydraena gracilis was common in both study periods (Table C.48). Site occupancy and distribution of abundance appear similar in both study periods (Figure C.48). Absolute abundance has increased significantly ($\chi^2_c = 30.003$ $p < 0.0001$) between 1960 and 2010 (Table C.48). *(a) Similar distribution in both study periods*.

Table C.48: Numerical summary of *H. gracilis* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	85	10.14 (± 8.09)	6
2010	136	17.57 (± 16.43)	5



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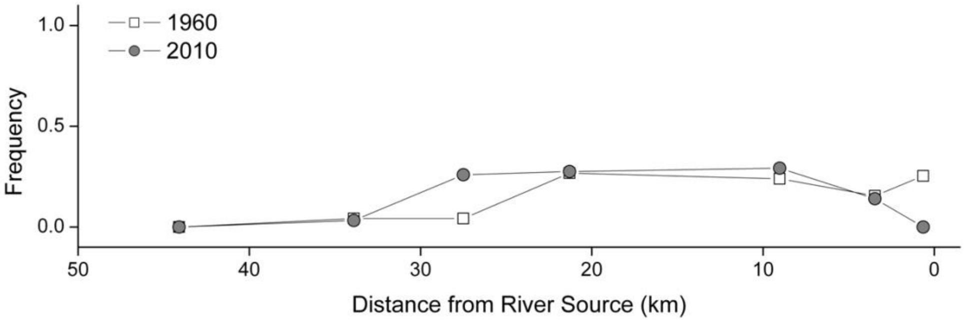


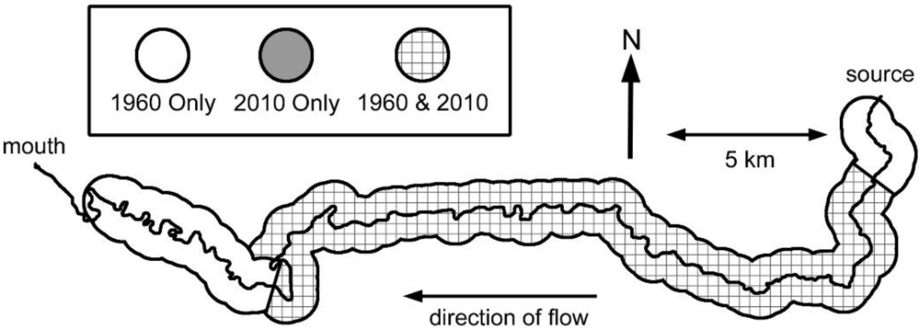
(b)

Figure C.48: Distribution of *H. gracilis* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *H. gracilis* in each study period.

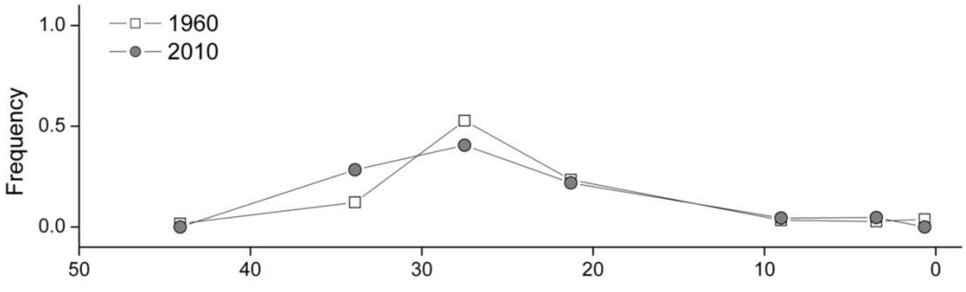
Limnius volkmari was common in both study periods (Table C.49). Site occupancy and distribution of abundance appear similar in both study periods (Figure C.49). Absolute abundance has increased significantly ($\chi^2_c = 1.5e^3$, $p < 0.0001$) between 1960 and 2010 (Table C.49). *(a) Similar distribution in both study periods*.

Table C.49: Numerical summary of *L. volkmari* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	610	105.14 (± 137.32)	7
2010	1572	237.37 (± 266.77)	5



(a)



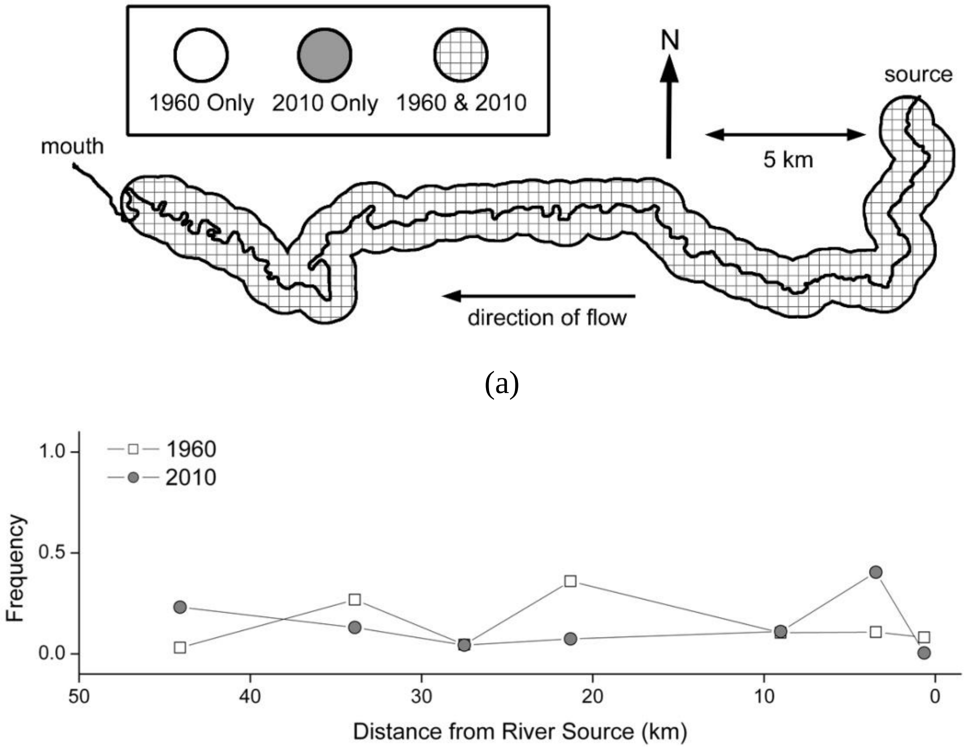
(b)

Figure C.49: Distribution of *L. volkmari* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *L. volkmari* in each study period.

Oulimnius tuberculatus was common in both study periods (Table C.50). Site occupancy and distribution of abundance appear similar in both study periods (Figure C.50). Absolute abundance has increased significantly ($\chi^2_c = 850.142$, $p < 0.0001$) between 1960 and 2010 (Table C.50). *(a) Similar distribution in both study periods*.

Table C.50: Numerical summary of *O. tuberculatus* collected in the 1960 and 2010 study periods; total number collected; river mean corrected for sampling effort (± standard deviation); number of sites at which species collected.

Study Period	Total Number	River Mean	Number of Sites
1960	283	87.29 (± 75.35)	7
2010	744	32.71 (± 31.31)	7



(a)

(b)

Figure C.50: Distribution of *O. tuberculatus* in the river Endrick in 1960 and 2010; (a) spatial distribution (site occupancy); (b) relative frequency of occurrence of *O. tuberculatus* in each study period.

Appendix D Keys used in the identification of macroinvertebrate species from the River Endrick

D.1 Tricladida

Reynoldson, T. B. 1978 A key to British species of Freshwater Triclads. Freshwater Biological Association, Ambleside. pp. 32.

D.2 Hirudinea

Elliot, J. M. & Mann, K. H. 1979 A key to the British Freshwater Leeches. Freshwater Biological Association, Ambleside. pp. 72.

D.3 Malacostraca

Gledhill, T., Sutcliffe, D. W. & Williams, D.W. 1976 Ket to British Freshwater Crustacea: Malacostraca. Freshwater Biological Association, Ambleside. pp. 72.

D.4 Ephemeroptera

Elliot, J. M., Humpesch, U. H. & Macan, T. T. 1988 Larvae of the British Ephemeroptera: A key with ecological notes. Freshwater Biological Association, Ambleside. pp. 145.

Macadam, C & Bennett, C. 2010 A pictorial guide to British Ephemeroptera. FSC Publications, Shrewsbury. pp. 128 + iv.

D.5 Plecoptera

Hynes, H. B. N. 1977 Adults and nymphs of British stoneflies (Plecoptera): A key. Freshwater Biological Association, Ambleside. pp. 92.

D.6 Odonata

Brooks, S. 1999 Field guide to the Dragonflies and Damselflies of Great Britain and Ireland. British Wildlife Publishing, Dorset. pp. 160.

D.7 Hemiptera

Jansson, A. 1996 Heteroptera Nepomorpha, Aquatic Bugs. In: Aquatic insects of North Europe – A Taxonomic Handbook Volume 1 (ed. Nilsson, A.N.) pp. 91-104.

Macan, T. T. 1965 A key to British Water Bugs (Hemiptera-Heteroptera). Freshwater Biological Association, Ambleside. pp. 78.

D.8 Neuroptera

Elliot, J. M. 1996 British Freshwater Megaloptera and Neuroptera: A key with ecological notes. Freshwater Biological Association, Ambleside. pp. 69.

D.9 Trichoptera

Eddington, J. M. & Hildrew, A. G. 1995 A revised Key to the Caseless Caddis Larvae of the British Isles, with Notes on their Ecology. Freshwater Biological Association, Ambleside. 134 pp.

Hickin, N. E. 1967 Caddis Larvae. Larvae of the British Trichoptera. Hutchinson & Co. Ltd., London. 476 + xi pp.

Wallace, I. D., Wallace, B & Philipson, G. N. 2003 Keys to the case-bearing caddis larvae of Britain and Ireland. Freshwater Biological Association, Ambleside. 259 pp.

D.10 Lepidoptera

Agassiz, D. J. L. 1996 Lepidoptera Pyralidae, (China Mark) Moths. In: Aquatic insects of North Europe – A Taxonomic Handbook Volume 1 (ed. Nilsson, A.N.) pp. 257-263.

D.11 Coleoptera

Friday, L. E. 1988 A key to the adults of British water beetles. *Field Studies* **7**:1-151

Hansen, M. 1996 Coleoptera Hydrophiloidae and Hydraenidae, Water Scavenger Beetles. In: Aquatic insects of North Europe – A Taxonomic Handbook Volume 1 (ed. Nilsson, A.N.) pp. 173-194.

Holland, D. G. 1972 A key to the larvae, pupae and adults of the British species of Elminthidae. Freshwater Biological Association, Ambleside. 58 pp.

Klausnitzer, B. 1996 Coleoptera Scirtidae, March Beetles. In: Aquatic insects of North Europe – A Taxonomic Handbook Volume 1 (ed. Nilsson, A.N.) pp. 203-208.

Nilsson, A. N. 1996 Coleoptera Chrysomelidae Donaciinae, Water Lilly Beetles. In: Aquatic insects of North Europe – A Taxonomic Handbook Volume 1 (ed. Nilsson, A.N.) pp. 209-216.

Nilsson, A. N. 1996 Coleoptera Dytiscidae, Diving Water Beetles. In: Aquatic insects of North Europe – A Taxonomic Handbook Volume 1 (ed. Nilsson, A.N.) pp. 145-172.

Nilsson, A. N. 1996 Coleoptera Dryopoidae, Riffle Beetles. In: Aquatic insects of North Europe – A Taxonomic Handbook Volume 1 (ed. Nilsson, A.N.) pp. 195-202.

Nilsson, A. N. 1996 Coleoptera Gyrinidae, Whirligig Beetles. In: Aquatic insects of North Europe – A Taxonomic Handbook Volume 1 (ed. Nilsson, A.N.) pp. 123-129.

Nilsson, A.N. 1996 Coleoptera Haliplidae, Crawling Water Beetles. In: Aquatic insects of North Europe – A Taxonomic Handbook Volume 1 (ed. Nilsson, A.N.) pp. 131-138.

Nilsson, A. N. 1996 Coleoptera Dytiscidae, Diving Water Beetles. In: Aquatic insects of North Europe – A Taxonomic Handbook Volume 1 (ed. Nilsson, A.N.) pp. 145-172.

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Anderson, H., Futter, M., Oliver, I., Redshaw, J. & Harper, A. 2010 Ternds in Scottish river water quality. Scottish Environment Protection Agency, East Kilbride, UK, pp 178

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