Metapopulation ecology of *Notonecta* in small ponds

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Abstract.

This thesis considers the application of metapopulation theory to a field system; two species of *Notonecta* (Hemiptera: Heteroptera, Notonectidae), a freshwater invertebrate predator, inhabiting a series of small man-made ponds known as dewponds, in the Peak District, Derbyshire.

Surveys of pond occupancy and habitat characteristics examined the habitat preferences and spatial population dynamics of the two species, and associations between *Notonecta* and other taxa. Interspecific competition and predation between nymphs were investigated in the laboratory and in field mesocosms to determine their potential influence on field distributions.

The two species have contrasting habitat preferences, and breed in a subset of all ponds in the area. Choice of oviposition substrate appears to be an important mechanism of habitat selection. The landscape scale population dynamics of *Notonecta* resemble those predicted by metapopulation models, but regional persistence is determined by the availability and distribution of suitable habitat across the landscape, rather than by a dynamic balance of stochastic colonisation and extinction. Where the species co-occur, competition is likely and the outcome is influenced by the amount of submerged vegetation present, which affects the feeding efficiency of the two species. Associations between *Notonecta* and other taxa largely appear to result from covariance in response to habitat factors; the distributions of *Notonecta* and potential prey do not seem to be strongly linked.

Most metapopulation models assume that habitat is static, but in common with many other field systems, metapopulation dynamics of *Notonecta* appear to be driven by dynamic changes in habitat of individual patches. This suggests that in order to be of greater practical value, future developments in metapopulation theory must incorporate effects of habitat dynamics on regional persistence and distribution.

Acknowledgements.

I would like to thank Phil Warren for his patient, supportive and always constructive supervision throughout the course of this work. Many thanks are also due to my wife, Kerrera, who tolerated the intrusion of research into 'normal' life, provided constant support and encouragement, and even came out to the dewponds in the snow. I am grateful to my parents, who actively encouraged my exploration of all things wet and wonderful. Anita Weatherby, John Brewington and Matt Spencer are thanked for providing a stimulating atmosphere in which to work and think. Allison Blake helped smooth the path in the lab and John Shutt provided assistance with diverse technical requirements.

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Contents.

1. Introduction.

1.1 General introduction.

All ecological processes are made up of events that are unevenly distributed in space (Weins 1989, Kareiva 1990, McLaughlin and Roughgarden 1993). However it is only in the last decade or so that significant attention has been focused on the importance of space and spatial scaling in the understanding of a wide range of ecological phenomena, from community structure to population persistence (Addicott *et al.* 1987, Giller and Gee 1987, Ricklefs 1987, Weins 1989, Ricklefs and Schluter 1993, May 1994, Tilman and Kareiva 1997). In community ecology, MacArthur and Wilson (1967) and MacArthur (1972) were among the first to focus attention on large scale processes and the importance of spatial scaling in patterns of species richness and diversity. In the field of population dynamics, the pioneering experiments of Huffaker (1958) and theories of Skellam (1951) and Slatkin (1974) amongst others demonstrated the potential importance of spatial environmental heterogeneity in interspecific interactions, but the general importance of spatial effects was not realised until some time later.

Prior to these developments, models of population dynamics and other ecological processes were based solely on local (within-population) processes, such as competition and predation (Kingsland 1985). The development of ecological theory that considers the effects of space, either implicitly or explicitly, has proved a challenge (Kareiva 1994), but significant progress has been made. In complement to this, there has also been considerable development in the understanding of large scale patterns in the distribution and abundance of species (macroecology, Brown 1995) and also processes acting at intermediate scales (mesoscale processes, Holt 1993).

Within the field of population dynamics, spatial theory has developed rapidly, but empirical tests of the emerging theories have lagged behind, due to the difficulties in carrying out experimental or observational work over the spatial (and temporal) scales required by the theory (Kareiva 1990, Steinberg and Kareiva 1997). Particular attention has been paid to the dynamics of populations that are scattered across the landscape, either naturally or as a result of anthropogenic habitat fragmentation. The widespread habitat fragmentation in the majority of ecosystems as a result of the activities of man has led to large numbers of species extinctions (Wilson 1992, Ehrlich 1995, Lawton and May 1995) and to many species existing as isolated populations in habitat fragments. Conservation biologists have therefore focused considerable attention on the conservation of species both rare and common which are found in fragmented habitats and have looked to developments in ecological theory for the best way to manage and conserve these species (Soulé and Simberloff 1986, Soulé 1987, Simberloff 1988, Doak and Mills 1994, Harrison 1994). Several approaches have been taken in investigating the implications for population dynamics of the spatial structuring of the populations across a landscape, such as reaction-diffusion and stepping-stone models (Kareiva 1990). However the most popular modelling framework for such populations has been that embodied by the concept of a metapopulation (Hanski and Gilpin 1991, Hastings and Harrison 1994, Hanski and Simberloff 1997, Hanski 1998). This thesis considers the application of metapopulation theory to the spatial population dynamics of insect species in small freshwater ponds at the landscape scale.

1.2 Metapopulations and metapopulation theory.

A metapopulation can be defined simply as a system of 'local populations which interact via individuals moving among populations' (Hanski and Gilpin 1991), and which show periodic local extinction and recolonisation. This definition highlights fundamental properties of metapopulations. Local populations must be present in discrete patches of habitat and hence 'islands' of suitable habitat must be able to be distinguished from the surrounding matrix of non-habitat. There must also be some degree of population turnover; local extinction of populations may occur, but regional persistence is achieved by complementary colonisation of unoccupied patches of habitat via dispersal.

Patch models.

The initial stimulus for the development of metapopulation theory was the model presented by Levins (1969, 1970), initially to explore strategies of pest control and group selection. Levins also introduced the term 'metapopulation' to describe the abstraction of the population to a higher level, where individual populations across a landscape are born and die in much the same way as individuals within a single population (Hanski and Simberloff 1997). The central parameter of the model is p, the proportion of suitable habitat that is occupied. This kind of model subsequently became known as a patch or occupancy model (Hanski and Gilpin 1991), which only considers whether a patch of habitat is occupied or not; no attention is paid to population dynamics within the patch. The change in the proportion of patches which are occupied, in a landscape of infinite patches, was described by the following equation

$$\frac{\mathrm{d}p}{\mathrm{d}t} = mp(1-p) - ep \tag{1.1}$$

where m and e are the rates of local population colonisation and extinction respectively. This equation has a single stable equilibrium occupancy value of $\hat{p} = 1 - e / m$. This highlights the fact that for a metapopulation to persist (i.e. $\hat{p}$ is positive) the rate of colonisation must be greater or equal to the rate of extinction. Stable equilibrial metapopulation level patch occupancy is an assumption common to all metapopulation models (Harrison and Taylor 1997). Other assumptions that are built into this model are that all patches are discrete and of equal size, isolation and suitability, local population dynamics are asynchronous and migration into presently occupied patches has no effect on local population dynamics (Hanski 1991).

From the original Levins model, there have been many developments and modifications to allow some of the assumptions to be relaxed (e.g. Hanski 1982, 1991). These have been intended to make the model more applicable to real population systems, which tend to deviate considerably from the structure envisaged by this model (Harrison 1991, 1994, Harrison and Taylor 1997). Most of these refinements have concentrated on incorporating a finite and explicit number of patches in the metapopulation, and their locations and sizes. This focus draws on empirical evidence that the probability of patch colonisation decreases with increasing isolation from sources of colonists, and that the likelihood of extinction declines with increasing patch (and by assumption population) size (Williamson 1981, Schoener and Spiller 1987, Hanski 1994b and references therein).

Incidence functions.

Hanski (1991, 1992, 1994a,b, 1997a,b, 1998, Hanski, Moilanen, Pakkala and Kuussaari 1996) has developed an alternative approach to the Levins model of metapopulation dynamics based on incidence functions (Diamond 1975), which originally described the change in the likelihood of species occurrence with changes in patch or island area (see also section 3.3). The incidence function models include patch-specific area and isolation measures, and are particularly attractive for use in real population systems, as they can be fitted using snap-shot patterns of occupancy that can be obtained from single surveys. From this it is possible to estimate other important parameters, such as rates of colonisation and extinction. They can also be easily modified to take account of other factors, such as the 'rescue effect' (Brown and Kodric-Brown 1977) which describes the reduction of local population extinction probability through immigration from surrounding occupied patches. Their practical value has been extensively demonstrated through the studies of endangered butterfly species in Finland by Hanski and his colleagues (e.g. Hanski, Moilanen, Pakkala and Kuussaari 1996) as well as other insect species (Eber and Brandl 1996) and plants (Quintana-Ascencio and Menges 1996).

Structured models.

Structured metapopulation models (e.g. Hastings 1991, Gyllenberg and Hanski 1992, Gyllenberg, Hanski and Hastings 1997) improve realism by explicitly incorporating local population dynamics within individual populations of the metapopulation, as opposed to the binary occupancy variable of the patch models. These models allow for migration between populations to influence the local population dynamics. Although they come to broadly similar conclusions to patch models, they demonstrate the possibility of alternative stable equilibria (Gyllenberg, Hanski and Hastings 1997) and have shown that optimal levels of migration may exist which enhance metapopulation persistence (Hanski and Zhang 1993). The chief drawback of these models is the complex mathematics involved and the proliferation of parameters which are hard to estimate in the field (Gyllenberg, Hanski and Hastings 1997).

Metapopulations and species interactions.

Although most metapopulation models consider single species dynamics, theory has also suggested that metapopulation dynamics may have a profound effect on interactions between species in a metapopulation (Nee, May and Hassell 1997). The basic premise of these models is that metapopulation dynamics allow regional persistence of species in the face of an unstable local interaction, whether that interaction be inter-specific competition (Slatkin 1974, Hanski 1983) or predator-prey and host-parasitoid relationships (Hastings 1977, Murdoch 1977, Crowley 1981, Sabelis, Diekmann and Jansen 1991, A.D.Taylor 1990, 1991). Some progress has also been made in extending these models to 'metacommunities' of many interacting metapopulations (Caswell and Cohen 1991, Holt 1993, 1995, 1997). There have been a limited number of studies that have shown evidence for these effects in field or laboratory systems (Hanski and Ranta 1983, Bengtsson 1989, 1991, Kareiva 1987, Holyoak and Lawler 1996, van de Meijden and van der Veen-van Wijk 1997) but the difficulties in studying multi-species metapopulations are even greater than for single species systems and most of the theoretical ideas remain to be tested convincingly in natural systems.

1.3 Dewponds.

The application of metapopulation models to field systems requires the clear and unambiguous delineation of habitat from non-habitat (Harrison, Murphy and Ehrlich 1988, Hanski 1997b, see above and also Chapter 3). In contrast to many other systems, the boundaries of habitat patches are clearly defined for most inhabitants of isolated freshwaters such as ponds, although some species such as amphibians and beetles spend part of their lifecycle away from the water. The analogy between isolated freshwaters such as ponds and oceanic islands has been repeatedly drawn (Keddy 1976, Barnes 1983, Probert 1989). Ponds are found scattered across the landscape, and therefore make ideal test systems for the study of population dynamics at the landscape scale. This thesis is based on studies carried out on a particular type of pond, known as dewponds.

Form and function.

Dewponds are small, shallow, man-made pools created to provide drinking water for livestock. They are found in areas with calcareous bedrock, which have little natural standing water due to the porous nature of the underlying rocks. The traditional construction method involved creating a saucer shaped depression in the earth which was then lined with layers of straw, sometimes with an additional layer of lime to prevent earthworms burrowing through the liner, followed by a layer of impermeable puddled clay, which gave the pond its water retaining abilities (Pugsley 1939). This top layer of clay was then protected from damage by the hooves of livestock by a layer of flint or limestone blocks or 'pitchers' (Hayfield and Brough 1987). There have been many variations on this basic construction scheme in attempts to improve the longevity and effectiveness of the ponds, and there is a certain mystique surrounding the art of successful dewpond siting and construction; in some cases methods have been passed down through several generations of the same family (Pugsley 1939, Hayfield and Brough 1987). Ponds with this type of construction are claimed to have existed in some areas since the 17th century, but most have more recent origins in the 19th and early 20th century (Hanney 1953, Darby 1968, Carpenter 1995), although ponds may have existed in the same sites much earlier. A more modern construction method that has become common in some areas is to create the impermeable liner from concrete, a practice that continued until the 1930s when construction generally declined or ceased (Darby 1968). The concrete ponds commonly have concentric ridges running intermittently around the liner to give a safe footing to livestock coming to drink from the ponds.

The name given to the ponds implies that they are dependent on dew and condensation for their water supply. This is far from true, as has been demonstrated exhaustively by the studies of Martin (1915, 1930) and Pugsley (1939). In fact, the majority of the water contained in these ponds is derived from rainfall, either directly, or indirectly via runoff from the surrounding pastureland. The collection of rainwater is facilitated by the siting of the ponds, which are often found in areas which naturally collect water due to their relief, and also through the design of the ponds. In many cases the ponds are not full to the top of the liner and hence the remainder of the impermeable liner above the level of water acts as an effective collecting surface for channelling water into the pond basin. Some of the more recently constructed concrete ponds adjacent to roads have channels built into their liners which extend towards the road to collect runoff.

Habitat, flora and fauna.

The physico-chemical environment of the dewponds is fairly consistent with most ponds being circum-neutral or slightly alkaline (Macan and Macfayden 1941, Warren *et al.* in press); this may be due to the geology of the land or in the case of the concrete ponds, their method of construction. The ponds often have a high conductivity as a consequence of fouling by livestock using the pond.

The extent and diversity of vegetation in the dewponds is variable, possibly due to isolation from sources of propagules and disturbance by cattle which can easily wade through ponds owing to their generally shallow depth and small size. However in some ponds the vegetation is well developed, and a considerable diversity of plants, both aquatic and terrestrial, have been recorded from dewpond sites (Chicken 1996). *Lemna minor* L., the common duckweed, is commonly found in dewponds (Macan and Macfayden 1941, Chicken 1996, Warren *et al.* in press) and often covers the entire surface of very eutrophic ponds, shading other plants. Submerged pondweeds, such as *Potamogeton*, *Ranunculus*, and *Elodea* are also found in more established ponds (Chicken 1996, Anderson and Shimwell 1981, Warren *et al.* in press). In a survey of ponds in the Peak District, Warren *et al.* (in press) found that concrete ponds tended to have less diverse vegetation compared to clay lined ponds, possible due to the poor rooting substrate provided by the liner.

Ponds that are neglected rapidly silt up and a successional sequence of terrestrial vegetation encroaches into the pond (Chicken 1996), often forming floating mats over the remaining water. Clay lined ponds are particularly vulnerable to this process as the plants can grow easily over the liner and subsequently down into the water. Concrete ponds seem less prone such encroachment; the liner above the water level may act as an effective barrier to colonisation by terrestrial grasses and other plants. A more detailed description of the ponds on which this study is based is given in section 2.6.

The dewpond fauna has not been particularly well studied although some general observations have been published by Gillespie (1932) and Hanney (1953) on ponds in Wiltshire and the Chiltern Hills respectively, but only a few studies have provided any detailed information on dewpond faunas. The hemipteran fauna of a series of fifty dewponds in Wiltshire and Sussex was studied by Macan and Macfayden (1941). They found a moderately diverse community in the ponds, including three species of *Notonecta*, and noted some habitat associations of the corixid fauna. Beebee (1977, 1997) has carried out surveys of ponds on the South Downs with regard to the diversity of amphibians. Because of the lack of other standing water, dewponds appear particularly important for newt species, including the great-crested newt, *Triturus cristatus* L and this, along with other newt species, also occurs regularly in dewponds in the Peak District (Peak National Park Authority, unpublished records). Warren *et al.* (in press) surveyed forty dewponds in the Peak District and found moderately diverse plant and invertebrate communities, with between 1 and 6 plant species and 8-27 invertebrate taxa per pond. They found that the method of construction (clay or concrete) had effects on the composition of the invertebrate communities, with groups such as Coleoptera and Diptera being more diverse in clay ponds and Hemiptera and Mollusca more diverse in concrete ponds.

Dewponds in the Peak District.

The Peak District is an upland area which forms the southern part of the uplands known as the Pennines in Northern England. It was the first of the British National Parks to be designated (December 1950) (Edwards 1962). The Peak District can be separated into two distinct regions, based on geology. The Dark Peak is an area of rugged acidic moorlands, with millstone grit as the predominant underlying rock type. The White Peak is an area of carboniferous limestone, which has been eroded by rivers, forming numerous dales separated by rounded hills. In the Peak District, dewponds are found only on the limestone White Peak, and despite their relatively recent vintage they have been regarded as 'historic features' (Berger 1979). Indeed the Peak Park Joint Planning Board makes provision for their conservation as a landscape feature within the structure plan for the Peak National Park (Peak Park Joint Planning Board 1994). In this area they are still reasonably numerous in comparison to other areas of calcareous upland, such as the South Downs (Beebee 1977, 1997), and many are still used for their traditional purpose. The survey by Warren *et al.* (in press) found that the ponds with concrete construction were more numerous than the more traditional clay-lined ponds, and this observation has been confirmed by the survey work undertaken during this study. Some landowners actively maintain the ponds for use by stock, even to the extent of piping or transporting water to them in times of drought. There are very few larger waterbodies in the area, but ponds are generally close together, with the nearest neighbour being typically no more than a kilometre away. The present studies are based on surveys of dewponds across an area of 380km^2 of the White Peak (see figures 1.1 and 1.2 and Appendix 1).

Rates of loss.

In the Peak District, despite the active use of many of the ponds, a large number have been lost in the past century, either neglected or removed and replaced by modern cattle troughs. This situation appears to be common to all districts containing dewponds, and is part of a more general decline in ponds and small water bodies of all types in Britain (Rackham 1986, Heath and Whitehead 1992, Boothby, Hull, Jeffreys and Small 1995). Across the country, agricultural intensification and the increasing availability of piped water to fill modern cattle troughs meant the dewponds declined in use. Following the decline in construction and maintenance of the dewponds in the 1930s (Darby 1968), there appears to have been little active conservation or upkeep of the ponds until relatively recently (Carpenter 1995). Limited protection or restoration (Peak Park Joint Planning Board 1994, Carpenter 1995) has failed to slow the decline in pond numbers.

It has been estimated that the life of a dewpond is approximately 100 years (Darby 1968, 1975), and the older clay construction ponds appear particularly susceptible to the silting and gradual succession characteristic of dewponds that are not actively managed (Chicken 1996).

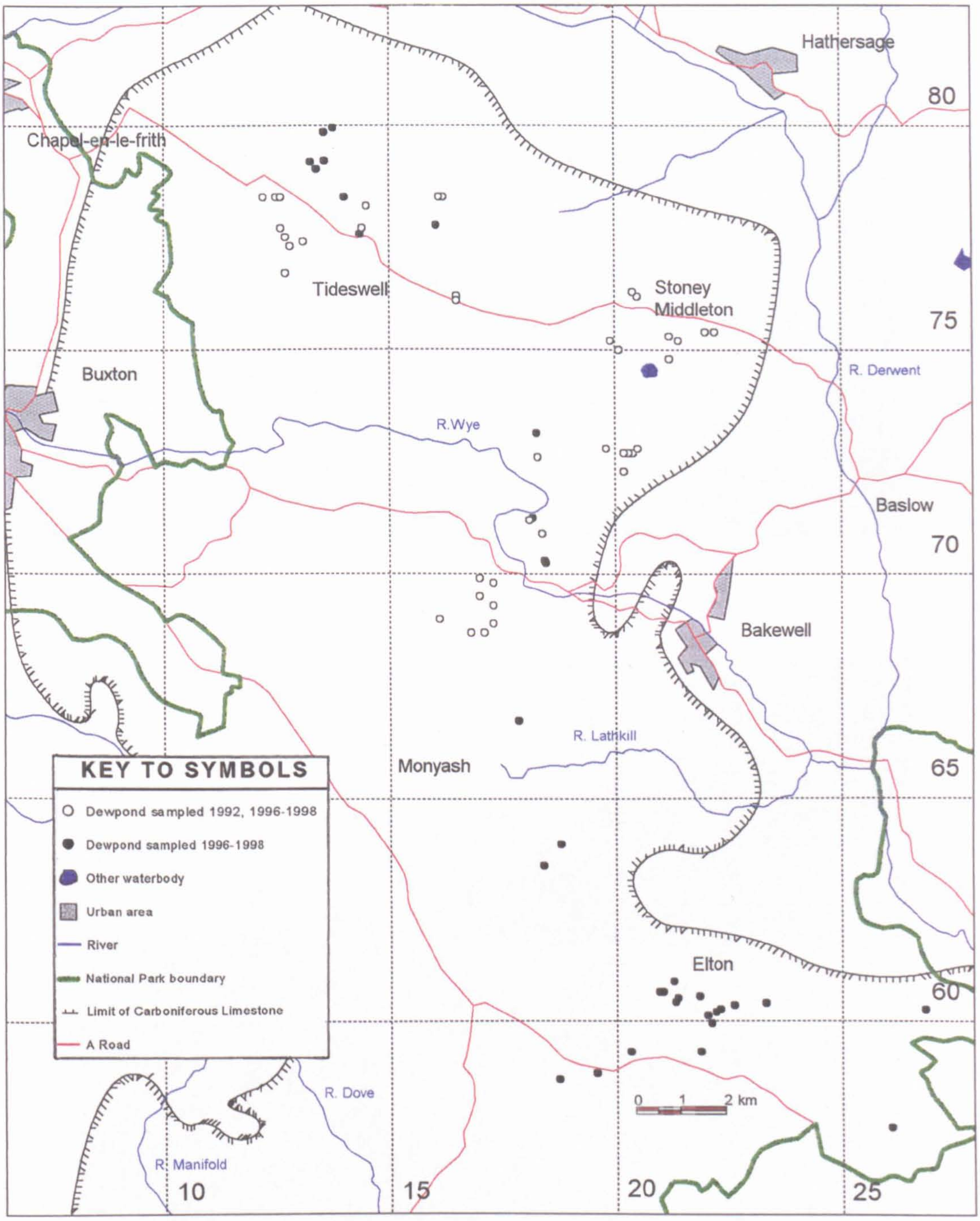

Figure 1.1 Map of the study area of the Peak District, showing the locations of the dewponds sampled during field surveys 1992-1998. The size of the grid squares is 5km^2. Figures along the edge of the map give National Grid References, grid square SK.

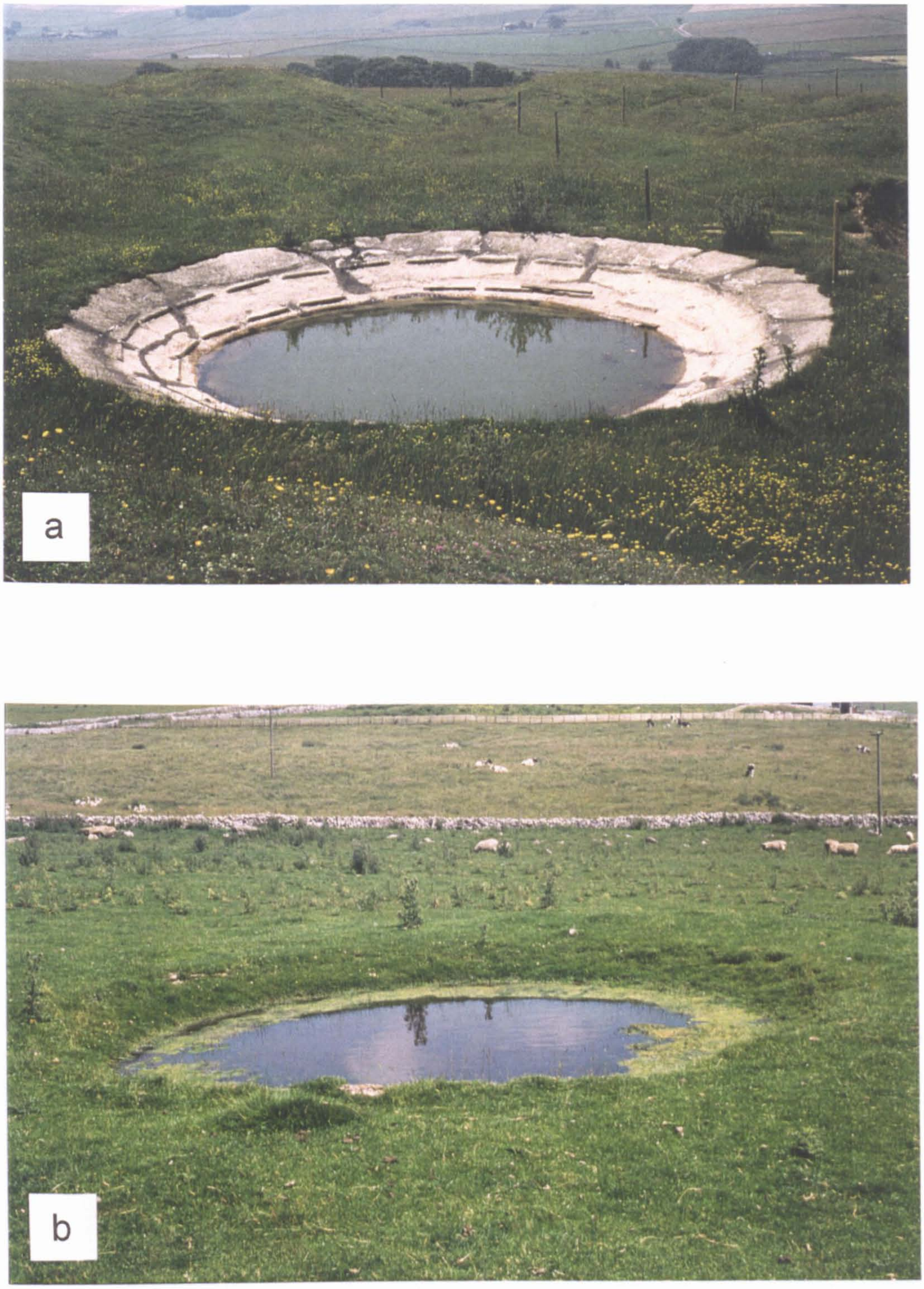

Figure 1.2 Examples of Peak District dewponds, a) typical concrete lined pond, b) typical clay lined pond, note grass growing down edges of liner, c) clay lined pond with extensive submerged vegetation (*Potamogeton* spp.), d) neglected dewpond, showing mats of terrestrial vegetation which have developed as the pond silted up.

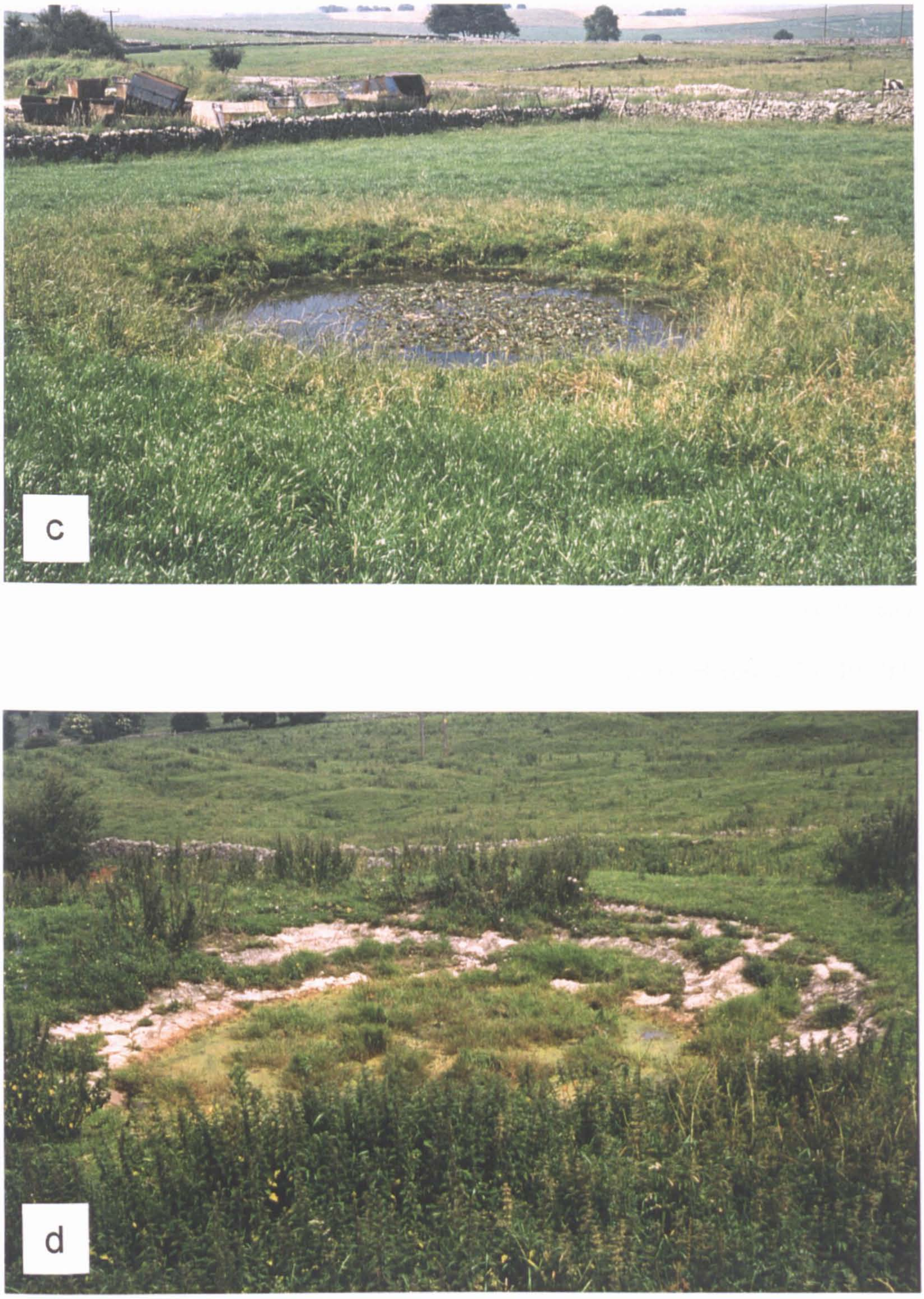

Figure 1.2 Continued.

The drought conditions of recent summers have probably increased the rate of dewpond loss. Despite their fabled water retaining abilities (Martin 1915, 1930, Pugsley 1939) immortalised in Kipling's poem, *Sussex* (1903), many of the ponds in the Peak District and other areas have dried out completely at least once in the last five years. Once dried out, the exposed pond liners, particularly in the clay lined ponds, are vulnerable to cracking, which is difficult to reverse. Concrete lined ponds are affected in a similar way by the action of frost, and many of the liners show signs of repair from cracking, with varying success.

Rates of loss are difficult to estimate, given the general lack of recording and mapping of dewpond locations. However the data that are available for recent periods all show high rates of loss occurring. Figure 1.3 shows a comparison of rates of loss for the South Downs (Beebee 1977, 1997), the Yorkshire Wolds (Chicken 1996) and the White Peak (Peak National Park Authority, unpublished survey). It can be seen that the density of ponds varies widely; the largest area surveyed, 150 km^2 of the South Downs (Beebee 1977, 1997) has the lowest density of ponds, whereas the density of ponds in the area of the White Peak surveyed (30km^2) was very high during the 1970s, and despite the considerable losses is still of comparable density to other areas such as the Yorkshire Wolds, but the rate of loss appears to be higher than for other areas.

1.4 Biology of *Notonecta.*

Many species of pond organisms are capable of actively dispersing between sites, particularly highly mobile orders such as the Hemiptera and Coleoptera (Brown 1951, Popham 1951, 1952, 1953, 1964, Fernando 1958, 1959, Nürnberger 1996, Briers 1997), and hence may exhibit metapopulation characteristics. This thesis focuses on two species of *Notonecta* (Hemiptera: Heteroptera, Notonectidae), *Notonecta maculata* Fabricius and *N. obliqua* Gallen which are common components of the dewpond fauna in the Peak District.

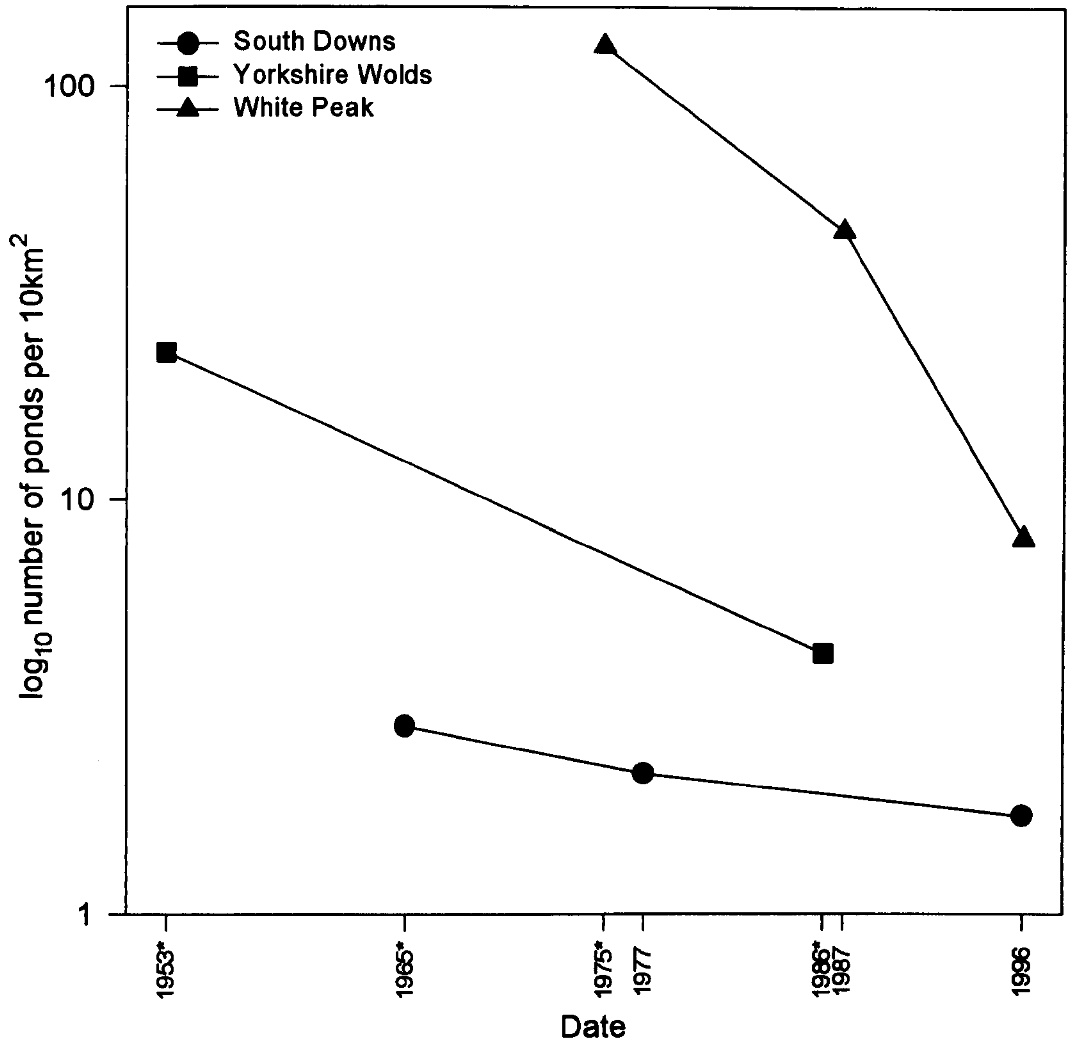

Figure 1.3 Rates of dewpond loss in different areas. * = figures based on map survey without field verification of pond presence. Sources: South Downs, area of survey approximately 150 km^2, data derived from Beebee (1977, 1997), Yorkshire Wolds, area of survey 30 km^2, data derived from Chicken (1996), White Peak area of the Peak National Park, area of survey 16 km^2, data derived from unpublished survey work by the Peak National Park Authority and personal survey work.

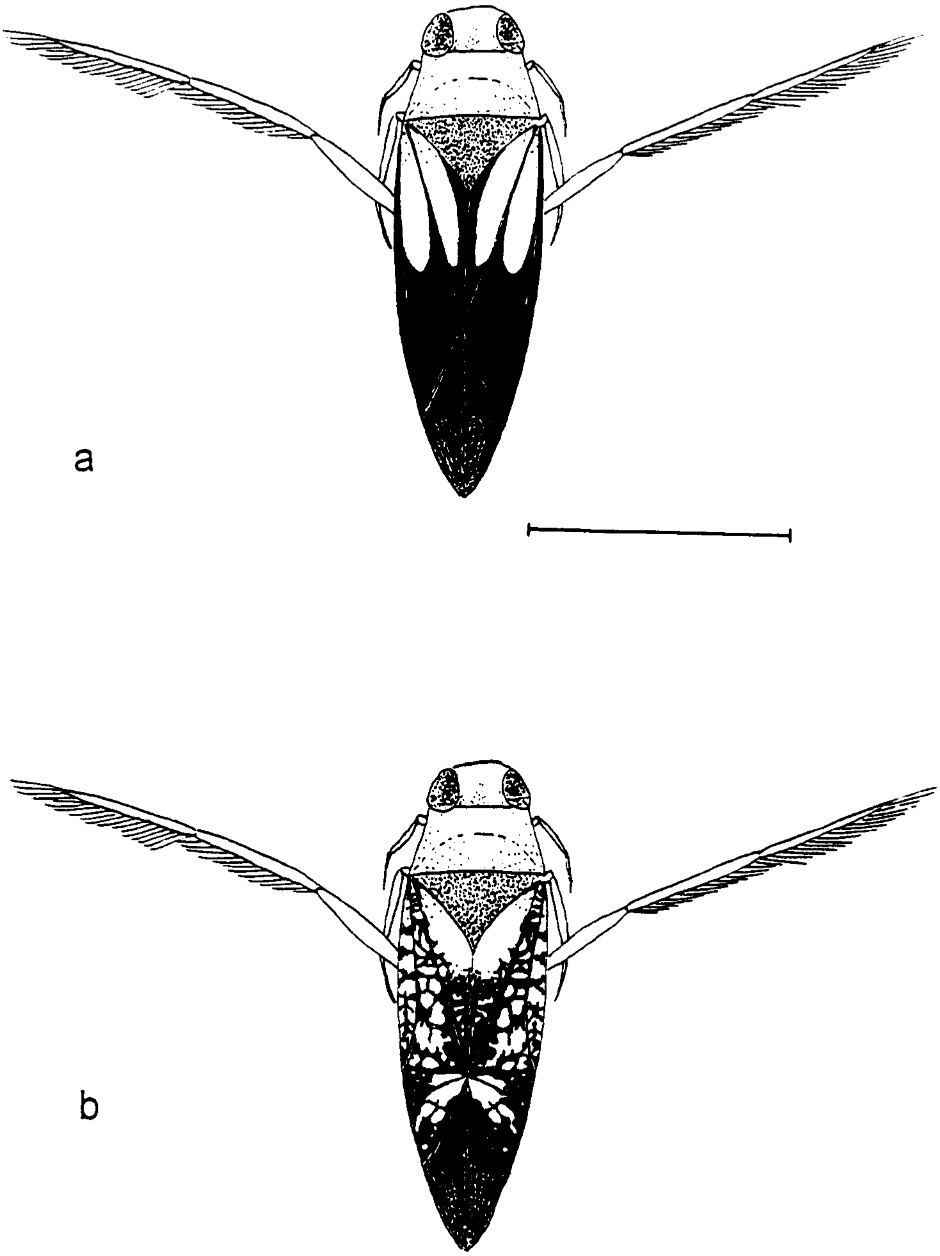

Figure 1.4 Dorsal view of adult *Notonecta*, a) *Notonecta obliqua*, b) *N. maculata*, showing hemielytral patterns used in identification. Scale bar = 10mm.

Distribution and life cycle.

Species in the genus *Notonecta*, are commonly known as back-swimmers or greater water-boatmen. There are 63 species of *Notonecta* and a further 14 subspecies, which are widely distributed around the world, with species found in the majority of landmasses in both hemispheres (Hungerford 1933). *Notonecta* are primarily found in still or slow flowing freshwaters, although one species successfully inhabits brackish water. They are easily distinguished from other aquatic Hemiptera by their habit of swimming on their backs. Only the much smaller Pleidae and Helotrephidae share this habit, and these can be distinguished from *Notonecta* by the hemielytra, which are joined apically (Hungerford 1933).

There are four species found in Britain, plus one variety. The following distributional information is summarised from Southwood and Leston (1959) and Savage (1989). *N. glauca* L. is the most widespread species, found in a variety of habitats throughout the country, mainly in lowland areas. *N. obliqua* (and its variety *delcourti*) tends to replace *N. glauca* in higher and more northern regions, and is generally less abundant. *N. maculata* tends to be found in barren or stony habitats, and is primarily a southern species, being absent from Scotland and infrequent in northern England. The final species *N. viridis* Delcourt is again largely found in the south of the country, although there is evidence that it may be extending its range further north and inland (Pearce and Walton 1939, P.Kirby, personal communication, R.A.Briers, unpublished records). The chief habitat of this species is brackish pools and other waterbodies in coastal areas.

The lifecycle is wholly aquatic, although the adults are capable of flight. The British species of *Notonecta* have a single generation per annum with five nymphal instars which develop through the summer months. Adults overwinter, and oviposition occurs in the autumn and in the spring, depending on species. The life cycles of *N. maculata* and *N.*

obliqua have been described by Walton (1936) and Southwood and Leston (1959) with additional information from Giller (1979) and are summarised in figure 1.5.

Respiration and locomotion.

Notonecta are air breathers, maintaining an air store under the forewings and on the ventral surface of the body (which due to the peculiar orientation is functionally the dorsal surface), where air is trapped under long hairs extending from either side of the abdominal sternites. The air supply is renewed by visits to the surface, where the posterior tip of the abdomen breaks the surface film and the hairs part, allowing the supply to be replenished. This store is supplemented by the action of the abdominal air bubble as a physical gill. However the physical gill is rather inefficient, particularly at higher temperatures, showing a more rapid decline in efficiency with increasing temperature than that of *Corixa punctata* (Illiger) or *Ilyocoris cimicoides* (L.) (Popham 1964).

Notonectids are active swimmers, using the long flattened metathoracic legs, positioned at the centre of the triangular cross sectioned body, and fringed with long swimming hairs. The bugs move with a jerky rowing action, interspersed with pauses, during which the positive buoyancy created by the air stores causes them to float back towards the surface. The muscle structure and articulation of the front and middle legs are adapted for capture and manipulation of prey organisms (Gittleman 1974, Gorb 1995).

Feeding.

Notonecta are all exclusively predaceous, feeding on both a wide range of aquatic prey and terrestrial prey trapped in the surface film (Hungerford 1933, Walton 1943, Southwood and Leston 1959, Fox 1975a), the latter being facilitated by their orientation. Individual species have been used in investigations of general predator-prey theory (Cook and Cockrell 1978, Fox and Murdoch 1978, Murdoch and Sih 1978, McArdle and Lawton 1979, Giller 1980, Sih 1982, 1984, Chesson 1989, Streams 1994) and also as potential biological control

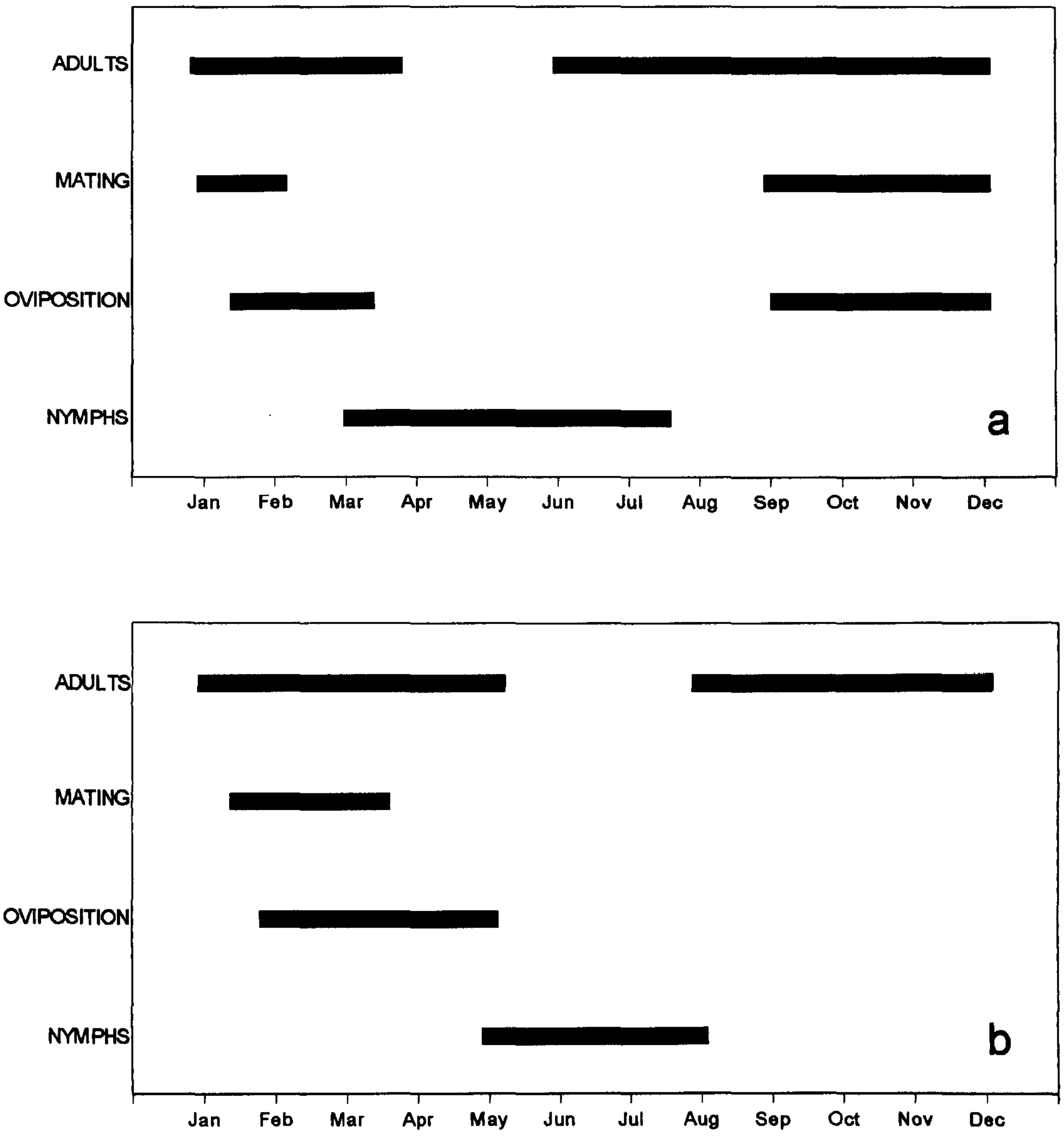

Figure 1.5 Life cycles of a) *N. maculata*, b) *N. obliqua*. Information derived from Walton (1936), Southwood and Leston (1959), Giller (1979) and personal observations.

agents for mosquito larvae (Ellis and Borden 1970, Toth and Chew 1972). However the majority of this work has been laboratory based, with one or a small number of prey species, and less is known about the diet of *Notonecta* in the field. This is largely due to the method of feeding, which in common with the majority of hemipterans, involves piercing their prey with stylet mouthparts and extracting the body fluids, making visual analysis of gut contents impossible. Giller (1982, 1986) addressed this problem by using electrophoresis as a method of determining the qualitative composition of the diet of insects in the field. Despite the well-cited polyphagous nature of notonectid predation, it was found that although a wide range of prey items may be taken, the bulk of the diet consisted of one or two prey types only (Giller 1986). The results of laboratory investigations into selective predation by *Notonecta* also suggest that relative attack rates for different prey are inflexible, i.e. its predatory behaviour is stereotyped (Scott and Murdoch 1983, Murdoch, Scott and Ebsworth 1984) and hence the natural diet may be more restricted than previously imagined.

Dispersal.

Adult *Notonecta* are strong fliers, capable of dispersing and colonising new habitats easily. Studies of the colonisation of new freshwater habitats have found that *Notonecta* may be among the first species to arrive at new sites (Macan 1939, Fernando 1959, Barnes 1983). The Notonectidae show some polymorphism in the development of wing muscles (Young 1961) along with other aquatic hemipteran groups such as Corixidae (Young 1965) and Gerridae (Brinkhurst 1959, Fairbairn and Deslanreau 1987) and hence there is potential for dispersal ability to vary between species. It has been shown for the Corixidae that there is a relationship between the dispersal ability and the type of habitat occupied in terms of stability and permanence, with species found in temporary waterbodies having a greater tendency to fly (Macan 1939, Brown 1951, Popham 1951, Fernando 1958, 1959). There is also some limited indirect evidence for similar variation in species of *Notonecta* (Streams and Newfield 1972, Streams 1987b).

Dispersal of Hemiptera, including *Notonecta*, tends to occur on warm, calm days (Fernando 1959, Popham 1964) suggesting a strongly seasonal pattern, with dispersal occurring in spring for the overwintered adults and in summer to autumn during favourable weather for the new generation of adults. Throughout the period of nymph development, dispersal is negligible as most of the overwintered adults will have died. Hemipterans appear to react to the development of thermal gradients in the water, choosing to occupy the warmest water in advance of dispersal (Fernando 1959, Popham 1964), presumably warming their flight muscles in preparation for flight. *Notonecta* take to the air directly from the surface of the water, individuals inverting themselves and drying their wings before attempting flight, unlike corixids which often crawl out of the water before dispersing (Popham 1964). There is a threshold temperature which must be reached before flight can be successfully initiated. Popham (1964) states that *N. glauca* failed to fly until water temperatures exceeded 18°C. *N. obliqua* and *N. viridis* apparently have similar flight threshold temperatures, but *N. maculata* requires a higher temperature (approximately 20°C) before it will fly (Southwood and Leston 1959). The wingstroke in Heteroptera, including *Notonecta*, is highly automated, and the associated musculature relatively simple compared to other pterygotes, and hence flight is not particularly versatile (Betts 1986a).

Once in flight, dispersing notonectids locate bodies of water using visual cues (Walton 1935). In common with many other bugs and beetles inhabiting water or a moist substrate, they detect water by the polarisation pattern of light reflected by the water surface (Schwind 1991, Horvath 1995). Light polarised in the horizontal plane causes *Notonecta* to exhibit the 'plunge reaction' (Schwind 1984) where the wings are rapidly folded back onto the abdomen and the bug drops into the water. Walton (1935) describes how individuals of *N. maculata* were seen to gain height having located a waterbody, before dropping into the water, purportedly to increase the chances of successfully breaking through the surface film. Unlike other Heteroptera, the wings of *Notonecta* are not folded flat over the abdomen, but instead fit closely along the sides of the abdomen, aided by an additional line of flexion in the region of the clavus (Betts 1986b), maintaining a streamlined shape suited to rapid locomotion under the water.

1.5 Overview of this study.

The aim of this thesis was to determine the extent to which the patterns in regional population dynamics of *Notonecta* in Peak District dewponds conform to the assumptions of standard metapopulation models, by examining the relative roles of within population (local) and between population (landscape or mesoscale) processes in influencing occupancy and distribution of *Notonecta* over a regional area.

The following chapter provides an overview of the methods used throughout this work and also gives some supplementary information on the biology of the species and the study system. Habitat preferences of the two species are explored in Chapter 3, in an attempt to determine the extent to which habitat influences pond occupancy, and define 'suitable habitat' for the species at the landscape scale. Chapter 4 focuses on the spatial population dynamics of *Notonecta* in relation to the proposition that they persist over a regional area as a metapopulation, and examines the processes driving the extinction of local populations and colonisation of unoccupied ponds. Competitive interactions between the two species of *Notonecta* are explored in Chapter 5, given the potential impact of competition on field population distributions and regional coexistence in a metapopulation. Chapter 6 provides a broader view of variation in the structure of dewpond communities, with reference to associations between predatory *Notonecta* and the rest of the invertebrate 'metacommunity'. The final chapter summarises the results of these investigations, with respect to the relative role of local and regional processes in influencing landscape distribution patterns of *Notonecta* in the dewponds, and sets them within the broader context of metapopulation theory.

2. General methodology and biological background.

2.1 Introduction.

This chapter provides some background information on the biology of the study species and the dewpond habitat, and describes the general methods and techniques that were used throughout this study.

2.2 Laboratory rearing of *Notonecta*.

Several parts of this study required nymphs and adults of both species of *Notonecta* to be maintained in the laboratory and the following methods were used throughout. Adult *Notonecta*, collected from field sites, were kept separately in groups of between 10 and 20 adults in large aquaria (45x30x30cm) containing approximately 40 litres of water. Strips of plastic mesh (mesh size approximately 4cm) were placed in the tanks to provide perch sites.

The adults were fed a mixture of *Daphnia magna* Straus and a variety of nymphal and adult Corixidae (mainly *Corixa punctata* [Illiger] and *Sigara nigrolineata* [Fieber]), all of which were obtained from field sites. Other food sources such as *Asellus aquaticus* (L.) were used on occasion. All aquaria were maintained under semi-natural lighting conditions at temperatures varying seasonally between 8 and 20°C.

In order to obtain nymphs, adults were collected in early spring each year and brought into the laboratory. The adults were observed intermittently and when they were seen to be mating a variety of suitable oviposition substrates was placed in the tanks (see also section 3.4). At intervals the substrates and attached eggs were removed, the eggs detached gently from the substrates using fine forceps and placed in separate smaller containers under similar conditions to the adults.

When the nymphs hatched, they were transferred using a wide necked pipette into transparent plastic cups containing 200ml of water and a small piece of plastic netting (mesh size approximately 5mm) to provide perch sites. Instar I nymphs were fed with *D. magna* obtained from field sites and laboratory cultures. Food density was kept high to reduce cannibalism which can be a major source of nymph mortality throughout development (Fox 1975a,b, Giller 1979). Subsequent instars were raised individually in the same plastic cups and fed a mixture of *D. magna*, instar I-III *C. punctata* nymphs and small *Sigara* spp. adults (mainly *S. nigrolineata*) depending on their size. When they reached the adult stage they were returned to the large aquaria in groups as detailed above.

2.3 Nymph identification.

Although the adults of *N. maculata* and *N. obliqua* are easily distinguished by the patterns of their hemielytra (Savage 1989), with additional characters provided by the genitalia (Macan 1965, Savage 1989), the nymphs are less easy to separate.

First instar nymphs can be separated on the basis of ventral abdominal colouration (Giller 1979, personal communication) as shown in figure 2.1. In an attempt to develop a key to the nymphal instars, the two species were reared and samples of all instars preserved in 70% alcohol for subsequent examination and description. Rice (1954) and Streams (unpublished key) give a number of key taxonomic characters for separation of nymphs of Michigan and New England *Notonecta* respectively, but none of these proved valid for the British species under consideration. However the two species can be separated in instar V by the extent of colouration of the hind tarsus (see figure 2.2). The dark colouration at the distal end of the hind tarsus extends over one-fifth of the total length in *N. maculata*, usually reaching the end of the anterio-ventral group of stout setae. The colouration extends no more than one-eighth of the total length in *N. obliqua*. This character is consistent in all nymphs of instar V except those on the verge of the adult moult, when the colouration is difficult to distinguish due to the development of the adult legs under the nymphal cuticle.

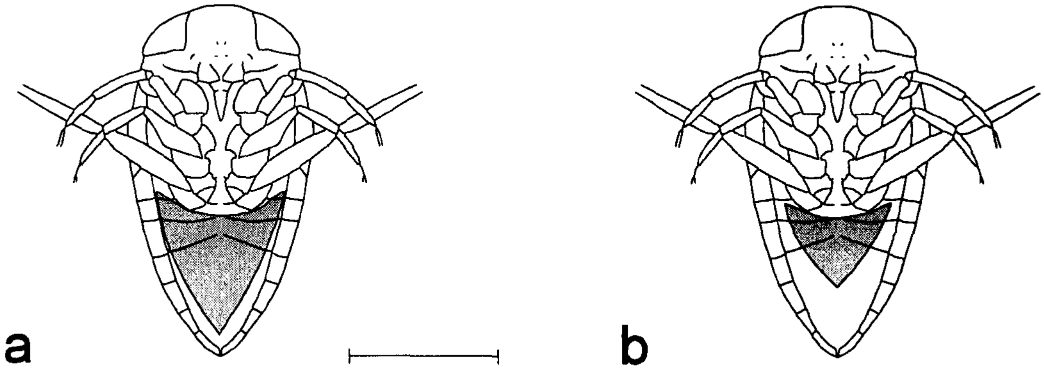

Figure 2.1 First instar *Notonecta* nymphs, showing approximate extent of coloration on ventral surface of the abdomen. a) *N. obliqua*, b) *N. maculata*. After Giller (1979) and personal observations. Scale bar = 1mm

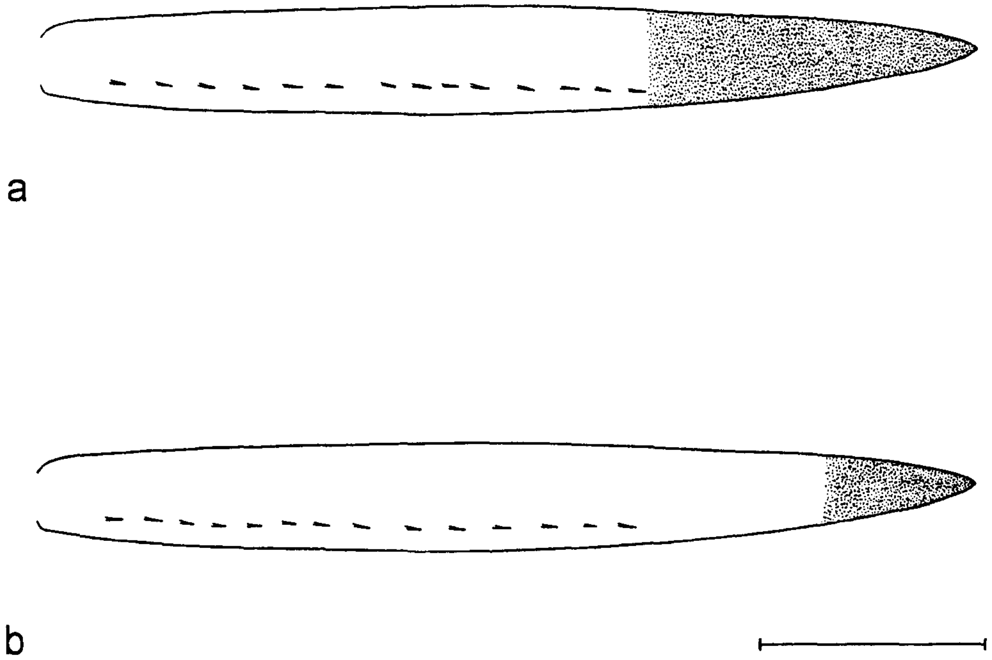

Figure 2.2 Hind tarsi of fifth instar *Notonecta* species, a) *N. maculata* b) *N. obliqua*, indicating extent of dark coloration at distal end of the tarsus. Swimming hairs omitted for clarity. Scale bar = 1mm.

2.4 Age:head width relationships.

The samples of nymphs taken for the purpose of identification were also used to produce age (instar):head width relationships for both species. The instars are generally easy to separate on the basis of size, but size within instar can vary significantly with feeding regime (Toth and Chew 1972, Fox and Murdoch 1978) and hence formalisation of instar sizes was preferable for identification purposes. The nymphs used had been raised on consistent feeding regimes throughout their lives and hence provide a standardisation for the laboratory reared nymphs. Field samples of nymph instars were of similar average size but may show greater size ranges due to natural variation in food availability. Figure 2.3 shows the derived relationships using natural log transformation of head widths. There is a significant difference between the mean head width of the two species in all instars (two-way ANOVA, species term $F_{[1, 193]} = 246, p < 0.001$; Tukey test, $p < 0.05$), with nymphs of *N. obliqua* being larger in all stages.

2.5 Field sampling techniques.

A large part of this study uses data derived from field surveys of dewponds. In order to be able to effectively sample the population of notonectids in a given site, a 10m long x 1m deep seine-type net was constructed. A flexible lead-cored rope provided weight (50g per metre) at the bottom of the net, allowing it to trail along the pond substrate, even when it is uneven. The top of the net is supported at the water surface by a series of square expanded polyethylene floats which prevent organisms from escaping over the top edge of the net. The net itself is constructed of 2mm polyester rot-proof mesh. In use the net was spread out around the edge of the pond with one end attached to a metal peg embedded in the pond bank. The free end was then slowly drawn across the pond and back towards the tethered end, and then gathered in until only a small amount of the net remains in the water. Both edges of the net were drawn in together to form a 'bag' which contained all the captured organisms. This

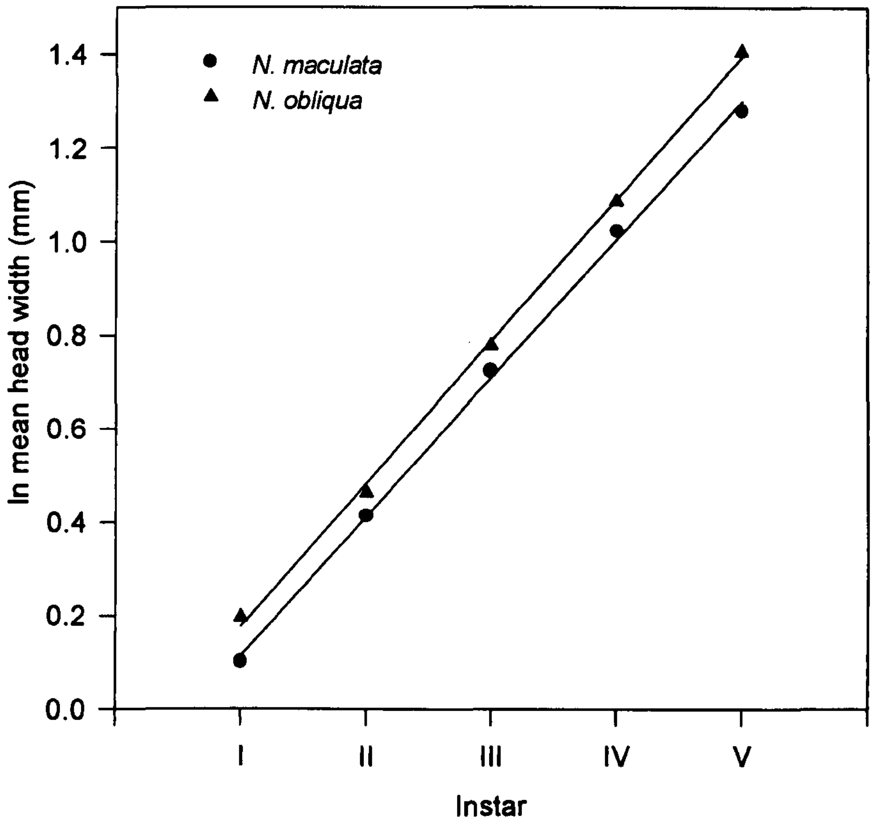

Figure 2.3 The relationship between mean head width (*W*) and instar number (*I*) for *N. maculata* and *N. obliqua*. Head widths were natural log transformed. The standard errors are smaller than the symbols. Regression lines fitted by linear least squares regression, regression equations are; *N. maculata*: $W = -0.183 + 0.297\, I$, $F_{[1, 85]} = 17907$, $p < 0.001$, $R^2 = 0.995$; *N. obliqua*: $W = -0.118 + 0.301\, I$, $F_{[1, 114]} = 10768$, $p < 0.001$, $R^2 = 0.989$.

bag was lifted clear of the water and the contents placed in a holding bucket for subsequent sorting. This method of sampling proved to be highly effective in the majority of the ponds surveyed. However it did not perform as well in ponds with abundant vegetation as the net rode up over the vegetation, allowing organisms to escape under the bottom edge. Therefore a three minute timed pond net sample was used in such environments, with all collected organisms removed to a holding bucket prior to sorting.

The two sampling techniques are not necessarily directly comparable and tests were carried out in order to compare the relative efficiency of the two methods. An individual notonectid, marked on the elytra with a waterproof marker pen, was released into a pond and left for ten minutes before sampling began. The tests were carried out in the largest pond sampled during the study, with little submerged vegetation cover, and hence in smaller ponds with similar habitat the efficiency of the techniques are likely to be higher.

Standardised sampling units were defined for each technique; for the seine-type net this consisted of one sweep of the net through the pond. For the pond net the standard sampling unit was a one minute timed pond net sweep, consisting of four fifteen second sweeps in different areas of the pond taken at equal intervals round the perimeter of the pond. The sweeps were carried out in a zig-zag fashion in concentric arcs from the sampling position, through the middle of the water column. For each technique this standard unit was carried out repeatedly until the notonectid was recovered. This allows the probability of recapture per sampling unit to be calculated (see figure 2.4). From this figure it is clear that the two techniques do not have comparable efficiencies in ponds of this type, with the seine-type net showing a much higher efficiency of recapture. However the use of the pond net is the only viable option in ponds with submerged vegetation cover, but this technique has a generally lower probability of recapture, even in ponds without submerged vegetation. Therefore the

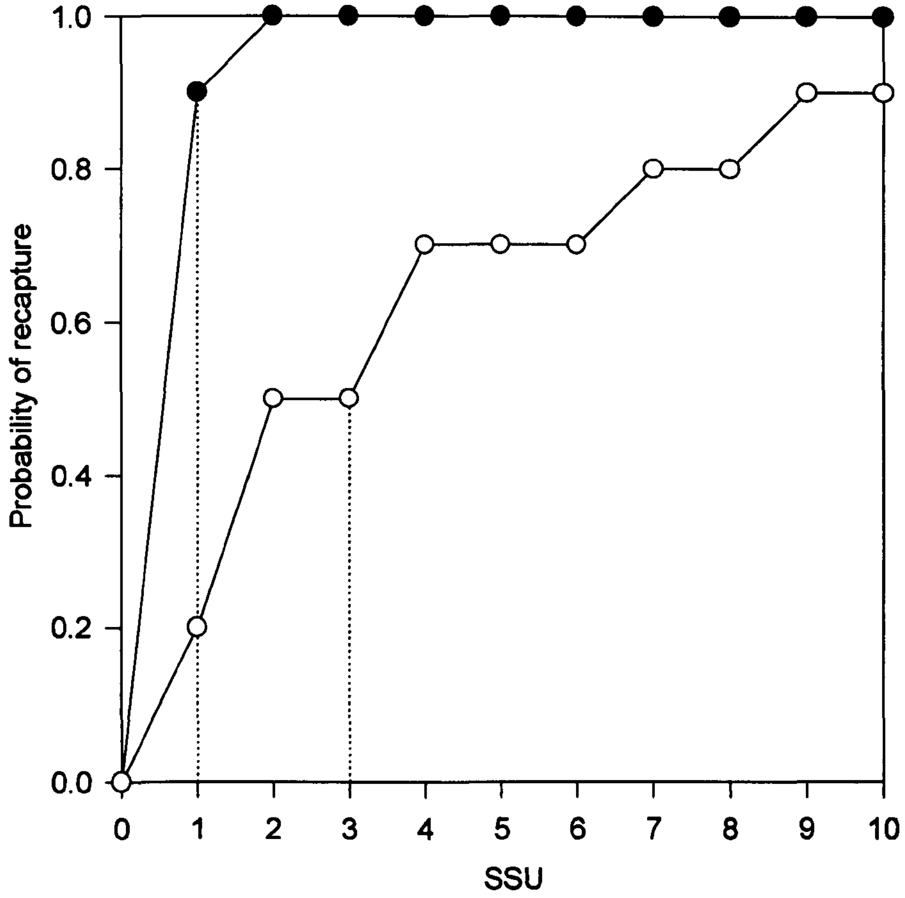

Figure 2.4 The relationship between number of standard sampling units (SSU) and probability of recapture of a single individual *Notonecta* adult from a pond with no submerged vegetation. Solid symbols = seine-type net, open symbols = pond net. See text for definitions of SSU for each sampling technique. Results are based on ten replicate trials for each SSU of each technique. Vertical dotted lines give the probability of recapture for the number of SSU used in field surveys.

differences in the sampling techniques have been taken into account when drawing conclusions from survey data in subsequent sections.

2.6 Habitat survey and dewpond characteristics.

In addition to recording pond occupancy by the species of *Notonecta*, a range of habitat variables were recorded at each site during the pond surveys. Pond basin and wetted width were estimated by pacing, and water, mud and Secchi disc depth measured at the centre of the pond using a graduated pole. Percentage cover of mud and macrophyte species were estimated visually. Conductivity and pH were recorded as the mean of five measurements taken at intervals around the pond using a portable meter. Altitude was estimated from 1:25,000 Ordnance Survey maps.

These data are used in several subsequent sections, but a summary of the habitat variables recorded in each survey year is given in figure 2.5. The box-plots summarise the habitat variables recorded in surveys of 68 dewponds during July and August 1996-1998. The filled symbols offset from the box-plots describe the habitat variables recorded from a subset of 32 of the dewponds where the habitat variables were recorded in 1992, 1996, 1997 and 1998. The data for 1992 was obtained from the survey by Warren *et al.* (in press). Altitude and other variables that did not change over the survey period, such as pond basin width, are not included in the figure. Changes in the variables between survey years are generally consistent, whether they were calculated for all 68 ponds, or the subset of 32. Most of the variables showed no directional trends over the survey period, with the exception of percentage cover of mud which showed a significant increase over the survey period (linear least squares regression, $F_{[1, 124]} = 30.0$, $p < 0.001$, $R^2 = 0.19$, calculated for the subset of 32 ponds).

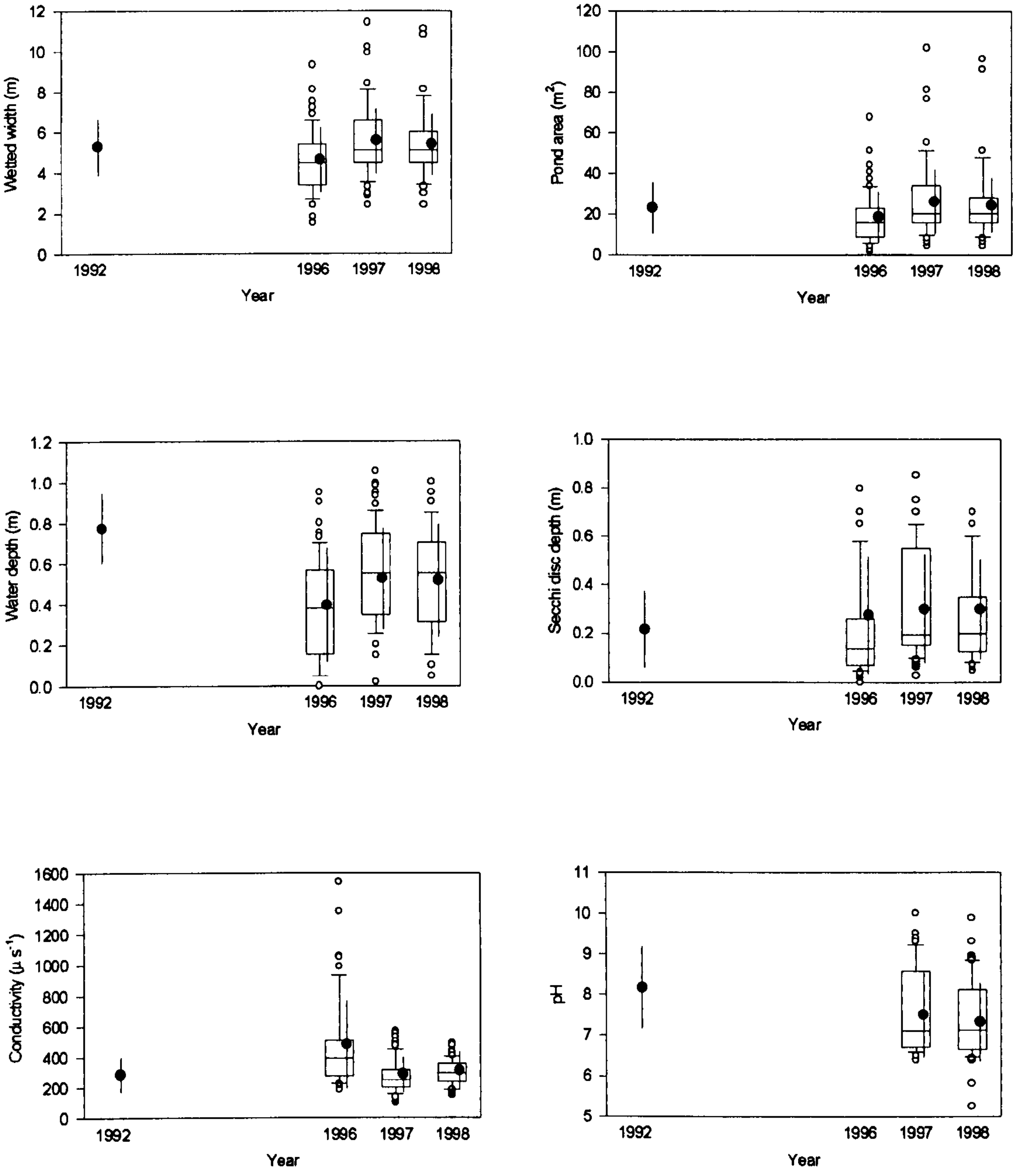

Figure 2.5 Summary of habitat variables recorded from dewponds in different survey years. Boxplots summarise data from 68 ponds. Limits of box are 25th and 75th percentiles, solid line is the median. Whiskers are 10th and 90th percentiles, open symbols = data points outside 10th and 90th percentile limits. Offset filled symbols = mean (+/- standard deviation) of habitat variables in subset of 32 ponds sampled in all years. No data available for pH in 1996.

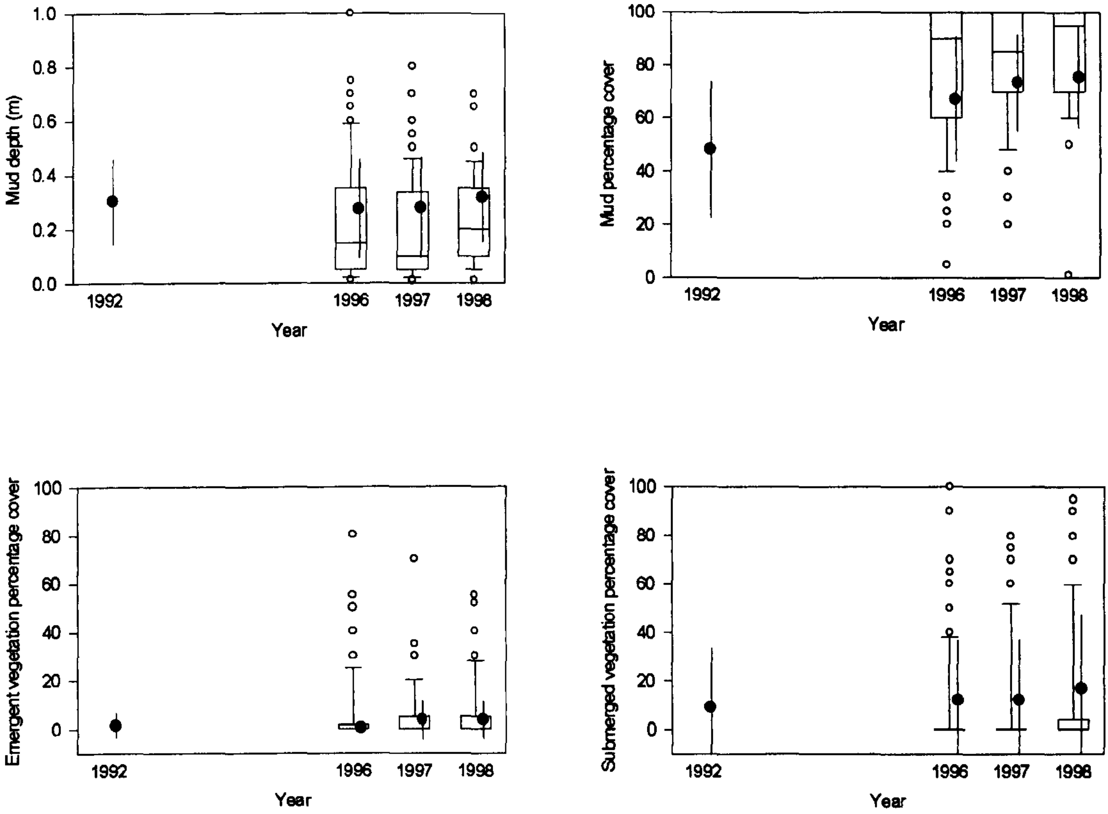

Figure 2.5 Continued.

2.7 Seasonal population dynamics.

Figure 2.6 shows the seasonal changes in the proportions of different instars in the dewponds for 1996. The data are derived from monthly samples of notonectids collected from 18 dewpond sites. At each site efforts were made to collect at least 50 nymphs, and these samples were pooled to give totals of different instars across all the dewponds. No attempt was made to differentiate between the species and hence the data are for the combined populations of both species. The timing of hatching varies with the prevailing environmental conditions, particularly temperature (Sjogren and Legner 1989) and development of notonectids is dependent on food availability (Toth and Chew 1972, Fox and Murdoch 1978), but nymphal development generally takes between two and three months, with the first adults appearing in mid July.

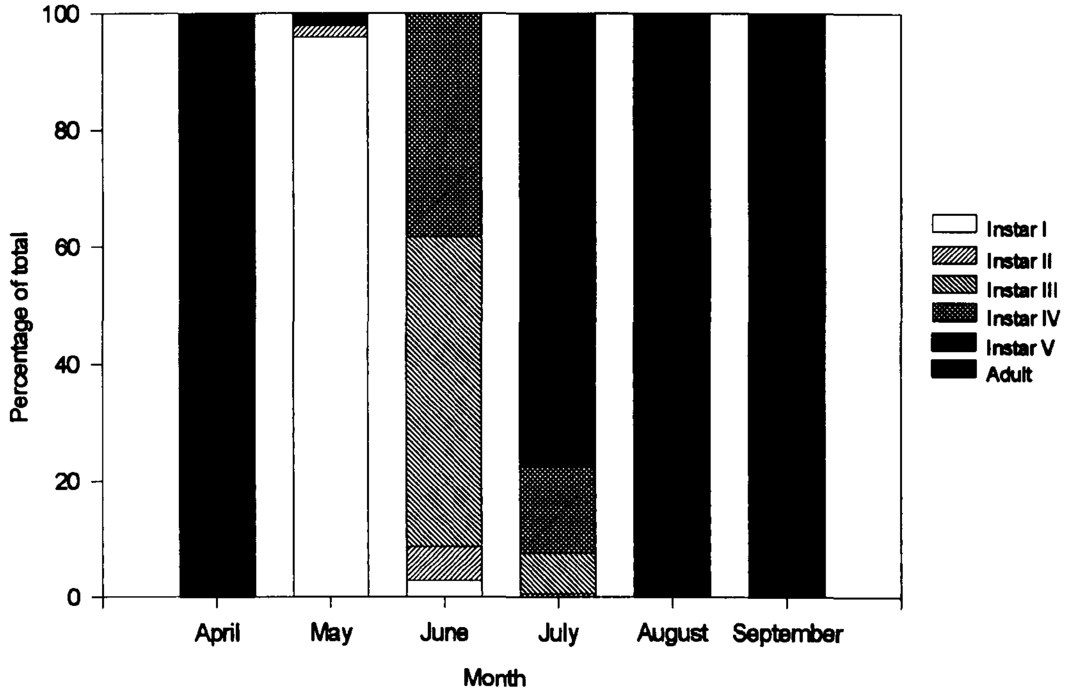

Figure 2.6 The proportions of different instars of *Notonecta* in a sample of 18 dewponds during the nymphal development period 1996. The periods from January to March and October to December are omitted as only adults are present.

3. Habitat preferences.

3.1 Introduction.

This chapter examines the habitat preferences of species of *Notonecta* in dewponds, in terms of habitat characteristics, and patterns of incidence in ponds of different area (incidence functions). I also explore one potential mechanism of habitat selection, oviposition substrate preferences, which may influence reproductive success in different habitat types.

Habitat fragmentation, either natural or anthropogenic, results in species occurring as multiple populations, in discrete habitat patches over a geographic area. The distribution of a species in such a situation is influenced by the amount of suitable habitat available and its spatial distribution (Dunning, Danielson and Pulliam 1992, Webb and Thomas 1994, Kozakiewicz 1995). Where a species regional distribution is determined by a balance of colonisation and extinction of local populations, the species is considered to be a metapopulation (Hanski 1991, Harrison 1994, see section 1.2). Most of the models used to describe metapopulation dynamics make the simplifying assumption that all habitat patches are suitable for occupancy. In order to begin to be able to apply these models to field population systems, a clear and unambiguous method of grading habitat suitability is required, to allow distinctions to be made between patches of habitat that are suitable but presently unoccupied, and those that are unsuitable (Harrison, Murphy and Ehrlich 1988, Lawton and Woodroffe 1991, B.Taylor 1991, Thomas, Thomas and Warren 1992, Hanski 1997a,b, Hanski and Simberloff 1997). However there is a growing awareness that metapopulation studies should take into account more explicitly the underlying habitat mosaic that the species inhabit (Wiens 1997) and that the models need to incorporate aspects such as patch area, isolation and habitat quality (Hanski 1994a,b, 1997a,b, Hanski, Kuussaari and Nieminen 1994, Gyllenberg and Hanski 1997, Moilanen and Hanski 1998).

Detailed autecological information, which would allow *a priori* definition of suitable habitat for a particular species, is very rarely available and most approaches to this problem rely on the use of multivariate statistical techniques to define the range of the habitat characteristics of suitable sites, based on observed patterns of occupancy (Harrison, Murphy and Ehrlich 1988, Jeffries 1989, Lawton and Woodroffe 1991). However, patches that are not capable of supporting a breeding population may be occupied temporarily, or even over many generations, through sustained immigration from surrounding patches, which offsets the population decline that would otherwise occur. Such patches, known as sink habitats (Pulliam 1988), complicate the assessment of habitat suitability based on occupancy patterns and may also be of ecological significance in terms of regional persistence and distribution patterns in their own right (Pulliam 1988, Howe, Davis and Mosca 1991). Definitions of habitat suitability are often linked to the reproductive success of a species at a site (Southwood 1977, Kozakiewicz 1995) and it is probably most ecologically useful to define 'suitable habitat' as those patches able to support a local breeding population.

Within the patches of suitable habitat, the effect of patch area on species occurrence is often considered separately (e.g. MacArthur and Wilson 1967, Hanski 1994a,b). All other things being equal, the area of a habitat patch imposes an upper limit on the population size, regardless of habitat quality, and hence there is a minimum patch area, below which a population cannot persist (MacArthur and Wilson 1967, Diamond 1975, Williamson 1981, B.Taylor 1991, Hanski 1994a). Diamond (1975) first described the species 'incidence function' - the pattern of increasing probability of occurrence with increasing island or habitat patch area, which has since been documented for a wide range of taxa (Diamond 1975, Gilpin and Diamond 1981, Adler and Wilson 1985, B.Taylor 1991, Hanski 1991, 1992, 1994b). Incidence functions typically take the form of a sigmoidal curve (Gilpin and Diamond 1981, B.Taylor 1991), but individual species show considerable variation in the shape and slope of their incidence function, reflecting differences in area requirements, and these differences have been interpreted in terms of species biology (Diamond 1975, Gilpin and Diamond 1981, Hanski 1992).

In a broad sense, notonectids are ecologically very similar (Hungerford 1933, Gittleman 1975). However at the level of the individual species, there are still important differences in aspects of their ecology, including habitat preferences (Giller and McNeill 1981, Savage 1989). Preferences for different habitat types may be evident as spatial segregation of species in relation to habitat within a patch (Streams 1987b) or on the basis of the patches occupied over a regional area (Taylor 1968, Streams and Newfield 1972, Giller and McNeill 1981). The size and permanence of habitat patches may also influence the distribution of species, with some species being characteristic of small and temporary waterbodies while others are generally found in larger waterbodies such as lakes (Southwood and Leston 1959, Streams and Newfield 1972, Streams 1987b). Adult *Notonecta* are capable of dispersing over a wide area, and hence selection of particular habitat types may be initiated by ovipositing females via the selection of certain oviposition substrates (Walton 1936, Streams 1987b), given that different methods of oviposition and oviposition substrates are used by different species (Hungerford 1933, Walton 1936).

3.2 Habitat characteristics.

In this section I aim to explore the habitat preferences of the two species of *Notonecta* in the dewponds using multivariate techniques, to quantify habitat suitability and hence provide a robust definition of 'suitable habitat' for use in subsequent sections.

3.2.1 Methods.

Pond survey.

The habitat preferences of *N. maculata* and *N. obliqua* were investigated using data on pond occupancy and habitat variables collected in surveys of 68 dewponds carried out in July and August 1996-1998 (see sections 2.5 and 2.6 for more details). Adult notonectids were identified by the hemielytral patterns (Savage 1989) and returned to the pond. In addition to identifying the adult notonectids present in a pond, samples of instar V nymphs were also taken, preserved in 70% alcohol and identified in the laboratory at a later date, using the taxonomic characteristics detailed in section 2.3, to confirm that the species found as adults were breeding in the sites.

Data analysis.

Associations between habitat variables and pond occupancy by the two notonectid species were investigated using two methods of analysis; principal components analysis and logistic regression.

Principal components analysis (PCA) was carried out using habitat variables that were identified from the available literature (summarised in Giller and McNeill [1981] and Savage [1989]) as potentially influencing habitat selection by the two species of *Notonecta*, with the exception of pH, which did not show substantial variation (ponds were generally circum-neutral to slightly alkaline), and hence was excluded from the analysis following initial testing. The variables included were pond width, mud depth, water clarity, conductivity and submerged vegetation cover. The PCA was repeated with other variables included in the analysis but in all years the inclusion of other variables did not markedly alter the overall ordination and hence the initial combination of variables was used. In this situation, by selecting the variables for entry into the analysis, PCA is used in a confirmatory manner (Tabachnick and Fidell 1996) where the interest is in revealing the patterns of variation in the variables relevant to the question being asked (in this case the habitat preferences of the two species), rather than to summarise the variation within the entire dataset (exploratory PCA). Suitable habitat was defined by drawing the minimum polygon that enclosed all the pond occupied by the species on a plot of the first two components of the PCA.

Logistic regression (Hosmer and Lemeshow 1989, Trexler and Travis 1993) was also applied to the analysis of habitat preferences, using the presence or absence of species as the binary response variable. Logistic regression was preferred to discriminant function analysis as it generally performs better under conditions of multivariate non-normality (Press and Wilson 1978, Tabachnick and Fidell 1996), which is the case in the dataset under analysis. Habitat variables were entered into the model using a forward stepwise procedure based on the likelihood ratio test. The probability for entry of variables into the model was set at $p = 0.1$ to avoid excluding potentially important variables which may result from using more stringent significance levels (Hosmer and Lemeshow 1989). A separate binary logistic regression model was fitted for each species. The use of multinomial logistic regression, which allows the response variable to take three or more values, would have allowed separate models to be fitted to distinguish between ponds occupied by one or other of the species and those occupied by both, but the iterative algorithm used for parameter estimation failed to converge to a stable solution and hence no further analysis by this method was possible.

3.2.2 Results.

Principal Components Analysis.

Plots of the first two components of the PCA of habitat variables for 1996, 1997 and 1998 are shown in figures 3.1 to 3.3. Table 3.1 gives the PCA summary statistics for each year. The habitat variable loadings on the first two principal components are highly correlated in different survey years, indicating that the variation in the habitat characteristics summarised by the ordination was very consistent between years, even if the habitat conditions in individual ponds changed. Although the first two components only accounted for just over 50% of the variance in all years, the ordination suggests that the two species do have different habitat preferences and despite considerable changes in the identity of the occupied ponds, the pattern of separation of the species is very similar in each year. In all years the maximum separation of the species is on the second component. The habitat variable loadings for this axis suggest that *N. maculata* is predominantly found in smaller ponds with little mud cover and submerged vegetation, whereas *N. obliqua* prefers larger habitats with higher mud cover and abundant submerged vegetation. The species show substantial overlap on component 1 suggesting less pronounced preferences. Subsequent components of the PCA were examined but no clear separation of the species was observed on these axes and hence no attempt was made to interpret them.

The habitat preferences of the two species, as defined by the PCA, are not mutually exclusive, there is some degree of overlap in occupancy and there is temporal variation in the amount of overlap. Ponds where the two species occur together are generally intermediate in terms of ordination position to those occupied by one or other of the species. In 1997 and 1998 there is a higher degree of overlap between the ordination position of the ponds occupied by the two species and also in terms of the number of ponds where both species are found (12 ponds as opposed to 6 in 1996) and hence the separation of the species in terms of habitat occupied is less clear.

Table 3.1 Summary statistics for principal components analysis of habitat data, a) cumulative percentage variance explained by each component, b) component loadings for habitat variables included in the analysis.

Year	1996		1997		1998	
	PC 1	PC 2	PC 1	PC 2	PC1	PC 2
a) Cumulative % variance	31.1	54.1	30.9	55.8	36.0	57.6
b) Variables						
Pond width	-0.033	0.633	-0.060	0.438	-0.031	0.404
Mud depth	-0.310	0.625	-0.256	0.474	0.177	0.670
Water clarity	0.678	0.091	0.706	0.092	-0.661	0.055
Submerged vegetation	0.453	0.437	0.431	0.647	-0.566	0.460
Conductivity	0.487	0.092	-0.497	0.395	0.458	0.417

Logistic Regression.

The results of the logistic regression analyses are given in table 3.2. Significant logistic regression models were fitted to the data in all years. Details of the model parameters at each step of the model building procedure have been omitted for the sake of clarity.

The fitted logistic regression models also suggest that pond occupancy by the two species is influenced by different habitat variables and hence that they have different habitat preferences. The regression coefficients (β) indicate the direction of influence of habitat variables on the probability of pond occupancy. For *N. maculata*, mud depth and conductivity have negative coefficients, indicating that the probability of occupancy decreases with increasing mud depth or conductivity, and water clarity has a positive coefficient, suggesting that *N. maculata* is more likely to occupy ponds with clear water. For *N. obliqua* all the variables included in the models have positive coefficients, hence the probability of occupancy increases with increasing values of percentage cover submerged vegetation, pond width and water depth.

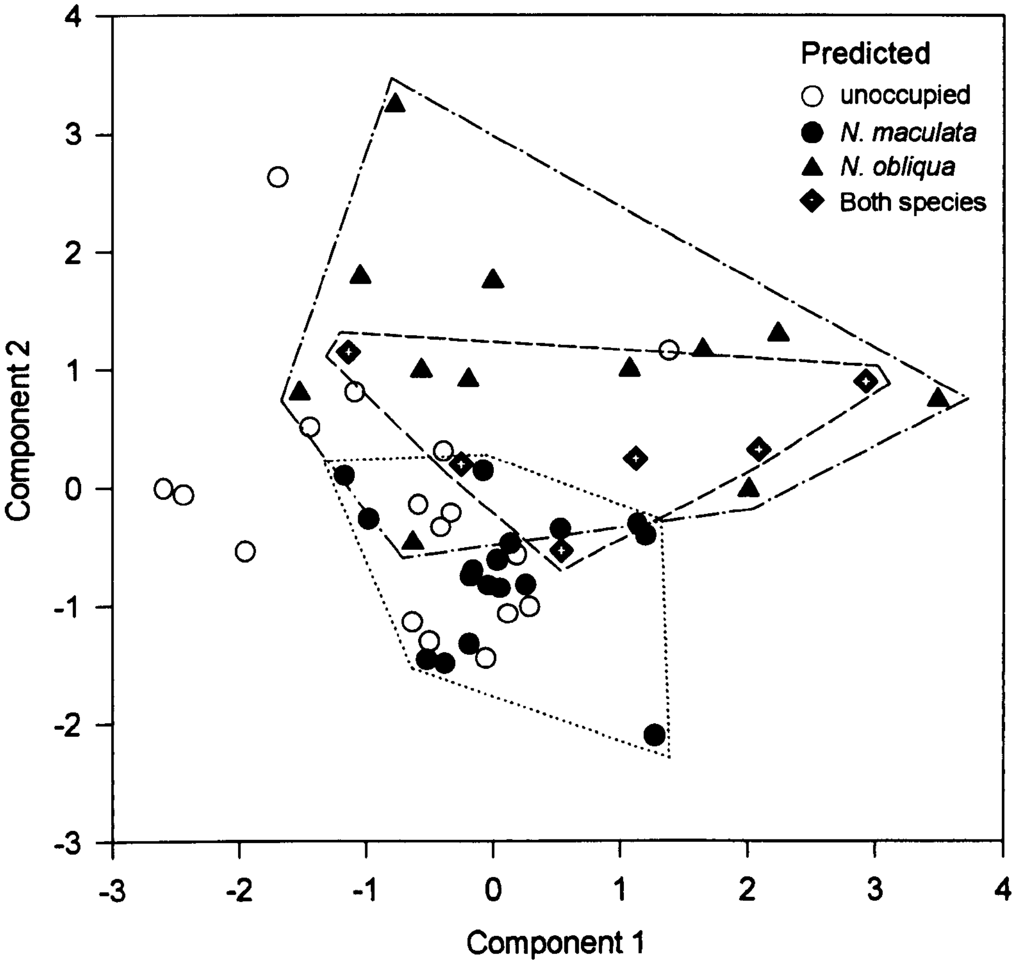

Figure 3.1 Plot of the first two components from PCA of habitat variables of ponds in 1996. For details of the PCA see table 3.1. Lines enclose groupings of ponds according to the species breeding.

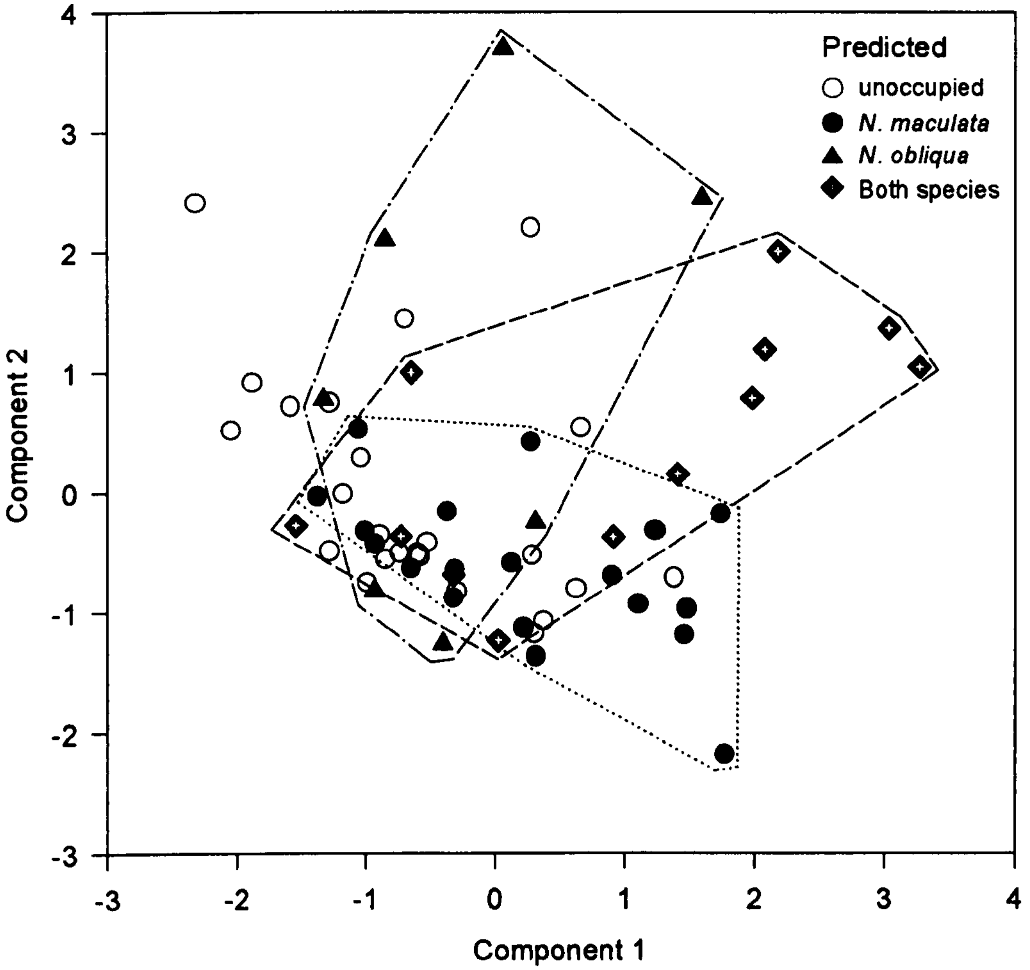

Figure 3.2 Plot of the first two components from PCA of habitat variables of ponds in 1997. For details of the PCA see table 3.1. Lines enclose groupings of ponds according to the species breeding.

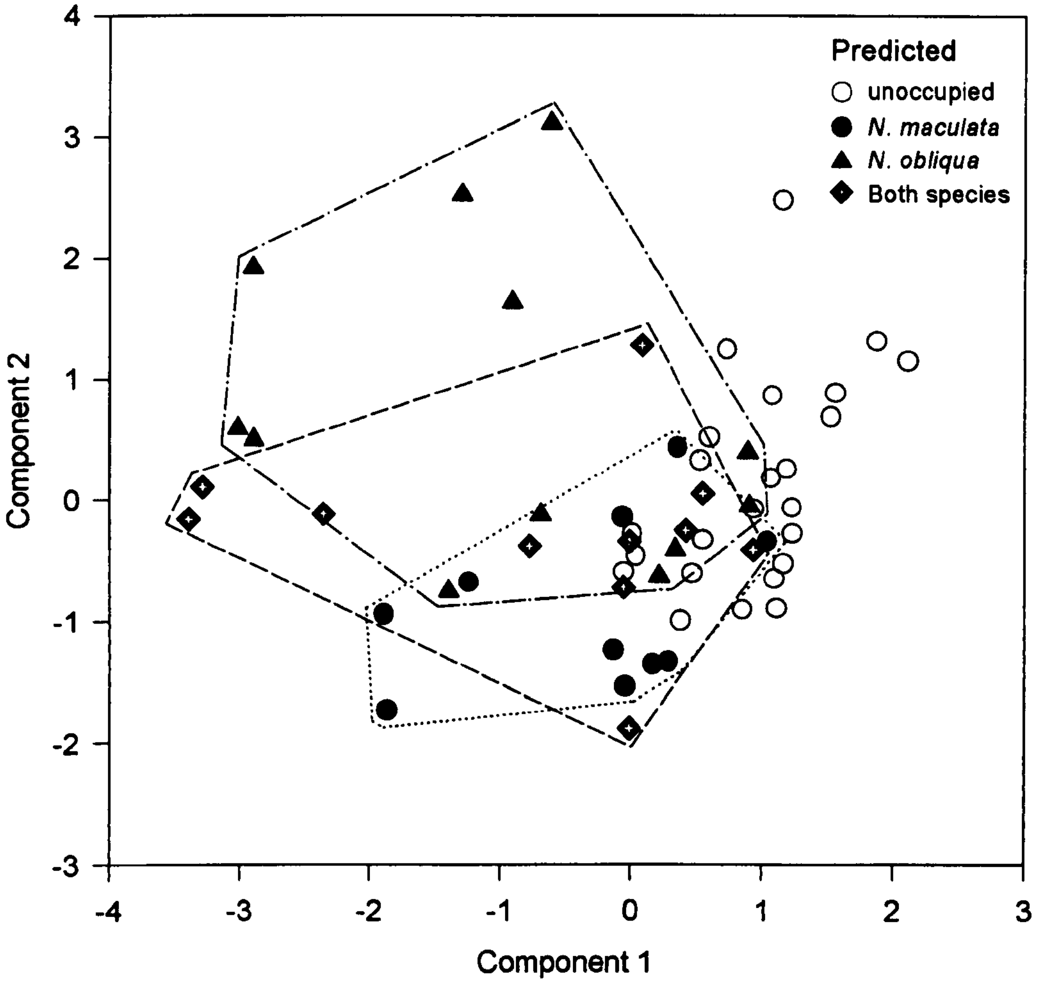

Figure 3.3 Plot of the first two components from PCA of habitat variables of ponds in 1998. For details of the PCA see table 3.1. Lines enclose groupings of ponds according to the species breeding.

Those variables that enter the model in more than one year always have the same direction of influence on the probability of occupancy, suggesting that the preferences for individual habitat variables remain similar between years. However, although some variables appear to consistently influence the probability of pond occupancy, for example percentage cover of submerged vegetation for *N. obliqua* (see table 3.2), the variables entering the models are different in different years. This may be the result of changes in the relative importance of the habitat variables in determining occupancy in different years, but alternatively may reflect stochastic variation in the patterns of occupancy and pond habitat.

Comparison of Techniques.

The primary separation of the species on the PCA is on the second component, which has high loadings for percentage cover of submerged vegetation, mud depth and pond width, and the first two of these variables are also consistently important in the logistic regression models of occupancy (see table 3.2). This would suggest that the two techniques of defining 'suitable habitat' are identifying similar trends in the data. In order to test whether the two methods of analysis give similar definitions of 'suitable habitat' for the two species, predicted pond occupancy was derived from the logistic regression models. By entering the habitat variables for each site into the fitted logistic regression equations, a probability of occupancy is obtained. This can be used to predict occupancy; typically the cut-off probability is 0.5 (Hosmer and Lemeshow 1989, Tabachnick and Fidell 1996). Therefore any site with a predicted probability of ≥ 0.5 was defined as suitable habitat. This process was repeated for each species in each year. Although sites where the two species co-occur are not defined directly by the logistic regression models, indirectly they are defined as those ponds where both species are predicted to be found.

Table 3.2 Results of forward stepwise logistic regression of pond occupancy in relation to habitat variables. a) Significance of logistic regression model. Model G^2 = log-likelihood ratio of the model, df = degrees of freedom of the logistic regression model, p = significance of logistic regression model. b) Logistic regression equation parameter estimates. β = coefficient of the variable entered, SE = standard error of the coefficient, p = significance of the variable entered (degrees of freedom for all variables = 1). Order of variables in the table indicates the order in which they entered the model.

a)

Species	Year	Model G^2	df	p
N. maculata	1996	12.38	2	0.002
	1997	12.03	1	< 0.001
	1998	17.77	2	< 0.001
N. obliqua	1996	24.85	2	< 0.001
	1997	16.40	1	< 0.001
	1998	24.23	2	< 0.001

b)

Species	Year	Variable entered	β	SE	p
N. maculata	1996	Constant	1.87	0.81	0.021
		Mud depth	-4.32	2.13	0.042
		Conductivity	-0.03	0.02	0.060
	1997	Constant	-1.33	0.48	0.002
		Water clarity	0.05	0.01	0.006
	1998	Constant	4.11	1.40	0.003
		Conductivity	-0.02	0.01	0.006
		Mud depth	-5.21	2.25	0.021
N. obliqua	1996	Constant	-6.89	2.06	< 0.001
		Submerged vegetation	0.06	0.02	0.009
		Pond width	0.69	0.23	0.003
	1997	Constant	-1.44	0.35	< 0.001
		Submerged vegetation	0.06	0.02	0.002
	1998	Constant	-3.43	0.99	< 0.001
		Water depth	4.65	1.65	0.004
		Submerged vegetation	0.04	0.02	0.040

The predicted pond occupancy from the logistic regression models was superimposed on the plot of the first two components from the PCA and compared with the polygons of suitable habitat from the PCA, defined by the grouping of ponds that were actually occupied (see figures 3.4 to 3.6). In all years the two classifications largely overlap, although the logistic regression predicted occupancy does not include all the ponds that were actually occupied in the surveys. Generally fewer ponds were predicted to be occupied by either or both of the species by the logistic regression classification and hence the suitable habitat does not include as many ponds as that defined by the PCA. Despite these minor inconsistencies, the overall patterns of actual and predicted occupancy are similar and the groupings of ponds according to the species present are found in the same areas of ordination space. This would suggest that the two techniques succeeded in deriving similar definitions of 'suitable habitat', and that the two species do indeed show different habitat preferences.

3.2.3 Discussion.

The aim of this analysis was to explore the habitat preferences of the two species of *Notonecta* in the dewpond system. Two method of analysis were used to attempt to define 'suitable habitat' for the species, and the resultant classifications of ponds were broadly consistent in terms the variables that appear to be important in determining pond occupancy by each species. The two sets of analyses taken together provide strong evidence that the two species have preferences for different types of habitat and that the preferences can be summarised by a relatively small number of habitat variables. The patterns of importance among variables defining habitat preferences do show some changes between years, but some variables appear to be consistently important in determining occupancy; for *N. maculata* these are mud depth and conductivity, whereas pond occupancy by *N. obliqua* is strongly influenced by the amount of submerged vegetation in a pond. The importance of the different habitat factors may be related to the relative variation exhibited by the factors across the ponds in each year, but may simply be a result of stochastic variation in the relationship between the observed patterns of occupancy and habitat variables, given the impact of stochastic events in pond community composition (Talling 1951, Jeffries 1989, 1997)

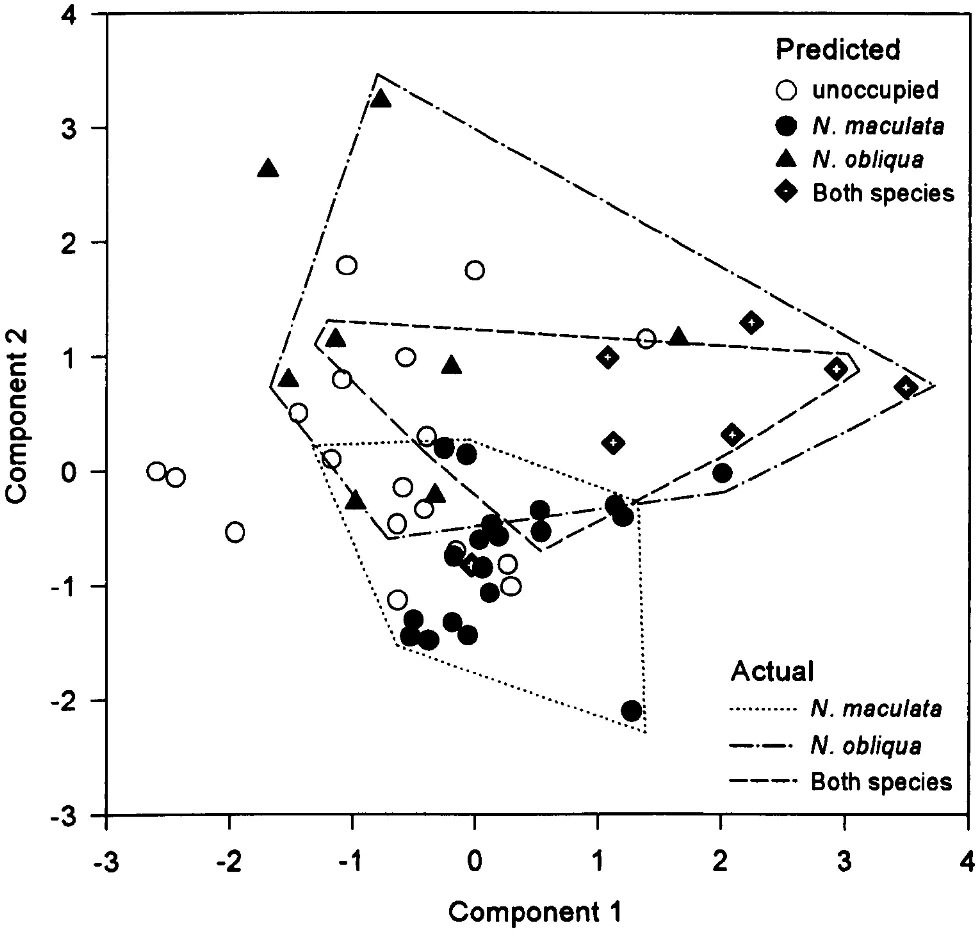

Figure 3.4 Plot of the first two components from PCA of habitat variables of ponds in 1996 with predicted occupancy derived from logistic regression model. For details of the PCA see table 3.1. Data points are labelled according to the species predicted to be present (see text for details). Lines enclose groupings of ponds actually occupied by the different species in the survey.

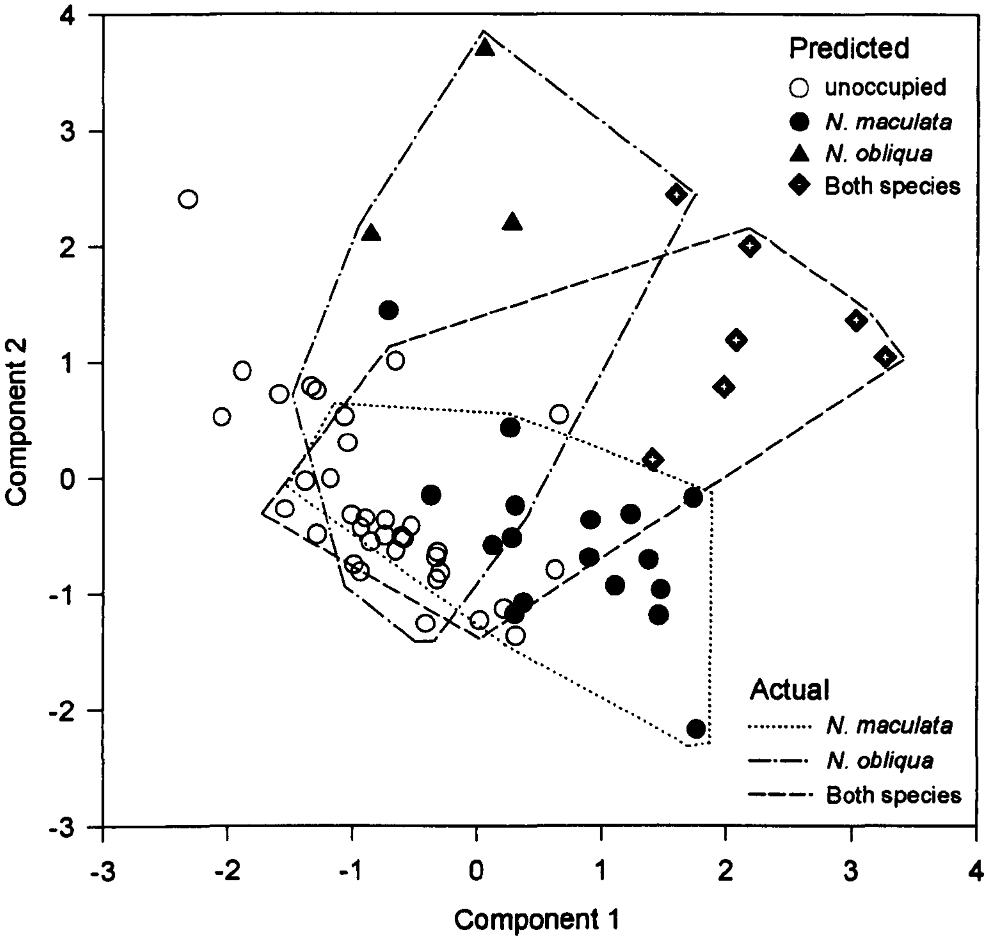

Figure 3.5 Plot of the first two components from PCA of habitat variables of ponds in 1997 with predicted occupancy derived from logistic regression model. For details of the PCA see table 3.1. Data points are labelled according to the species predicted to be present (see text for details). Lines enclose groupings of ponds actually occupied by the different species in the survey.

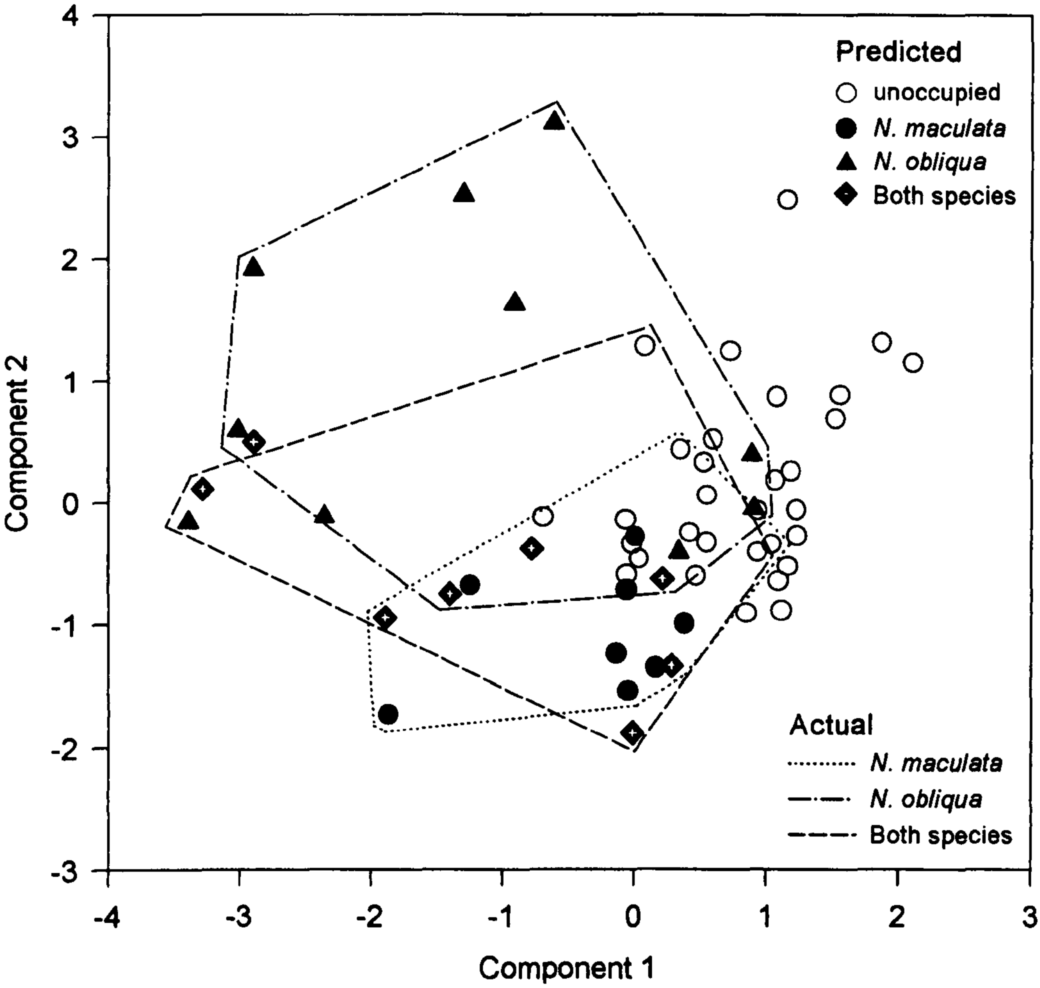

Figure 3.6 Plot of the first two components from PCA of habitat variables of ponds in 1998 with predicted occupancy derived from logistic regression model. For details of the PCA see table 3.1. Data points are labelled according to the species predicted to be present (see text for details). Lines enclose groupings of ponds actually occupied by the different species in the survey.

The preferences exhibited are consistent with the literature data on observed patterns of pond occupancy and habitat types (Giller and McNeill 1981, Savage 1989). The habitat preferences may be related to the foraging abilities of the species in different environments. Giller and McNeill (1981) found that the two species had different foraging efficiencies in environments of varying complexity, with *N. maculata* showing the highest foraging efficiency in simple environments, whereas *N. obliqua* was better able to exploit complex habitats with more abundant submerged vegetation. Foraging efficiency and competition between the two species in different environments is further explored in Chapter 5. There is also evidence that the species exhibit preferences for different oviposition substrates (Walton 1936) which may serve to initiate habitat selection. This is explored further in section 3.4.

Although the two methods produced similar results, the output from the two sets of analyses are suited to different purposes. The definition of 'suitable habitat' from the PCA analysis is in essence a summary of the type of habitat occupied by the species in any one year. This method of assessing habitat suitability is best suited to situations where the interest is in the observed patterns of occupancy in the field data, for example the derivation of incidence functions (see section 3.3).

In contrast, the definition of 'suitable habitat' obtained using logistic regression, which is becoming an increasingly popular method of defining habitat requirements (e.g. Peeters and Gardiniers 1998), can be used to derive a predictive model of pond occupancy based on the probability of observing the pond being occupied by a species given the habitat characteristics of the site. The inclusion of different variables in the models in different years of survey limits the value of the models in predicting the future pond occupancy. However alternative models can be fitted to the data, using just those variables that appear to be consistently important. For *N. maculata* these are mud depth and conductivity and for *N. obliqua*, submerged vegetation cover. Models containing only these variables still give highly significant fits to the data in all years and have similar percentages of correct predictions (based on the ratio of observed to predicted occupancy) as the models fitted by the stepwise variable selection (see table 3.3).

Table 3.3 Comparison of logistic regression models for predicting pond occupancy in different years. Stepwise = model fitted by forward stepwise procedure (see table 3.2), standard = model fitted with the same variables each year (*N. maculata*: variables = mud depth and conductivity, *N. obliqua*: variable = percentage cover of submerged vegetation). Model G^2 = log-likelihood ratio of the model, df = degrees of freedom of the logistic regression model, p = significance of logistic regression model.

Species	Year	Model	Model G^2	df	p	% correct prediction
N. maculata	1996	Stepwise	12.38	2	0.002	73.1 *
		Standard	20.64	2	< 0.001	75.8 *
	1997	Stepwise	12.03	1	< 0.001	66.7
		Standard	11.55	2	0.003	68.8
	1998	Stepwise	17.77	2	< 0.001	77.2
		Standard	17.77	2	< 0.001	77.2
N. obliqua	1996	Stepwise	24.85	2	< 0.001	86.5
		Standard	16.59	1	< 0.001	83.6
	1997	Stepwise	16.40	1	< 0.001	82.5 *
		Standard	16.68	1	< 0.001	82.8 *
	1998	Stepwise	24.23	2	< 0.001	82.5
		Standard	14.31	1	< 0.001	79.7

* Although both of these models contain the same variables, the stepwise model included other variables for selection, and missing values in these variables reduced the number of cases used in the analysis, affecting the fit of the model. Only the two variables were entered into the standard model and hence all cases were used, leading to a higher percentage correct prediction.

The differences between the two sets of models reflects the methods used in their construction. Stepwise selection of variables will tend to fit the most parsimonious model that is a significant fit to the data. In addition, the iterative procedure used to fit the models is biased towards the largest classification group (in this case whether or not the pond is occupied) (Hosmer and Lemeshow 1989). Given that there were more ponds with the species absent than present, the model is optimised to fit the observed frequencies of absence with the highest percentage correct prediction. However this may give a lower overall percentage correct prediction when combined with the predictions of presence, and it is these data which are presented in the table above.

In conclusion, this section has demonstrated that there are consistent effects of habitat type on pond occupancy by the two species and that the two species have different habitat preferences. Two definitions of 'suitable habitat' were obtained using different methods of analysis. These definitions gave similar results in terms of the habitat types that appeared to be preferred by the different species, but are suited to different purposes.

3.3 Incidence functions.

This section deals with the construction and interpretation of incidence functions for the two species of *Notonecta* in the dewponds to establish whether there are any differences between the habitat patch area requirements of the species.

3.3.1 Methods.

Incidence functions were constructed for the two species of *Notonecta* in all survey years using pond area and occupancy data collected in the habitat surveys. Potentially suitable habitat was defined using the output from the PCA of habitat variables (see section 3.2.1 and figures 3.1 to 3.3) by defining the ponds occurring within the minimum polygon enclosing all the ponds that were occupied by the species in question, as potentially suitable for occupancy. The PCA analysis used pond width as one of the variables and this variable had a fairly high loading on the second component in all years. Therefore some of the habitat variation summarised by the PCA incorporates an effect of pond size, and it has already been suggested that the species show different area requirements (section 3.2.2). However the purpose of constructing the incidence functions is to examine the distribution of the species in ponds of different area within the 'suitable habitat', regardless of whether the species shows a preference for generally larger or smaller ponds.

Ponds that were occupied by more than one species were included in both species analyses. Ponds occupied by one species that occurred within the polygon of suitable habitat of the other species were counted as unoccupied as they could still act as potential habitat, and hence any effects of biotic interactions between the species were ignored. Ponds that were of suitable habitat were grouped by surface area into $10m^2$ classes and the proportion of ponds within each class that were occupied calculated. Logistic regression was used to analyse the pattern of occupancy in relation to pond area. The fit of the logistic function is sensitive to the number of samples in each size class and their distribution along the predictor (area) axis (Hosmer and Lemeshow 1989, B.Taylor 1991) and for this reason area classes with a sample size of less than 5 were excluded from the analysis. In all years this meant excluding ponds with an area of greater than $40m^2$. A jackknife cross-validation procedure (Efron and Gong 1983, B.Taylor 1991, Manly 1997) was used to test whether there were any errors associated with the fitted logistic function, due to the high influence of a single sample driving the shape of the function. This involved sequentially removing each of the samples from the dataset in turn and refitting the logistic function to assess whether the sample removed had a strong influence on the fit of the function. In all cases the error structure was consistent over the range of areas used to estimate the regression parameters, with no individual sample strongly influencing the fit. The maximum and minimum deviation were calculated from the jackknifing procedure and plotted to indicate the amount of error associated with the fitted function.

3.3.2 Results.

The observed incidence functions and fitted logistic equations for the two species are shown in figures 3.7 to 3.9. Logistic regression gave a significant fit to the observed data in all cases except *N. maculata* in 1996, and the functions fitted indicated that proportional occupancy increases with increasing pond area. The test statistics and logistic regression equations are given in table 3.4.

The observed patterns of pond occupancy may be the result of area-dependent habitat quality if changes in pond area are correlated with changes in other habitat variables important in determining pond occupancy. However in all years there were no significant correlations between pond area and any of the other habitat variables recorded.

Table 3.4 Results of logistic regression of pond area and occupancy. a) Test statistics. Model G^2 = log-likelihood ratio of the model, p = significance of the model. b) Logistic regression equation and parameter estimates. Note: logistic regression was not significant for *N. maculata* and therefore no equation was derived. β = coefficient of the variable entered, SE = standard error of the coefficient, p = significance of the logistic regression model. Degrees of freedom for all tests = 1.

a)

Species	Year	Model G^2	p
N. maculata	1996	0.02	0.961
	1997	4.71	0.030
	1998	4.57	0.033
N. obliqua	1996	6.44	0.011
	1997	3.91	0.047
	1998	6.56	0.010

b)

Species	Year	Variable entered	β	SE	p
N. maculata	1996	Constant	-	-	-
		Pond area	-	-	-
	1997	Constant	-1.04	0.87	-
		Pond area	0.10	0.05	0.051*
	1998	Constant	-0.97	0.78	-
		Pond area	0.05	0.03	0.100*
N. obliqua	1996	Constant	-2.12	1.45	-
		Pond area	0.14	0.06	0.029
	1997	Constant	-2.03	0.93	-
		Pond area	0.07	0.04	0.069*
	1998	Constant	-2.61	1.25	-
		Pond area	0.13	0.58	0.026

* Note: although the probability does not reach the standard level for significance ($p < 0.05$), Hosmer and Lemeshow (1989) recommend that a significance level of $p < 0.1$ is more appropriate to ensure that important variables are not excluded.

Comparison of incidence functions.

In order to allow interpretation and comparison of the fitted logistic regression equations which describe the incidence functions of the species, the structure of the logistic regression model must be examined.

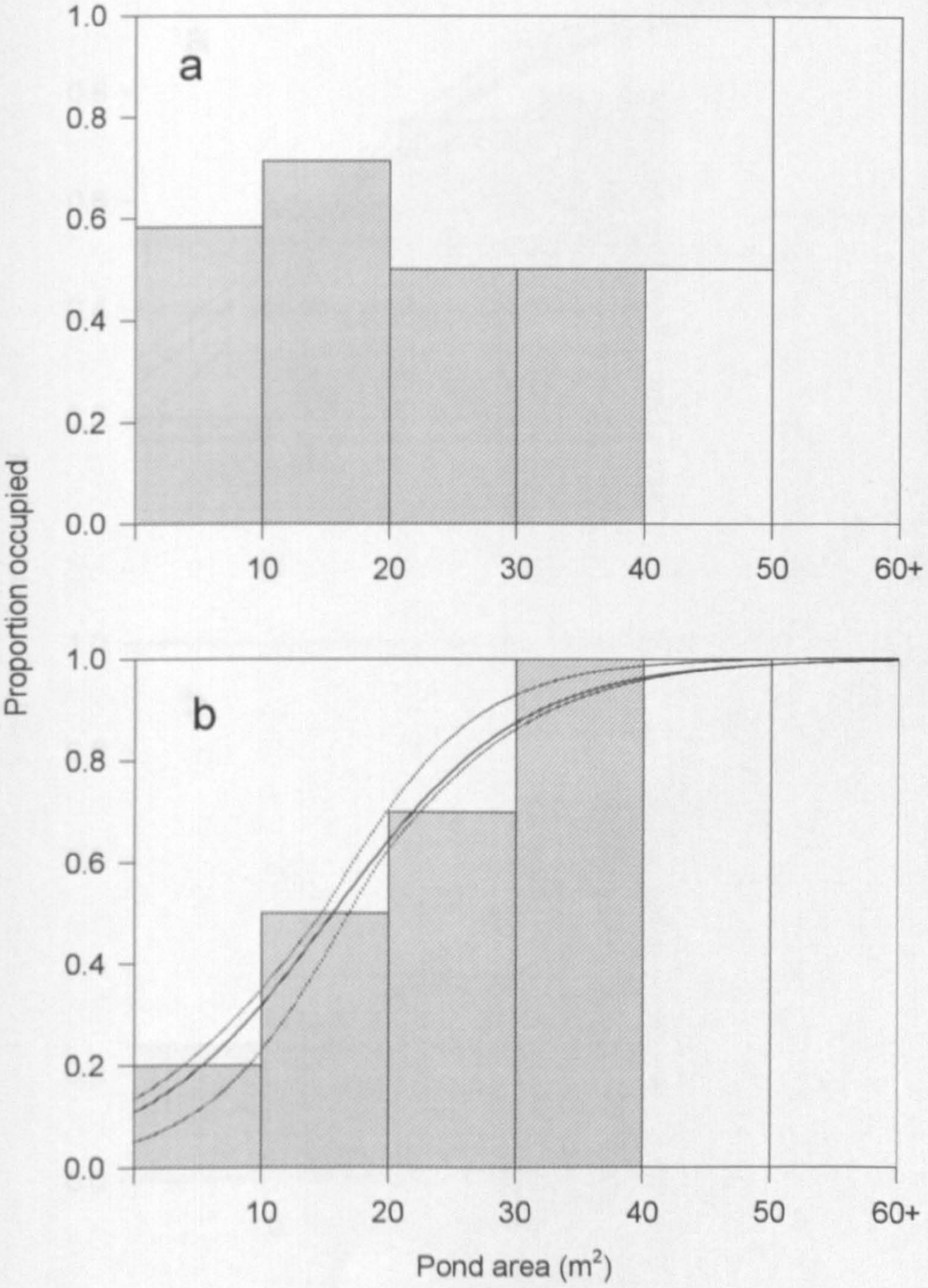

Figure 3.7 Incidence functions for 1996 survey data, a) *N. maculata*, b) *N. obliqua*. Unhatched bars were excluded from data used to fit logistic regression function due to small sample size. Fitted lines are logistic regression function (solid line) and maximum and minimum deviation from this function (derived from jackknifing procedure) (dotted lines). Logistic regression was not significant ($p > 0.1$) for *N. maculata* and hence no lines were fitted.

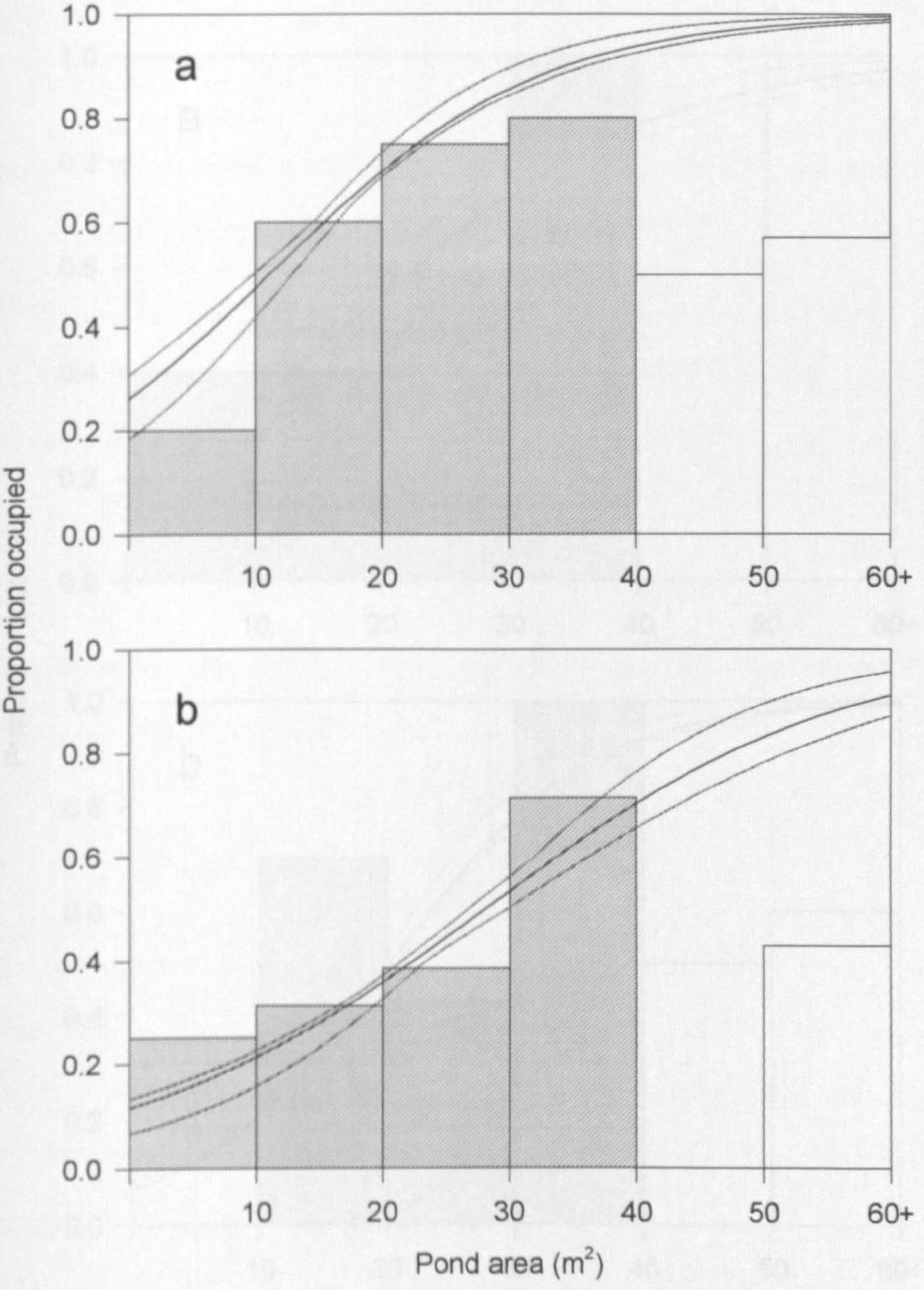

Figure 3.8 Incidence functions for 1997 survey data, a) *N. maculata*, b) *N. obliqua*. Unhatched bars were excluded from data used to fit logistic regression function due to small sample size. Fitted lines are logistic regression function (solid line) and maximum and minimum deviation from this function (derived from jackknifing procedure) (dotted lines).

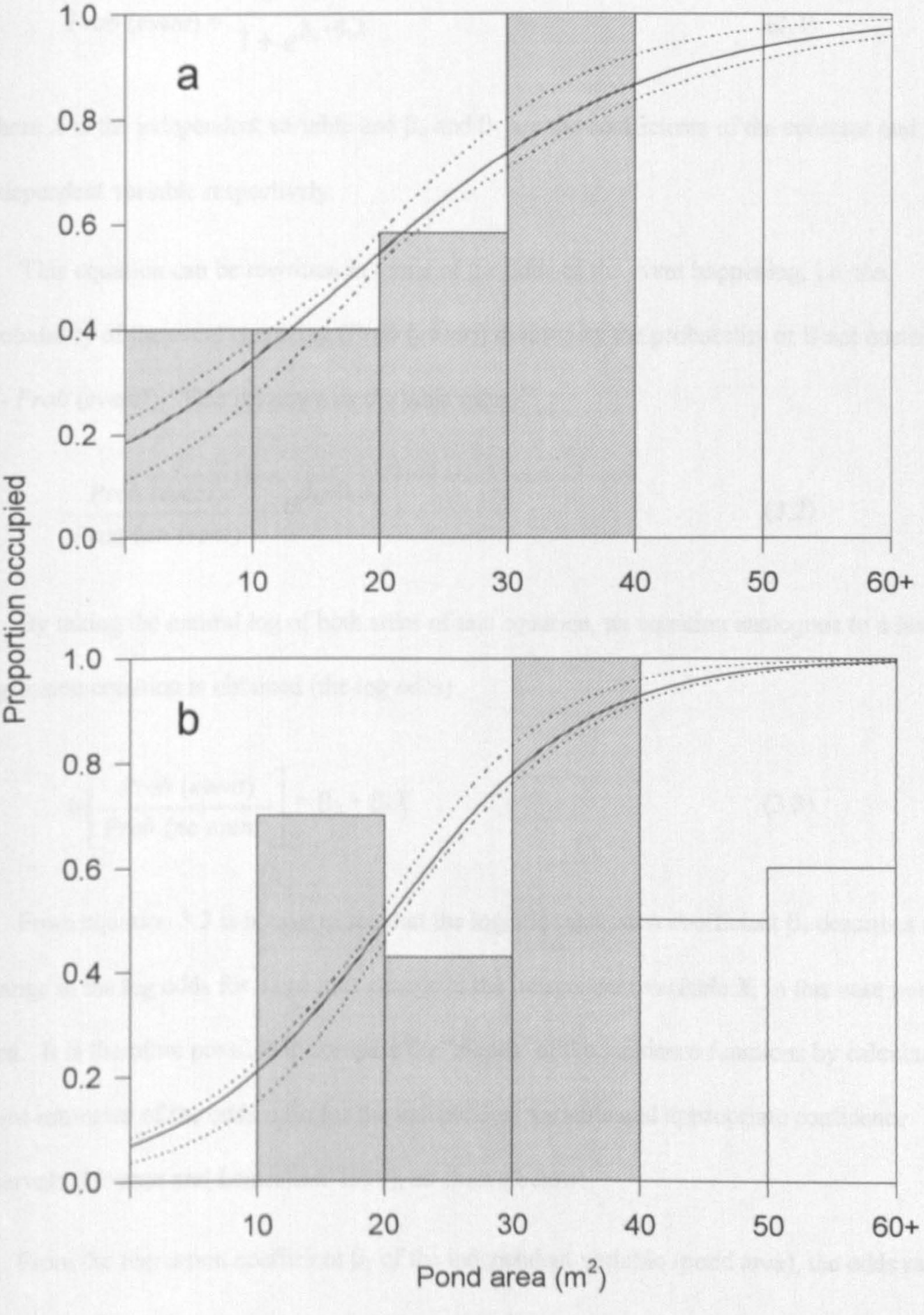

Figure 3.9 Incidence functions for 1998 survey data, a) *N. maculata*, b) *N. obliqua*. Unhatched bars were excluded from data used to fit logistic regression function due to small sample size. Fitted lines are logistic regression function (solid line) and maximum and minimum deviation from this function (derived from jackknifing procedure) (dotted lines).

The equation for a logistic regression model with one independent variable can be written as follows

$$Prob\ (event) = \frac{e^{\beta_0+\beta_1 X}}{1+e^{\beta_0+\beta_1 X}} \qquad (3.1)$$

where X is the independent variable and β_0 and β_1 are the coefficients of the constant and the independent variable respectively.

This equation can be rewritten in terms of the odds of the event happening, i.e. the probability of the event occurring (*Prob* (*event*)) divided by the probability of it not occurring (1- *Prob* (*event*)). This is known as the odds ratio.

$$\frac{Prob\ (event)}{Prob\ (no\ event)} = e^{\beta_0+\beta_1 X} \qquad (3.2)$$

By taking the natural log of both sides of this equation, an equation analogous to a linear regression equation is obtained (the log odds).

$$\ln\left[\frac{Prob\ (event)}{Prob\ (no\ event)}\right] = \beta_0 + \beta_1 X \qquad (3.3)$$

From equation 3.3 is it easy to see that the logistic regression coefficient β_1 describes the change in the log odds for a one unit change in the independent variable X, in this case pond area. It is therefore possible to compare the 'slopes' of the incidence functions by calculating point estimates of the odds ratio for the independent variable and appropriate confidence intervals (Hosmer and Lemeshow 1989), as shown below.

From the regression coefficient β_1 of the independent variable (pond area), the odds ratio, ψ which reflects changes in the probability of pond occupancy is calculated as

$$\psi = e^{\beta_1} \qquad (3.4)$$

If ψ is greater than one then the probability of the event (in this case the pond being occupied) increases with increasing pond area and *vice versa*. Confidence intervals for the estimate of ψ, at an appropriate level of α (typically 95%), can be constructed from the following equation

$$100(1-\alpha)\%\ \mathrm{CI} = \exp[\beta_1 \pm z_{1-\alpha/2}\ \mathrm{SE}(\beta_1)] \qquad (3.5)$$

Table 3.5 gives the odds ratio and 95% confidence intervals for the incidence functions of the different species in all years. Due to the large standard errors of the regression coefficients, the confidence intervals overlap completely in all cases, limiting comparison of the slope coefficients. Standard errors of this magnitude are commonplace in logistic regression and do not invalidate the fit of the model (Hosmer and Lemeshow 1989). Therefore further interpretation is based solely on the shape of the fitted incidence functions (figures 3.7-3.9) which can be interpreted to a limited extent. Although incidence functions generally exhibit the same basic shape, the steepness of the curve and its relative position along the area axis can be interpreted in terms of the areas requirements of the different species (Gilpin and Diamond 1981).

Table 3.5 Odds ratio (ψ) and 95% confidence intervals derived from logistic regression incidence functions. Dashes indicate no model fitted and hence no calculation carried out.

Year	*N. maculata*			*N. obliqua*		
	ψ	+ CI	-CI	ψ	+CI	-CI
1996	-	-	-	1.15	1.29	0.94
1997	1.09	1.21	0.95	1.08	1.16	0.96
1998	1.08	1.22	0.95	1.14	1.28	0.95

3.3.3 Discussion.

This section examined the incidence functions of the species of *Notonecta* in the dewponds. Both species of *Notonecta* show the typical pattern of increasing proportional occupancy with increasing pond area, with the exception of *N. maculata* in 1996. Although the species show generally similar patterns, there is considerable variation in the incidence functions exhibited by the species in different years, suggesting that stochastic variation in species' incidence functions may be considerable. The changes in the observed incidence functions may reflect changing availability of ponds of different areas within the 'suitable habitat' for each species. Pond occupancy is dynamic, with considerable changes in the identity of the occupied ponds between years, and there are also changes in the habitat of individual ponds. Therefore the pattern of incidence in ponds of different area may be influenced by the changing habitat mosaic on which it is superimposed.

There are also some differences in the incidence functions of the two species. In all years, the intercept on the area axis of the fitted logistic function for *N. maculata* is higher than for *N. obliqua*, suggesting that it has higher proportional occupancy in the smaller ponds. This is confirmed by examination of the proportional occupancy of the smallest area class of ponds (0-10m^2) and to a lesser extent for the next smallest area class, and is consistent with the types of habitat this species occupies. *N. maculata* is found in a range of small and temporary habitats (Southwood and Leston 1959) such as desert pools (Blaustein, Kotler and Ward 1995, Blaustein 1998), and has been found successfully breeding in metal cattle troughs in the Peak District (area approximately 0.5m^2). *N. obliqua* conversely has generally low proportional occupancy of the smallest ponds, and shows a stronger area dependent occupancy effect, with proportional occupancy consistently high in the larger pond area classes, and hence the slope of the incidence function is steeper. Indeed a comparison of the mean area at which proportional occupancy equals 0.5 shows that *N. maculata* reaches this level of occupancy at a smaller pond area (mean area for *N. maculata* = 14.8m^2, *N. obliqua* = 21.4m^2), although it is difficult to ascribe significance to this difference given the small sample size. Although the PCA analysis suggests that *N. obliqua* prefers larger ponds in general, there is still a consistent area effect within the habitat defined as suitable.

Hanski (1991, 1992) has suggested that further interpretation of the slope of incidence functions is possible based on models of population extinction. According to this approach, the persistence of species with steep incidence functions is primarily influenced by demographic stochasticity, whereas species with shallow incidence functions are more strongly affected by environmental stochasticity (Hanski 1991, 1992). However, the differences in slope of the incidence functions for the two species of *Notonecta* are not of sufficient magnitude or consistency to draw any firm conclusions on this basis. The variation in the shape of the functions in different years suggests that longer term data on the patterns of incidence in the dewponds would be required to determine whether there are any consistent differences between the incidence functions of the two species, but the present data suggest that pond occupancy by *N. maculata* is less strongly area dependent than *N. obliqua*.

3.4 Oviposition preferences.

Given the potential mobility of adult *Notonecta* via dispersal, any active selection of oviposition sites by females could be an important component in determining patterns of occupancy and habitat preferences at the landscape scale. In this section I examine the oviposition preferences of the two species of *Notonecta*, with regard to their potential role in habitat selection. In Britain, female *Notonecta* lay batches of eggs, usually eight per batch up to a total of 64, in the autumn or spring depending on species (Walton 1936) (see figure 1.5). The majority of the species attach the eggs to the surface of substrates using a waterproof adhesive, but some species are capable of embedding eggs into the stems of aquatic plants (Hungerford 1933, Walton 1936).

3.4.1 Methods.

Oviposition preference experiments were carried out in plastic containers (27x15x9cm) containing 2.5 litres of water. The outer surfaces of the containers were covered in black plastic so that light penetrated only from above, giving a more natural lighting regime. All experiments were carried out under a 12hr light:12hr dark regime in a constant temperature room at 15°C. A choice of four oviposition substrates were presented in each container (table 3.6). These substrates were selected to present the species with a range of substrates similar to those available in the dewponds. Additionally, the inclusion of pairs of similar substrates, such as natural and artificial plants, allowed me to investigate whether it was the form or shape of the substrate which was important, or other physical characteristics, such as surface texture. For example, the natural and artificial plants were of similar shape, size and colour, but only the real plants would allow eggs to be embedded into the stems.

All *Notonecta* used were obtained from field sites. Both sexes were collected and maintained in aquaria under conditions described in section 2.2 until mating was observed. Individual female *Notonecta* were then collected and placed in the experimental containers.

All trials lasted 72 hours, after which the *Notonecta* were removed and the number of eggs laid on each of the substrates recorded. Twelve replicates were carried out for each species.

Table 3.6 Oviposition substrates presented to adult female *Notonecta*.

Treatment	Substrate
Stone	Autoclaved sandstone block (approx. 80x50x45mm)
Supports	Green plastic mesh strip (60x40mm, mesh size 15mm)
Artificial	Artificial plastic aquarium weed (90mm in length)
Elodea	Length of *Elodea canadensis* Michx. (90mm in length)

3.4.2 Results.

The mean number of eggs laid on the substrates for each species is shown in figure 3.10. There were significant differences in the number of eggs laid on each substrate for both species (Kruskal Wallis test: *N. maculata* $H_{[3]} = 41.3, p < 0.001$, *N. obliqua* $H_{[3]} = 40.1, p < 0.001$). *N. maculata* showed a significant preference for stone oviposition sites and *N. obliqua* for oviposition on *Elodea*. Very few eggs were laid on any substrate other than the preferred in both cases.

3.4.3 Discussion.

The preferences for oviposition sites shown experimentally by the two species in this study are broadly consistent with previous field and laboratory observations (Walton 1936, Southwood and Leston 1959). However, although observations have been made previously, this is the first time that a comparative experimental study of the preferences has been carried out. *N. obliqua* has a strong preference for oviposition on natural weed. Observations of the act of oviposition by this species indicate that it normally uses its relatively long ovipositor to embed individual eggs into the substrate (Walton 1936), and macrophytes provide a suitable

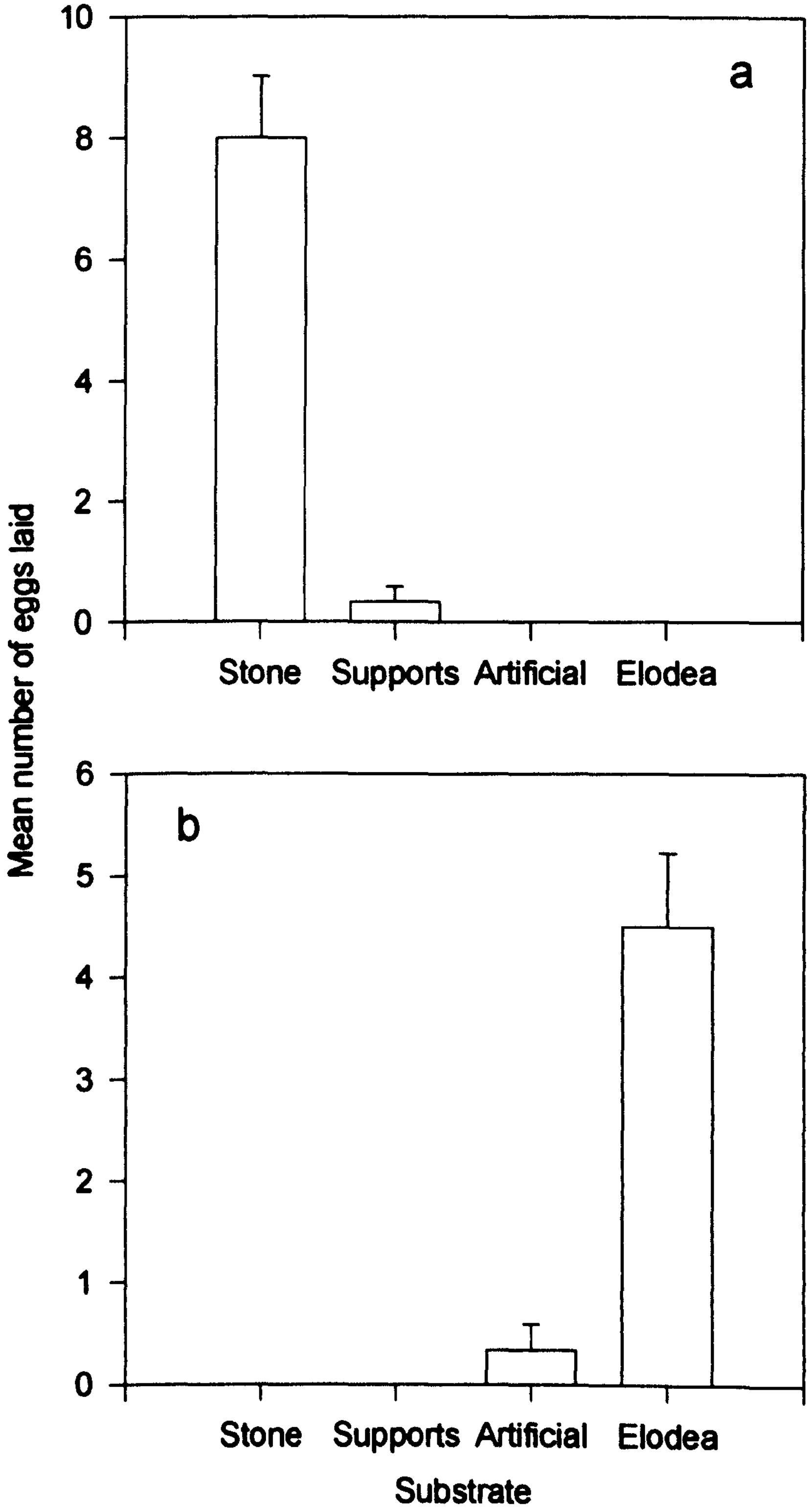

Figure 3.10 Mean number of eggs laid on different substrates by a) *N. maculata*, b) *N. obliqua*. Error bars = 1 standard error.

substrate for this method of oviposition. When laying on solid substrates, *N. obliqua* rapidly runs short of the waterproof 'glue' used for egg attachment and hence the eggs are more susceptible to dislodgement (Walton 1936). Only a very small number of eggs were laid on the artificial weed, which is structurally similar to *Elodea*, and none on the other substrates indicating that it is capable of accurate discrimination between substrates, and that it is the ability to embed the eggs into the substrate that appears most important for *N. obliqua*.

N. maculata was found to oviposit almost exclusively on stone, again only a small number of eggs laid on the supports suggesting that it can accurately discriminate between substrates. Oviposition on solid material of some description is the most widespread method of oviposition in the Notonectidae (Hungerford 1933), but *N. maculata* rarely oviposits on any support other than stone, using the spines on its relatively short ovipositor to scrape the surface of the substrate before oviposition (Walton 1936).

The strength of the observed oviposition preferences suggests that they could strongly influence habitat preferences, and the selection of oviposition substrates is consistent with the habitat preferences demonstrated by the species in the dewponds (section 3.2). *N. obliqua* was found primarily in ponds with submerged vegetation, its preferred oviposition substrate, whereas *N. maculata* was associated with ponds with low mud depth. The amount of mud present in the ponds affects the availability of solid substrate (primarily the concrete pond lining or the limestone blocks embedded in the clay linings) for oviposition. The close correlation between the habitat types occupied and oviposition preferences suggests that selection of different oviposition substrates by the two species is an important factor contributing to habitat preferences in the field (Bennett and Streams 1986, Streams 1987b).

3.5 Conclusions.

This chapter examined the habitat preferences of the *Notonecta* species in the dewponds. It has been demonstrated fairly conclusively that the two species occupy markedly different habitat types and not all the sites constitute suitable habitat for either species. For the purposes of predicting distribution patterns, the preferences can be summarised in terms of a relatively small number of the variables recorded. The species also demonstrated different patterns of pond occupancy in relation to area, with *N. obliqua* showing a stronger dependence of occupancy on pond area than *N. maculata*. This suggests that *N. obliqua* prefers larger habitats, whereas *N. maculata* can be found across a wide range of habitats, including fairly small waterbodies. These habitat preferences, both in terms of the variables that appear to be important in habitat selection and occupancy in relation to pond area, are consistent with available literature data (Southwood and Leston 1959, Giller and McNeill 1981, Savage 1989). Experimental examination of choice of oviposition substrate demonstrated that the species have strong and contrasting preferences. The preferred substrates are consistent with previous observational studies (Walton 1936) and with the observed habitat preferences in the dewponds. This would suggest that oviposition preferences have a significant impact on habitat selection by *Notonecta*.

Habitat preferences have implications for regional population dynamics and distribution of *Notonecta* species. At the level of the individual species, not all the dewponds constitute suitable habitat for breeding populations and hence potential occupancy is likely to be limited to a subset of the total number of ponds. This may influence the regional population dynamics of the species, which are explored in Chapter 4, through the spatial distribution of, and temporal changes in, suitable habitat across the landscape. The habitat preferences may also affect coexistence of the species at the landscape scale, by influencing the degree of overlap in distribution and hence the likelihood of competition between the two species. The competitive interactions between the species are examined in Chapter 5.

4. Spatial population dynamics.

4.1 Introduction.

Species occurring as multiple populations in a landscape of discrete habitat patches often show temporal changes in their spatial distribution. These changes in distribution result from extinction of local populations and establishment of new populations by colonisation of previously unoccupied patches of habitat. The colonisation-extinction dynamics of local populations are known as population turnover. The importance of local population turnover in population dynamics was first highlighted in the seminal text by Andrewatha and Birch (1954), who placed emphasis on frequent local extinction of populations and subsequent re-establishment. Interest in population turnover over a regional area has crystallised in recent years into a distinct field of studies centred around metapopulation dynamics (Hanski and Gilpin 1991, Hanski and Gilpin 1997, Hanski 1998).

Population turnover is of central importance in metapopulation dynamics because the persistence of a species as a metapopulation depends upon a balance between the rates of local extinction and recolonisation (Hanski 1991, Harrison 1994, see section 1.2). Although individual populations become extinct and currently vacant patches are colonised, the fraction of patches that are occupied remains at a dynamic equilibrium. If the rates of colonisation and extinction are not balanced, the system is termed a non-equilibrium metapopulation (Harrison and Taylor 1997) and the species will undergo a regional decline or expansion of distribution, depending on the direction of the inequality.

This chapter explores the spatial population dynamics and turnover of *N. maculata* and *N. obliqua* in the dewpond system. The first section is concerned with general patterns of pond occupancy and population turnover in relation to the persistence of *Notonecta* species as metapopulations. The results of these analyses provide a framework for the development of the subsequent sections, which focus explicitly on the processes of colonisation and extinction of local populations of *Notonecta* within the dewpond system.

4.2 Occupancy dynamics and population turnover.

4.2.1 Introduction.

Metapopulation models, starting with that of Levins (1969, 1970), make certain assumptions about the systems of populations under analysis. Although no field system is likely to meet all these assumptions (Hanski and Simberloff 1997, Harrison and Taylor 1997), there are certain suggested conditions that should be fulfilled in order for metapopulation dynamics to be considered important in regional persistence (Harrison 1991, 1994, Hanski, Pakkala, Kuussaari and Lei 1995, Thomas 1996, Hanski 1997a, Harrison and Taylor 1997). Here I will examine the patterns of pond occupancy and population turnover to assess whether the spatial population dynamics of *Notonecta* species in dewponds resemble those predicted by metapopulation models. Principally, I will investigate whether the levels of occupancy of *Notonecta* species appear to be at a dynamic equilibrium, whether all populations are at risk from extinction and the extent of population turnover over the period of study.

All of the following data are derived from the annual surveys of dewpond habitat and occupancy described in sections 2.5 and 2.6. For univoltine insects such as *Notonecta*, annual surveys are the most appropriate for the study of population turnover. Longer census intervals are likely to result in inflated apparent turnover rates (Diamond and May 1977, Clark and Rosenzweig 1994).

4.2.2 Changes in regional occupancy.

Figure 4.1 shows the number of ponds occupied by the two species of *Notonecta* in all years which surveys were carried out. The data are shown for the annual survey of 68 ponds between 1996-1998 and also for the subset of 32 ponds which were sampled in 1992 (data from Warren *et al.* in press) as well as in the years 1996-8. The survey by Warren *et al.* (in press) was carried out using a three minute timed pond net sweep through different habitat types, which was the technique used in heavily vegetated ponds during this study (see section

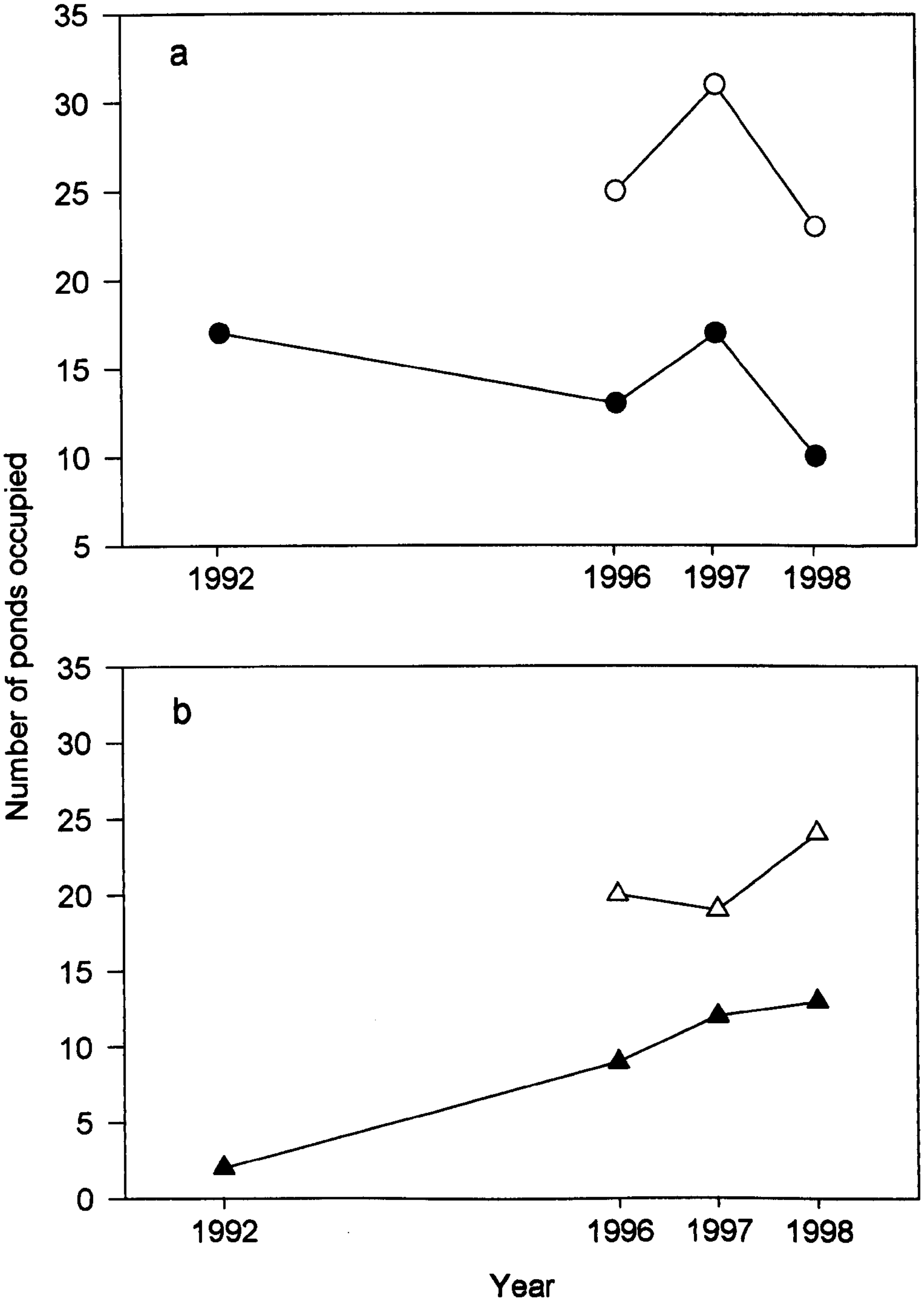

Figure 4.1 Changes in pond occupancy by the two species of *Notonecta* period of survey. a) *N. maculata*, b) *N. obliqua*. Open symbols refer to occupancy of 68 dewponds surveyed between 1996-1998, solid symbols refer to a subset of 32 of the dewponds that were sampled between 1992 and 1998.

2.5), and hence the pond occupancy data derived from this previous study is of similar accuracy to that derived from the surveys carried out in the course of these studies.

From figure 4.1 it is clear to see that there are some changes in the number of ponds occupied by the two species over the period of survey. For *N. maculata* there was a slight overall decline in occupancy of the 32 ponds that were surveyed between 1992 and 1998, although the scale of the changes relative to the number of ponds occupied is fairly small. Comparison between the occupancy recorded for the 32 ponds and that for the surveys of 68 ponds (1996-8) indicates that occupancy over a wider area appears to closely follow the changes that were observed in the 32 pond sample. However in such a short time series it is difficult to ascertain whether the fluctuations in occupancy at different scales are synchronous. *N. obliqua* however, showed a considerable increase in occupancy of the 32 pond sample between 1992 and 1998, being found in only two ponds in 1992, compared to 13 in 1998. These changes in occupancy are less clearly mirrored in the patterns of occupancy in the 68 ponds; the variation in this larger sample of ponds is again small compared to overall occupancy.

The trends in occupancy that are evident may be the result of stochastic variation around an equilibrial level of occupancy, which is of approximately similar magnitude for both species in the sample of 68 ponds (between 23 and 31 ponds occupied by *N. maculata*, and between 19 and 24 by *N. obliqua*). *N. maculata* appears to show fairly stable occupancy in both the 68 ponds and in the subset of 32 ponds, whereas *N. obliqua* shows a definite trend of increasing occupancy over time in the longer time series available for the 32 pond sample. These changes in occupancy may be the result of changes in the habitat of the ponds. Evidence from Chapter 3 suggests that not all the ponds are suitable for occupancy for a particular species. Submerged vegetation is a key habitat characteristic for *N. obliqua* and there is a significant positive correlation between the number of ponds with submerged vegetation present, and occupancy by *N. obliqua* ($r_{[4]} = 0.969, p = 0.031$, 1992-1998 dataset), although the small number of datapoints in the time series makes assessment of the relationship difficult. There was no evidence of any correlation between the changes in occupancy of *N. maculata* and habitat variables that appear important in habitat preferences (see Chapter 3), but the changes in occupancy over the same period have no clear trend.

4.2.3 Population turnover.

The turnover of populations was fairly high over the survey period. Considering only the surveys of 68 ponds between 1996 and 1998, only 12 ponds out of the 68 were occupied continuously from 1996 to 1998, five by *N. maculata*, four by *N. obliqua* and 3 with both species present. Eleven of the ponds were never occupied, with the remainder undergoing at least one turnover event in the three years of survey. From the data on changes in pond occupancy over the survey period, it is possible to derive the rates of colonisation and extinction, and also the amount of population turnover (colonisation and extinction combined). Although the processes of colonisation and extinction will be dealt with in greater detail in subsequent sections, a summary of population turnover over the survey period is given in table 4.1. The information in this table was derived using the following formulae:

Colonisation rate, C was calculated as: (the number of ponds colonised at $t + 1$)/(number of unoccupied ponds at time t), with t measured in years. This formula assumes that all the unoccupied ponds were suitable for occupancy. The rate of colonisation is likely to be influenced by the number of ponds that are presently occupied (in the original Levins metapopulation model [1969, 1970] and derivatives, the colonisation parameter, m is multiplied by the proportion of ponds occupied, p, see section 1.2). Therefore, in order to account for the potential variation in colonisation resulting from different levels of regional occupancy, a modified colonisation rate C_{pop} was defined as C/number of ponds occupied at time t. This effectively gives the colonisation rate per extant population.

The extinction rate, E was defined as: (the number of populations that had gone extinct by $t + 1$)/(the number of ponds occupied at time t), and the degree of turnover, T (not calculated as a rate) was defined as: (the number of turnover events [colonisations plus extinctions] between time t and $t + 1$)/(number of populations persisting over the same time period).

Table 4.1 Population turnover (colonisation and extinction) for the two species of *Notonecta* in a sample of 68 dewponds from 1996-1998. For abbreviations and details of calculations see text.

Variable	Species			
	N. maculata 1996-1997	1997-1998	*N. obliqua* 1996-1997	1997-1998
Colonisations	13	5	7	7
Extinctions	7	13	8	2
C	0.302	0.135	0.146	0.143
C_{pop}	0.012	0.004	0.007	0.008
E	0.280	0.419	0.400	0.105
T*	1.111	1.059	1.250	0.529

* Note: Values of T greater than one indicate that more populations underwent turnover than persisted over the same period.

4.2.4 Discussion.

Detection of trends in regional pond occupancy depends on the length of time over which the surveys are taken. In the surveys of 68 ponds in three consecutive years, the proportion of ponds occupied did not show notable variation over the survey period, suggesting that the levels of occupancy may be at a dynamic equilibrium. However when the trends in the subset of 32 ponds were examined over a six year period, there were more pronounced fluctuations in the number of ponds occupied, particularly for *N. obliqua*, which showed a substantial increase in occupancy between 1992 and 1998. There is some evidence that the changes in occupancy exhibited by *N. obliqua* were related to changes in the availability of suitable habitat (see also Chapter 3).

Proportional occupancy was examined assuming that all the ponds were suitable for occupancy by either species, but this is unlikely to be the case (see Chapter 3). Therefore, it is possible that the species exist at a dynamic equilibrium of occupancy within the set of sites that constitute suitable habitat, and it is changes in the habitat availability (i.e. number of suitable sites) that result in fluctuations in regional occupancy. Models have explored the implications of the destruction of habitat patches on metapopulation dynamics (e.g. Hess 1996) but have so far largely ignored the effects of habitat dynamics on regional persistence (Wiens 1997, Thomas and Hanski 1997, but see Stelter, Reich, Grimm and Wissel 1997).

Whatever the reasons behind the fluctuations in occupancy, the changes have implications for the choice of scale for studying regional population dynamics of *Notonecta* in the dewponds. The dewpond system is 'open', with no natural boundaries defining the edge of the metapopulation. It was not feasible to survey all the dewponds in the White Peak area (assuming that similar densities of ponds are found across the survey area, the total number of dewponds within the Peak National Park is estimated to be approximately 1500), but the scale of study affects the observed patterns of occupancy. The occupancy of *N. obliqua* was very low in 1992 (two ponds occupied), suggesting that if observations were based on a sample size of 32, species may be observed to 'go extinct', even though it is likely that they will persist in the broader landscape. Simulations based on randomised resampling with replacement (Manly 1997) of the observed patterns of occupancy, for pond networks with differing numbers of ponds, show that the variation in observed proportional occupancy increases with decreasing number of ponds sampled (figure 4.2). Even for a sample size of 68, there is considerable variation around the mean occupancy level, resulting from random variation in the ponds sampled. The species are likely to appear to be 'extinct' if the survey was based on a sample of between 9 and 21 ponds, depending on species and initial level of occupancy (see figure 4.2). These simulations assume that all the ponds are suitable for occupancy. In addition to the errors inherent in basing estimates of proportional occupancy

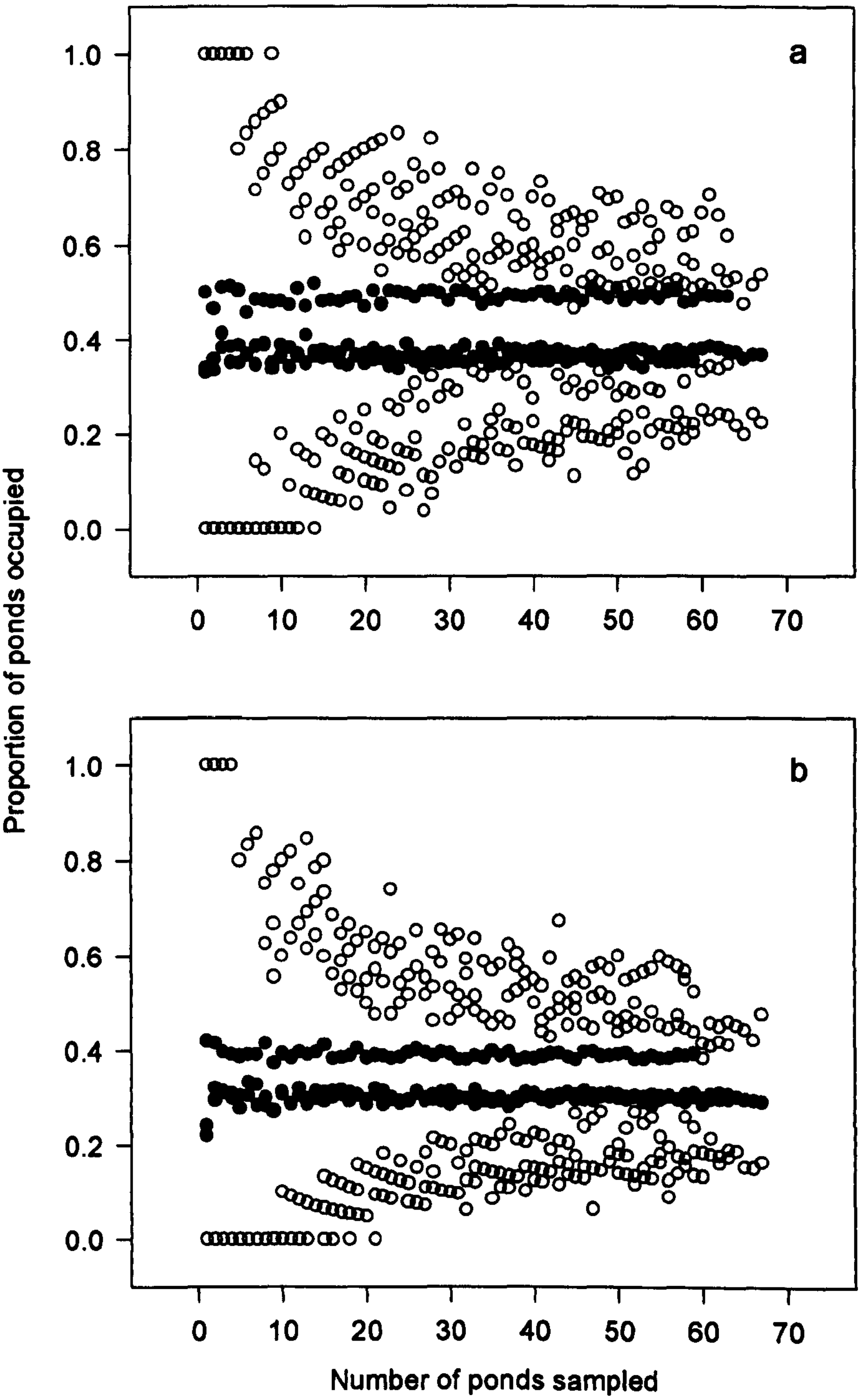

Figure 4.2 Simulated changes in observed proportional occupancy with number of ponds sampled for a) *N. maculata* and b) *N. obliqua*. Simulations are based on randomised sampling with replacement of observed proportion of ponds occupied in each survey between 1996-1998. Solid symbols show mean occupancy from 100 replicate trials for each year and open symbols represent maximum and minimum number of ponds occupied from the same trials.

on a limited sample of ponds, variation in the number of ponds suitable for each species within the sample will potentially further increase the temporal variation in observed occupancy.

The rate of population turnover is quite high in both species, with more populations undergoing turnover than persist over the same period in 3 out of 4 cases (table 4.1). Although the rates of colonisation seem quite high, they are comparable with other studies of annual insect species (e.g. Eber and Brandl 1996). The rates of colonisation and extinction are not constant, although *N. obliqua* shows remarkably consistent colonisation rate between years. However the calculations do not take into account the suitability of patches for colonisation and hence may be slightly misleading. Between 60 and 90% of populations persist from one year to the next (population persistence = 1-E), but the relatively small number of ponds that were continually occupied during the survey period suggests that it is reasonable to assume that all the populations have a substantial risk of extinction. The ponds that did have persistent populations showed no characteristics that would suggest that they are extinction resistant 'mainland' populations (Harrison 1991, 1994).

The relatively high rates of turnover would tend to suggest that the dewpond system lies towards the high dispersal end of the continuum of metapopulation types, superficially resembling a 'patchy population' (Harrison 1991, 1994). However the ponds do appear to represent local breeding populations. The lack of transfer of individuals during the period of nymphal development (almost all adults die before the summer) prevents mixing of populations from occurring all year round. Dispersal is limited to certain periods of the year (Fernando 1959, Popham 1964, see section 4.3), preventing the individual ponds from becoming demographically united, which would blur the distinction between local and regional timescales that is central to metapopulation functioning (Hanski 1983, Harrison 1991, Drechsler and Wissel 1997). Thus, at least from these data, it would seem reasonable to conclude that the regional dynamics of *Notonecta* species in the dewponds show at least some of the characteristics of a metapopulation.

4.3 Colonisation and dispersal.

4.3.1 Introduction.

Colonisation and extinction are the key processes on which metapopulation persistence is based (Hanski 1991, Hanski and Gilpin 1991, Hanski 1998), yet both of these processes are relatively difficult to study empirically, and colonisation especially so, due to infrequent occurrence in most systems, and difficulties in distinguishing the different stages of the process involved (Ebenhard 1991, Ims and Yoccoz 1997). In this section I will investigate aspects of the colonisation processes for the species of *Notonecta*.

In common with island biogeographical models (e.g. MacArthur and Wilson 1967), in a metapopulation setting all habitat patches are assumed to be suitable for occupancy, and colonisation is seen as an entirely stochastic process (Ebenhard 1991). The view of static underlying habitat, onto which stochastic patterns of colonisation are superimposed, is unlikely to be true in most natural systems. Habitat suitability will vary in different patches (see Chapter 3) and is likely to show temporal variation. In this situation, colonisation may be linked to habitat suitability (Thomas 1994b,c). This contrasting view of regional spatial dynamics regards changes in spatial distribution as being driven by deterministic habitat change, with species attempting to track the suitable habitat through time (Southwood 1977, Thomas 1994b,c, Webb and Thomas 1994, Harrison and Taylor 1997). Successional processes and disturbance regimes may be of prime importance in these situations (see Stelter, Reich, Grimm and Wissel 1997); these are themes more closely associated with patch dynamics (Pickett and White 1985, Levin, Powell and Steele 1993) than metapopulation dynamics. However, in structured population systems, stochasticity in habitat selection is likely to be greater than in other situations, due to the limited scope for organisms to sample the available habitat, which is distributed unevenly in time and space (Ims and Yoccoz 1997). Therefore I aim to test whether the colonisation of dewponds is linked to habitat characteristics or changes in the habitat, or is predominantly stochastic in nature as would be predicted for a metapopulation.

The probability of colonisation is also influenced by the isolation of patches; empirical evidence has shown that the rate of colonisation decreases with increasing patch isolation, due to the reduced probability of individuals arriving at a given patch (Hanski 1994b and references therein). The distribution of dispersal or migration distances is commonly modelled by negative exponential or inverse power functions, or regression equations based on the logarithm of distance (Wolfenbarger 1959, Harrison, Murphy and Ehrlich 1988, Kovats, Ciborowski and Corkum 1996, Thomas and Hanski 1997). Most dispersing individuals will not reach a very isolated patch, reducing the probability of successful population establishment. To assess the likelihood of recolonisation of ponds following extinction and the degree of connectivity of the dewpond system, I investigate the rate and pattern of colonisation over a year and use mark-release-recapture experiments to examine the distribution of dispersal distance by adult *Notonecta*.

4.3.2 Methods.

Annual survey.

Colonisation is one component of the turnover events analysed in section 4.2. Using the data from the surveys of 68 dewponds between 1996 and 1998, the number of colonisation events over each one year census interval was calculated for each species. Forward stepwise logistic regression, using the likelihood ratio method of variable selection and the same entry criteria as used in previous analyses (section 3.2.1), was used to test whether colonisation of ponds was related to the habitat variables recorded in the year which colonisation occurred, or the change in the variables between surveys.

Monthly colonisation rates.

The 32 ponds remaining of the 40 sampled in 1992 (Warren *et al.* in press) were sampled monthly from April 1996 to May 1997, using standard methods (section 2.5), to assess the pattern of pond colonisation by adult notonectid over the course of a year. Each month all the adults captured were identified to species. The colonisation rate for each species was defined as: (the proportion of empty sites at time t colonised at time $t+1$)/(the proportion of ponds occupied at time t), where t is in months. The dewpond system is 'open' in so far as it has no easily definable boundaries, and it was not possible to survey all the ponds over the survey area. Therefore the above formulation makes the assumption that the ponds surveyed were a random sample, so that the proportion of ponds occupied by each species in the survey area is a reflection of the overall occupancy across the whole system. However it is likely to underestimate colonisation rates as it does not include immigration to already occupied ponds. As a result of the inverse relationship between the number of ponds occupied and the number available for colonisation, the calculated colonisation rates are not independent of the number of ponds occupied in each survey. Due to this non-independence, the relative magnitude of colonisation rates cannot easily be interpreted and hence only the pattern of colonisation over the year will be considered. The definition of colonisation in this section is distinct from the use of the term to describe the establishment of a breeding population at a site, as it is used in *Annual survey* above and in population turnover calculations.

Mark-release experiments.

A mark-release-recapture study of adult dispersal distances was undertaken in the Autumn of 1997 and Spring of 1998 using a technique similar to that of Freilich (1989). A computer spreadsheet was used to generate three digit sequential numbers in a two point sans-serif font. These numbers were printed on a 600 dpi monochrome laser printer and individual tags (size 3x2mm) made by cutting the numbers out of the paper. Notonectids were collected in the field by standard sampling methods (section 2.5) and placed in a holding bucket. Individual adult *Notonecta* were removed using a small hand net and surface dried using paper towelling. They were then loosely restrained in the paper towelling and the tags were attached to the central region of the pronotum using cyano-acrylate adhesive (UHU® Superpower Universal Superglue, UHU [UK] Ltd, Middlesex). A liquid glue was used as this effectively penetrated the paper fibres and waterproofed the tag as well as providing adhesion. Following attachment of the tag, the tag number, the pond from which the individual was collected and the species were recorded. Due to the quick drying nature of the glue, individuals were generally out of water for one minute or less before being returned to another holding bucket and subsequently returned to the pond.

Preliminary tests indicated that the tags did not affect the ability of the notonectids to fly, but it was not possible to assess whether there were any effects on duration or distance of flights. Given the small size and weight of the tags it seems reasonable to assume that they would have a negligible effect. Individual marked adults were maintained in laboratory aquaria in order to assess tag retention and adult mortality. Although cyano-acrylate glue is not recommended for use under water or on waxy or oily surfaces (Freilich 1989) such as the pronotum of hemipterans, tags were retained by captive individuals for 5 months and adults in the field were recaptured with the tag attached after 4 months. Similar tags have been retained by aquatic Coleoptera in the field for up to 18 months (J. Bowker, personal communication) No effects of tagging on the mortality of captive adults were observed. Following marking, a large number of surrounding dewpond sites were visited intermittently and collections of notonectids made. All adults collected were examined for tags and if any were found, the number, species and pond from which the individual was recovered was recorded.

4.3.3 Results.

Annual survey.

For *N. maculata*, none of the habitat variables recorded in 1997 were significant in predicting the colonisation of ponds. However when the analysis was repeated using the change in habitat variables between 1996 and 1997, a significant logistic regression model was fitted to the data. The results of the stepwise logistic regression of pond colonisation between 1996 and 1997 by *N. maculata* in relation to changes in habitat variables are summarised in table 4.2. Two of the habitat variables recorded, change in mud depth and submerged vegetation cover, caused a significant increase in the log-likelihood ratio ($p < 0.1$) and hence were included in the final model. The regression coefficients (β) indicate the direction of influence: in both cases the coefficients are negative, indicating that the probability of colonisation increases with a decline in mud depth and submerged vegetation cover between years. From the final logistic regression equation, the colonisation probability surface can be derived. This is shown in figure 4.3, over the range of habitat variables found in the field. In 1998 no significant model could be fitted to the data for either the habitat variables recorded in 1998 or the changes in the variables between 1997 and 1998, suggesting that there was no systematic link between pond colonisation by *N. maculata* and the habitat variables recorded.

For *N. obliqua* in 1997, submerged vegetation cover in 1997 initially entered the logistic regression model, but the large standard error of the coefficient (standard error approximately 6 times larger than the coefficient) indicated that the model was a poor fit to the data (Tabachnick and Fidell 1996). Subsequent screening of the data indicated that the model was being driven by one outlying value of submerged vegetation cover in the ponds colonised by *N. obliqua* and hence the model was rejected. A similar situation occurred in 1998 and hence again no model was fitted to the data.

Table 4.2 Results of forward stepwise logistic regression of pond colonisation by *N. maculata*. a) Test statistics and steps of logistic regression. Model G^2 = log-likelihood ratio of the model, df = degrees of freedom of the logistic regression model, p = significance of logistic regression model. b) logistic regression equation parameter estimates. β = coefficient of the variable entered, SE = standard error of the coefficient, p = significance of the variable entered. Degrees of freedom of all variables entered = 1.

a) Test statistics

Year	Model G^2	df	p
1996-1997	13.19	2	0.001

b) Logistic regression equation

Year	Variable entered	β	SE	p
1996-1997	Constant	-1.68	0.56	0.003
	Change in mud depth	-7.22	2.95	0.014
	Change in submerged vegetation cover	-0.08	0.05	0.074

Monthly colonisation rates.

The colonisation rates for both species (figure 4.4) show a strongly seasonal pattern, with peaks of dispersal in spring and late summer. Following the spring dispersal phase, the adult population rapidly declines and hence dispersal is zero until the new cohort reaches maturity between July and August. There is then another peak of dispersal which gradually declines during the autumn as conditions become less favourable for flight. The dispersal rate of *N. obliqua* appears to be generally higher than *N. maculata*, but the significance of this cannot easily be judged due to the problems with the calculation of colonisation rates. Only three out of the 32 ponds were not occupied at some point during the study, and the ponds that were not occupied were very close to other ponds, suggesting that isolation was not the cause of the lack of occupancy in these cases.

Mark-release experiments.

A total of 248 individuals were marked during the Autumn of 1997 from 6 different ponds. Of these 30 were subsequently recovered, giving a recovery rate of approximately

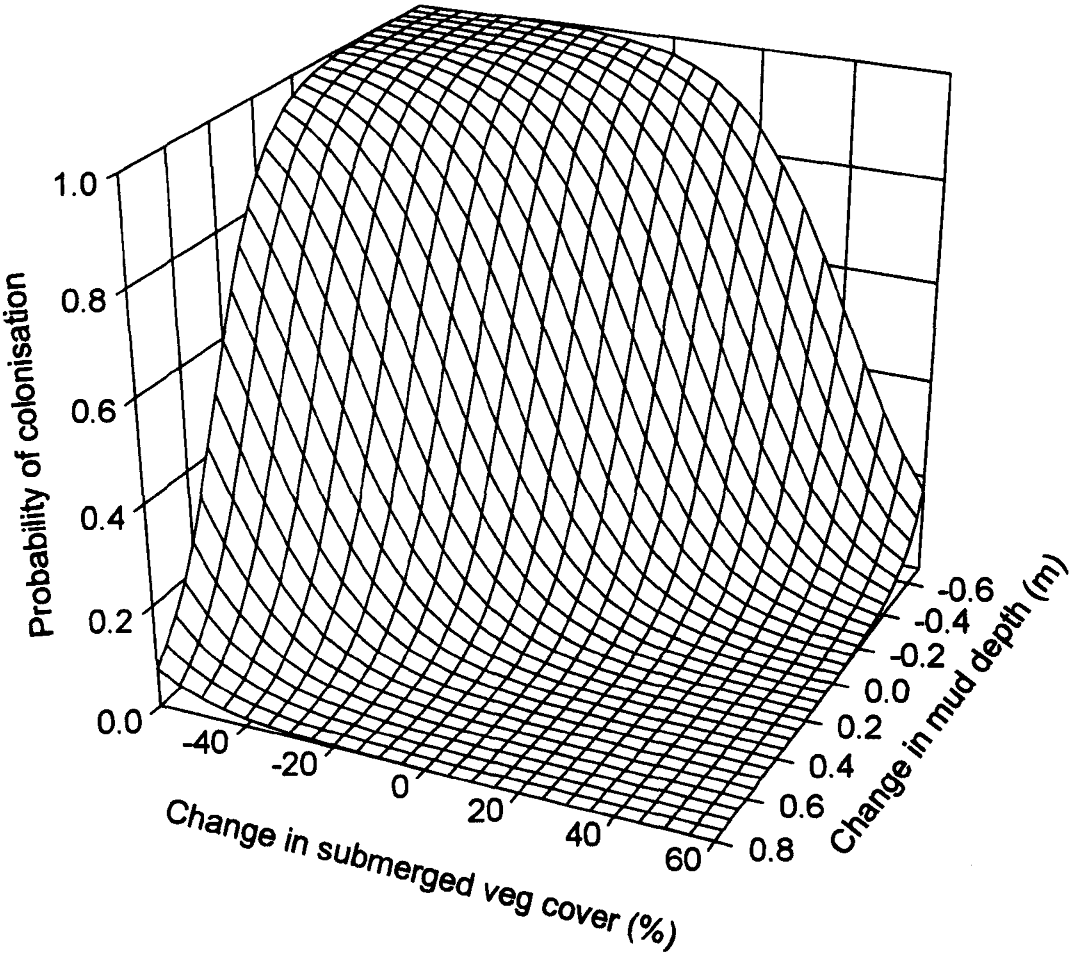

Figure 4.3 Probability of pond colonisation between 1996 and 1997 by *N. maculata* in relation to changes in mud depth and submerged vegetation cover over the same period. Probability surface derived from logistic regression equation (see table 4.2) over the range of values in the field data.

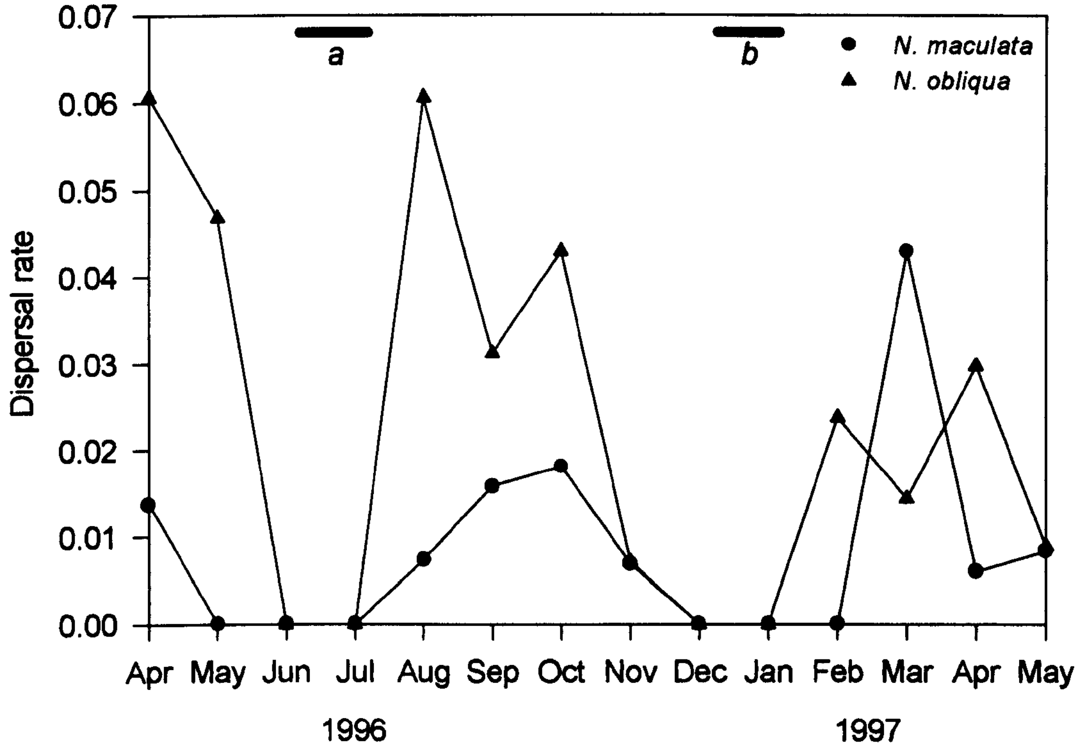

Figure 4.4 Monthly rates of colonisation of *Notonecta* species from 1996 to 1997 for a sample of 34 dewponds. Solid bar *a* between June and July indicates the period where only nymphs were present and the bar *b* between December and January indicates the period over which the ponds were frozen; in both cases dispersal was zero during these periods.

12%. Only three of the 30 individuals recovered had migrated between ponds (post migration recovery = 1.3%), and hence the conclusions that can be drawn from these data are very limited. Two individuals moved 90m between ponds, and one individual migrated 1640m.

4.3.4. Discussion.

Annual Survey.

The results of the logistic regression analyses suggest that there is some evidence for a link between colonisation of ponds and habitat variables, or the change in variables between years for *N. maculata*. There is no evidence of such a link between habitat and colonisation for *N. obliqua* but problems with the distribution of the data affected the model fitting process in the logistic regressions. Therefore it is difficult to draw conclusions from these results.

The variables included in the logistic regression model for *N. maculata* make biological sense in relation to the habitat and oviposition preferences demonstrated by this species (Chapter 3). However the link between habitat and colonisation is not consistent between years, suggesting that habitat is not the sole determinant of colonisation. This may be the result of the influence of stochastic elements in the colonisation process (Ims and Yoccoz 1997). For example, dispersal, and hence colonisation, is highly dependent on the prevailing weather conditions (Fernando 1959, Popham 1964). Therefore year-to-year variation in the timing and extent of suitable weather conditions for dispersal may influence the link between habitat and colonisation by restricting the chance of individuals dispersing and finding suitable habitat.

Monthly colonisation rates.

Both species of *Notonecta* showed a strongly seasonal pattern of colonisation common to other Heteroptera, both aquatic (Johnson 1969, Savage 1989) and terrestrial (Southwood 1960, Johnson 1969). The two peak periods of colonisation coincide with prevailing weather conditions that are suitable for dispersal (Fernando 1959, Popham 1964, Savage 1989). The seasonal pattern of colonisation prevents the exchange of individuals all year round, and during winter and the summer nymphal development period (see figure 1.2) the ponds are effectively isolated from each other. Therefore, although the rate of turnover is high (see section 4.2.3), each pond represents a local breeding population.

Although *N. obliqua* appears to have a higher colonisation rate, it is difficult to assess the significance of the differences between the species due to the problems inherant in the calculation of colonisation rates, and the data on the annual rate of colonisation over the same period (table 4.1) suggest a converse pattern with *N. maculata* having a higher colonisation rate. There is considerable evidence for a negative association between dispersal ability in insects and stability of the habitat occupied (Southwood 1962, Johnson 1969), as demonstrated by Brown (1951) for species of Corixidae. *N. maculata* is commonly found in temporary or unstable habitats, whereas *N. obliqua* is more often found in larger and more stable habitats (Southwood and Leston 1959, Blaustein, Kotler and Ward 1995, Walton 1943). If the relationship holds true for notonectids, it would suggest that *N. maculata* should have a higher dispersal rate than *N. obliqua*.

Mark-release experiments.

The very small number of individuals recaptured following dispersal limits the discussion of the results of these experiments. However the percentage recovery following migration was comparable to other studies (e.g. Nürnberger 1996) and this, combined with the successful retention of the tags for several months, suggests that it is a useful technique for examining dispersal and colonisation by mobile aquatic Hemiptera. The only conclusion that can be drawn from the results is that adult *Notonecta* are capable of dispersing at least 1.6km, but no further inferences are possible regarding the distribution of dispersal distances, and whether there are any differences between species. However, the distance to the nearest neighbour pond in the sample that were surveyed is generally less than 1km, and all but three of the ponds sampled for the monthly colonisation rate calculations was occupied at some point. It seems unlikely therefore, that any of the study ponds were too isolated for recolonisation to occur.

Conclusions.

This section aimed to evaluate the factors influencing the colonisation of dewponds by *Notonecta* and investigate the rate and pattern of dispersal by the two species. There is some limited evidence for a link between changes in the habitat and colonisation for *N. maculata*, but problems with the analysis prevent any conclusions regarding *N. obliqua* from being drawn. The link between pond colonisation by *N. maculata* and changes in habitat is not consistent between years; in 1998 there was no evidence of any habitat influence on pond colonisation. Stochasticity in the process of dispersal (Ebenhard 1991, Ims and Yoccoz 1997) may mean that species may not show effective 'habitat tracking', possibly due to limited opportunities to sample the available habitat due to seasonal dispersal, and hence colonisation is influence by both habitat change and chance effects.

The influence of isolation on dispersal and colonisation seems rather limited in the dewpond system, as the distance between ponds appears to be well within the dispersal range of the species. This would tend to suggest that connectivity between individual ponds is high, and hence individual ponds may be demographically united into a larger single population - a 'patchy population' (Harrison 1991, 1994). However the strongly seasonal pattern of colonisation limits the amount of dispersal that can take place between ponds and hence the individual ponds can still be considered to be local breeding populations.

4.4 Local extinction.

4.4.1 Introduction.

Local extinction of populations can occur as a result of the influence of numerous factors (Pimm, Jones and Diamond 1988, Lawton 1995), and it is the relative importance of the different factors that is fundamental to understanding the overall process of extinction in the content of a metapopulation or any population system showing local extinctions but regional persistence.

May (1973) and Shaffer (1981) developed schemes to characterise these different factors and 'types' of extinction. The primary division is between deterministic and stochastic extinction events. Deterministic local extinctions occur when there is an inexorable change in the environment, for example changes in the habitat occupied by the population (such as succession) which lead to it being no longer suitable for occupancy. Stochastic extinctions however, are the result of chance events (Goodman 1987, Foley 1997) and can be further subdivided by the nature of the chance process that is acting to cause extinction.

Demographic stochasticity refers to the chance events in birth-death processes that lead to population extinction (Goodman 1987, Pimm, Jones and Diamond 1988). Generally, the effects of demographic stochasticity are only important when the populations has been reduced to a fairly small size by the action of other factors (Goodman 1987, Harrison 1991, Foley 1997), although the precise population size depends on species' demographic traits (Ebenhard 1991). Similarly, genetic stochasticity, the effects of inbreeding and loss of genetic diversity on the likelihood of population extinction, are again generally only important in populations that have reached a critical size (Frankham 1995, Saccheri *et al.* 1998). Environmental stochasticity is concerned with random changes in population size due to the influence of external environmental factors such as food supply (Foley 1997); the final stochastic factor, catastrophes (Ewens, Brockwell, Gani and Resnick 1987, Lande 1993), refers to the effects of infrequent extreme environmental events such as drought or fire, which result in extinction. These terms apply to individual local populations, but the same principles can also be applied over a wider scale. Hanski (1991) described immigration-emigration stochasticity and regional stochasticity; the metapopulation level equivalents of demographic and environmental stochasticity respectively. The former describes extinction events caused by chance imbalances in immigration and emigration at a site, while the latter describes correlated environmental events which affect all the sites across a region and may reduce the lifetime of a metapopulation (Harrison and Quinn 1989, Gilpin 1990).

Most metapopulation models make the assumption that local extinction of populations occurs solely as a result of stochastic processes (such as environmental or demographic stochasticity) (Hanski 1991, 1994b, Harrison 1991, Foley 1997) and that deterministic processes are unimportant. This stems partly from the fact that all habitat patches are generally assumed to be equally suitable (an assumption that began with the first metapopulation model of Levins [1969, 1970]). If habitat quality, including such aspects as habitat patch area, does not vary then deterministic habitat change cannot influence population persistence. Some models incorporate loss of habitat through destruction (Nee and May 1992, Moilanen and Hanski 1995, Gyllenberg and Hanski 1997) which has the same end result as deterministic habitat change, but these models do not allow for habitat to be recreated. Obviously this simplifying assumption may limit the use of the current models in situations where changes in the habitat are an important driving force in spatial population dynamics (e.g. Stelter, Reich, Grimm and Wissel 1997).

Harrison and Taylor (1997), reviewing the empirical evidence for metapopulation dynamics, state that environmental stochasticity is the most likely factor driving local extinctions in the majority of metapopulations that have been studied (see also Harrison 1991) and it is this factor that is most commonly incorporated into extinction models (e.g. Foley

1997). However Thomas (1994b,c) suggests that the emphasis placed on stochastic factors in most metapopulation studies may be misplaced. Drawing mainly on studies of butterfly metapopulations, Thomas (1994b) suggests that most local extinctions are the result of deterministic changes in the local habitat which lead to extinction, and prevent recolonisation of the patch until further changes in the habitat have occurred to make the habitat suitable for occupancy again. Svensson (1985) and Sjogren Gulve (1994) also found evidence of deterministic extinctions of local populations of gyrinid beetles and pool frogs respectively, correlated with changes in the local habitat conditions in small ponds and Svensson (1985) documented recolonisation when the habitat became more suitable.

Given that most metapopulation models are based on the assumption of stochastic extinction as a result of environmental stochasticity, it is important to assess the importance of different factors acting to cause local extinctions when studying field systems that resemble metapopulations. Here I examine the extinction of populations to determine whether there is a link between habitat change and local population extinction. I then investigate the relationship between notonectid population size and dewpond area. A positive relationship is a central assumption of incidence function and other spatially explicit metapopulation models, which substitute patch area for population size in calculating extinction probabilities (see section 1.2). Finally I assess the rates of mortality experienced by overwintering populations of *Notonecta* to determine whether this is likely to be an important cause of local extinction.

4.4.2 Methods.

Annual survey.

Extinction events, recorded as part of the study of population turnover (section 4.2) were analysed in the same manner as described for colonisation rates (4.3.2). The number of extinction events was calculated for each species over each one year census interval and stepwise logistic regression used to analyse the probability of extinction in relation to the habitat variables recorded in the first census year or the changes in the habitat variables between years.

Quantitative survey.

A quantitative sample of the notonectid population was taken from 12 dewponds in August 1998, using the seine-type net method of sampling (section 2.5), to test whether there was a relationship between population size and pond area or other habitat variables. In order to attempt to reduce the variability due to differences in pond habitats, the ponds that were sampled were all concrete lined and contained no submerged vegetation. Ponds where both species occurred were also excluded due to the potential of interspecific interactions influencing the abundance attained by each species. The number of ponds within this classification that were occupied by *N. obliqua* was very small and hence estimates of population size were only obtained for ponds occupied by *N. maculata*.

Overwintering mortality.

Monthly surveys of five dewponds were carried out from November 1997 to March 1998 using the standard methodology (section 2.5). The counts of notonectids obtained from these surveys were used to provide a standardised population estimate for each pond in each month, allowing changes in overwintering population size to be investigated. The ponds were chosen to provide a range of starting population sizes whilst having broadly similar habitat characteristics. Only a total population census, regardless of species, was recorded and no comparison between the survival of the different species was made. In addition, intermittent visits were made to the ponds between surveys and relevant environmental conditions (for example extended ice cover) recorded. During this work it was noted that there was considerable variation in the degree of freezing of ponds following a frost. Therefore a survey of ice thickness at one metre from the pond edge was undertaken following a three day period of sub-zero temperatures across the whole survey area, to test whether there was a relationship between the severity of freezing and pond altitude.

4.4.3 Results.

Annual Survey.

The results of the stepwise logistic regression of local extinction are shown in table 4.3. For *N. maculata*, none of the habitat variables recorded in 1996 entered the logistic regression model. However when the change in habitat between years was used in the analysis, one of the habitat variables recorded, change in mud depth between years, was included in the final model, causing a significant increase in the log-likelihood ratio ($p < 0.1$). From the results it can be seen that an increase in mud depth between years caused an increase in the probability of population extinction (the regression coefficient for change in mud depth is positive, table 4.3b). Figure 4.5 shows the function derived from the logistic regression equation plotted over the range of values of mud depth change recorded in the field. In 1998 a significant logistic regression model was fitted to the data which included mud percentage cover in 1997 (table 4.3). A high percentage cover of mud in 1997 was associated with an increasing probability of extinction between 1997 and 1998 (figure 4.6). No model could be fitted using the change in variables between 1997 and 1998.

For *N. obliqua*, when the analysis was carried out on extinction between 1996 and 1997 using habitat variables recorded in 1996, one habitat variable entered the logistic regression model, percentage cover of submerged vegetation. A low percentage cover of submerged vegetation in 1996 was related to a increased probability of population extinction in 1997 (negative regression coefficient of submerged vegetation cover, table 4.3b). The function derived from the logistic regression model is shown in figure 4.7. When the analysis was repeated with change in habitat variables between census years, no significant logistic regression model could be fitted. For the 1998 data no model could be fitted as only two extinction events were recorded between 1997 and 1998. The small number of cases in one classification category (extinction events) lead to unstable parameter estimates and overfitting of the model due to the high variable to event ratio for this category (Tabachnick and Fidell 1996).

Table 4.3 Results of forward stepwise logistic regression of local extinction of *Notonecta* species in relation to habitat variables. a) Significance of logistic regression model. Model G^2 = log-likelihood ratio of the model, df = degrees of freedom of the logistic regression model, p = significance of logistic regression model. b) Logistic regression equation parameter estimates. β = coefficient of the variable entered, SE = standard error of the coefficient, p = significance of the variable entered (degrees of freedom for all variables = 1).

a)

Species	Year	Model G^2	df	p
N. maculata	1996-7	4.71	1	0.029
	1997-8	6.59	1	0.010
N. obliqua	1996-7	7.34	1	0.007

b)

Species	Year	Variable entered	β	SE	p
N. maculata	1996-7	Constant	-1.28	0.58	0.027
		Change in mud depth	9.80	5.33	0.066
	1997-8	Constant	-5.03	2.30	0.029
		Mud percentage cover	0.06	0.03	0.029
N. obliqua	1996-7	Constant	0.74	0.72	0.305
		Submerged vegetation cover	-0.08	0.04	0.061

Quantitative survey.

N. maculata population size, as estimated by the quantitative survey, was not correlated with pond area ($r_{[12]} = 0.111$, $p = 0.732$ using $\log_{10}$ transformed data, figure 4.8). Although it was examined over a limited range of pond and population sizes, there is little evidence of any relationship. The populations that were established between 1997 and 1998 did not appear to be any smaller than those that persisted over the same period, and one newly colonised population reached a very high abundance (350 individuals) (figure 4.8). Although no

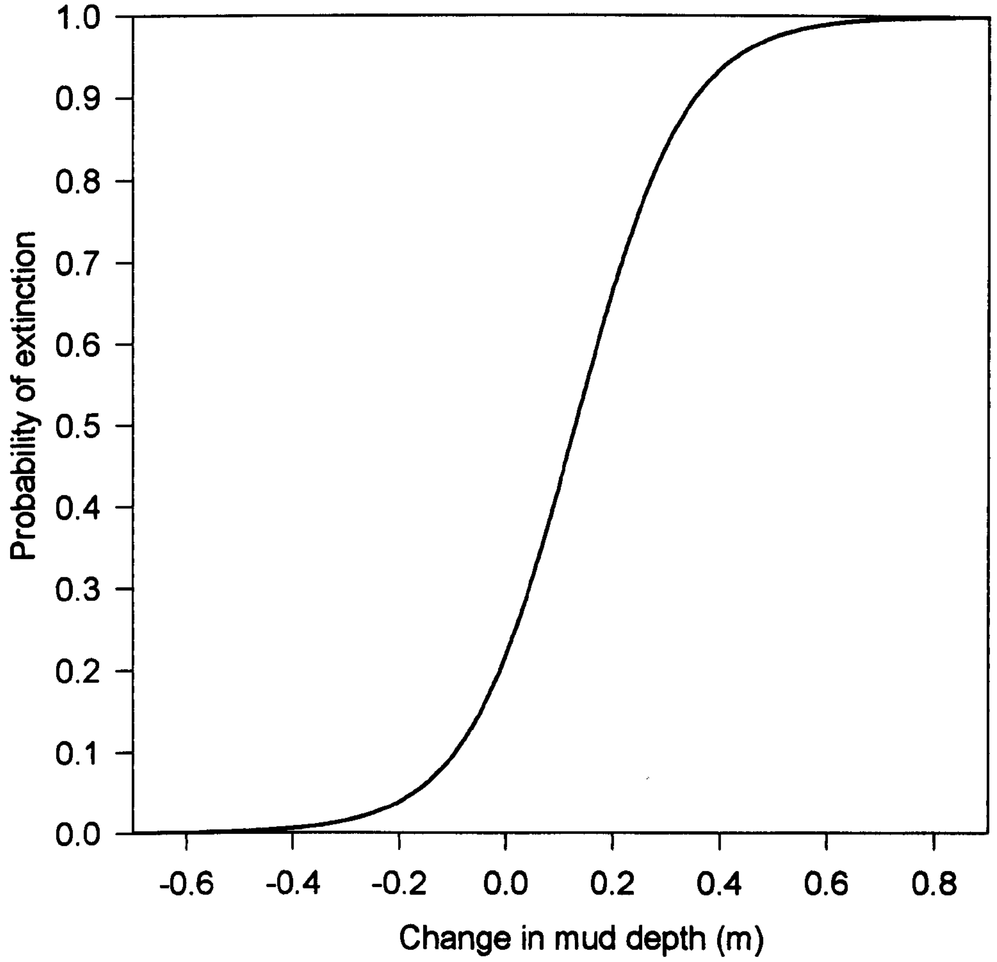

Figure 4.5 Probability of local extinction between 1996 and 1997 of *N. maculata* in relation to changes in mud depth. Fitted line derived from logistic regression equation (see table 4.3) over the range of values in the field data.

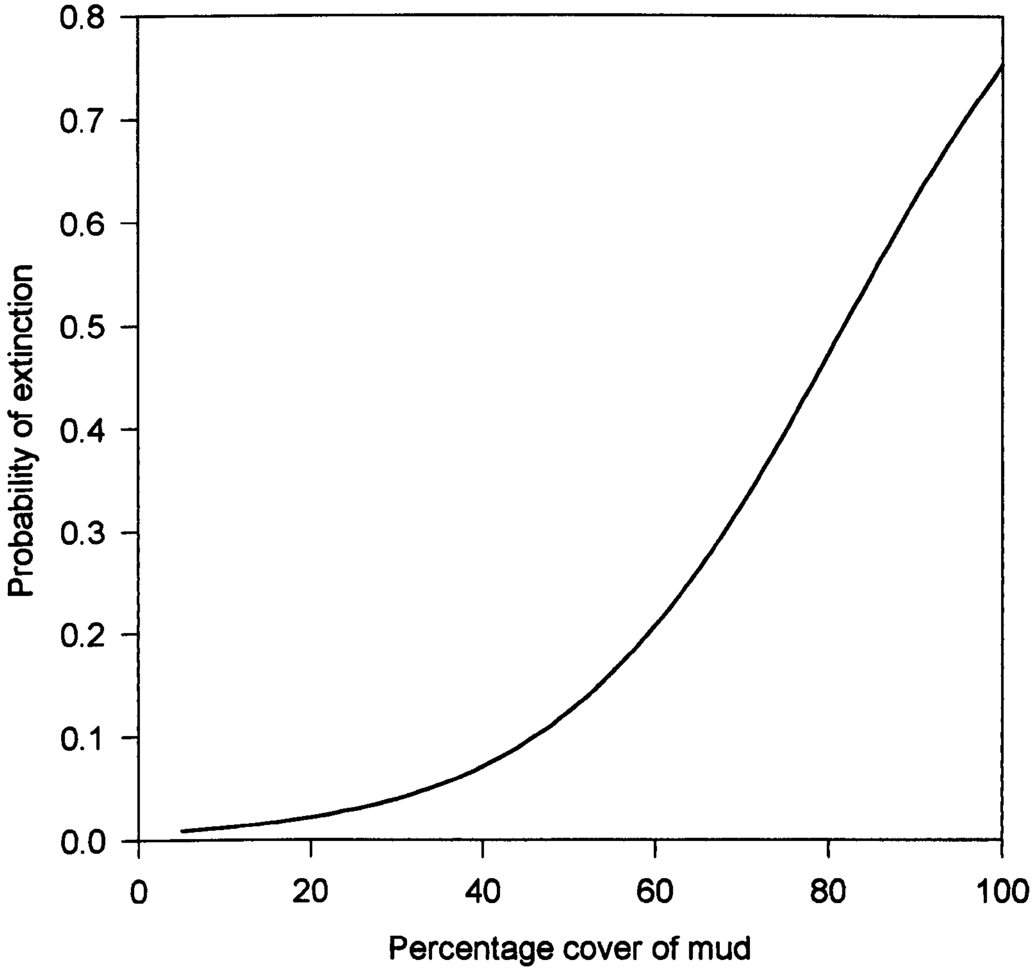

Figure 4.6 Probability of local extinction between 1997 and 1998 of *N. maculata* in relation to 1997 percentage cover of mud on the substrate. Fitted line derived from logistic regression equation (see table 4.3) over the range of values in the field data.

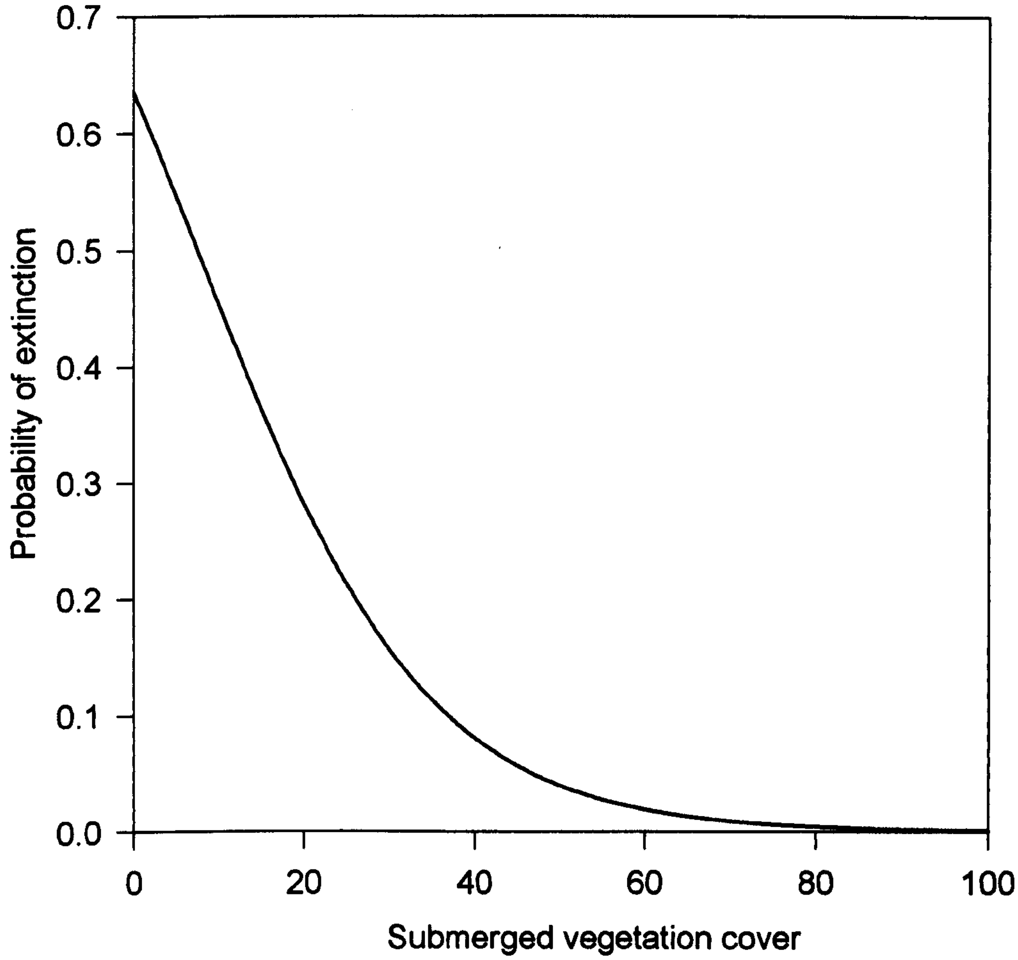

Figure 4.7 Probability of local extinction between 1996 and 1997 of *N. obliqua* in relation to 1996 percentage cover of submerged vegetation. Fitted line derived from logistic regression equation (see table 4.3) over the range of values in the field data.

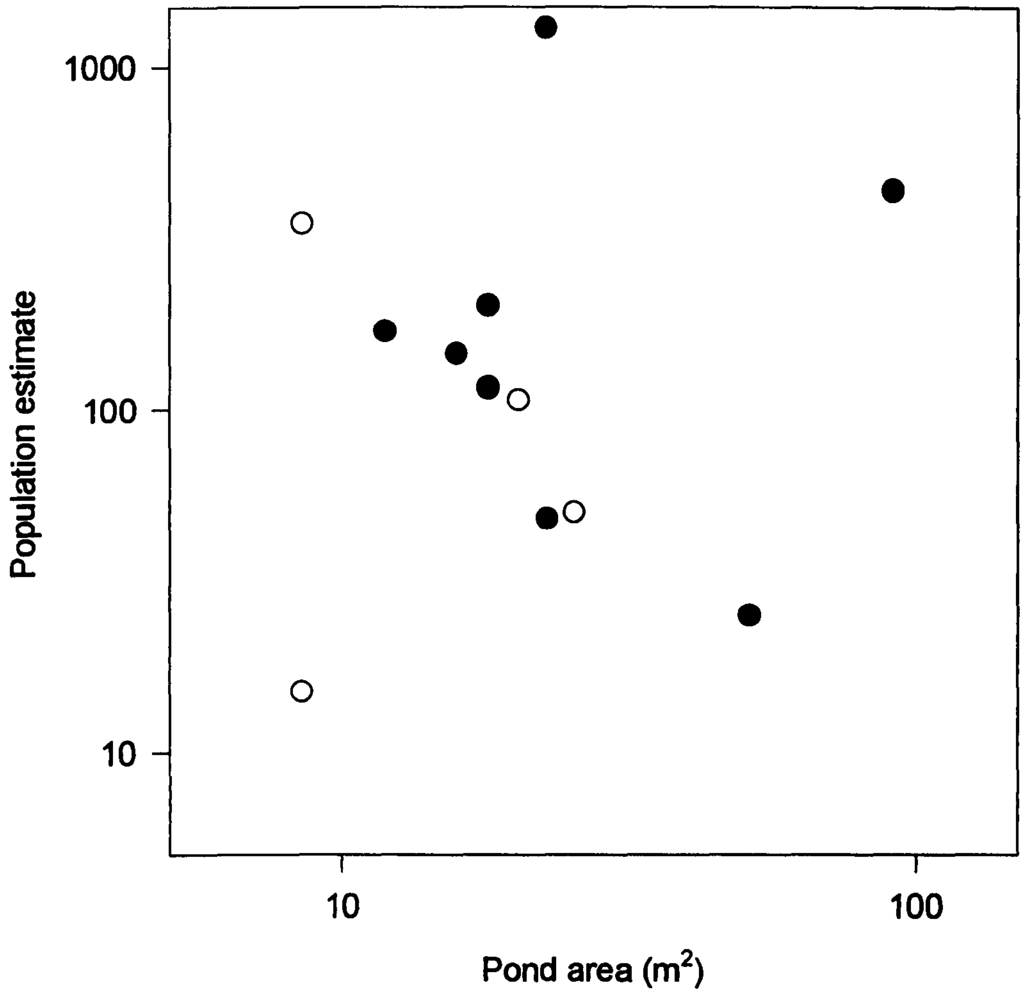

Figure 4.8 Correlation of local population size with pond area in 1998. Note $\log_{10}$ scale of both axes. Open circles represent populations that colonised between 1997 and 1998. Filled symbols are populations that persisted between 1997 and 1998.

information was obtained for *N. obliqua*, there is no reason to presume that this species would demonstrate a significantly different relationship.

Correlations were also calculated between *N. maculata* population size and percentage mud cover, the variable which was included in the logistic regression model of extinction for the period 1997-1998, to test whether the changes in extinction probability were correlated with local population sizes. The correlation between population size and percentage mud cover was not significant ($r_{s\,[12]} = -0.01$, $p = 0.974$), suggesting this has little influence on population size.

Overwintering mortality.

There was a general decline in the overwintering population in all ponds throughout the period of sampling (figure 4.9a), with some suggestion of ponds with larger starting population sizes (e.g. pond 28) showing a more rapid numerical decline. However in order to test for differences between the proportional rates of decline in the different ponds, the population abundances were converted into survival data, with the population estimate each month expressed as cumulative survival from the start of sampling (figure 4.9b). These data were analysed using the logrank (Mantel-Cox) test of survival (Miller 1981, Pyke and Thompson 1986). There were significant differences between the survival of populations in different ponds ($Z_{[4]} = 46.0$, $p < 0.001$). Pairwise comparisons of the populations were carried out (using a Bonferroni correction of the observed significance to correct for the number of comparisons being carried out [Norusis 1993]) to determine where significant differences occurred (see table 4.4). The population in pond 18 showed a significantly greater decline in overwinter survival than all the other ponds (figure 4.9b).

Given the assumption that the survival estimates obtained from the different ponds (which had different starting population sizes) are independent estimates of a common survival curve, then the data from the individual ponds can be combined to obtain an overall survivorship

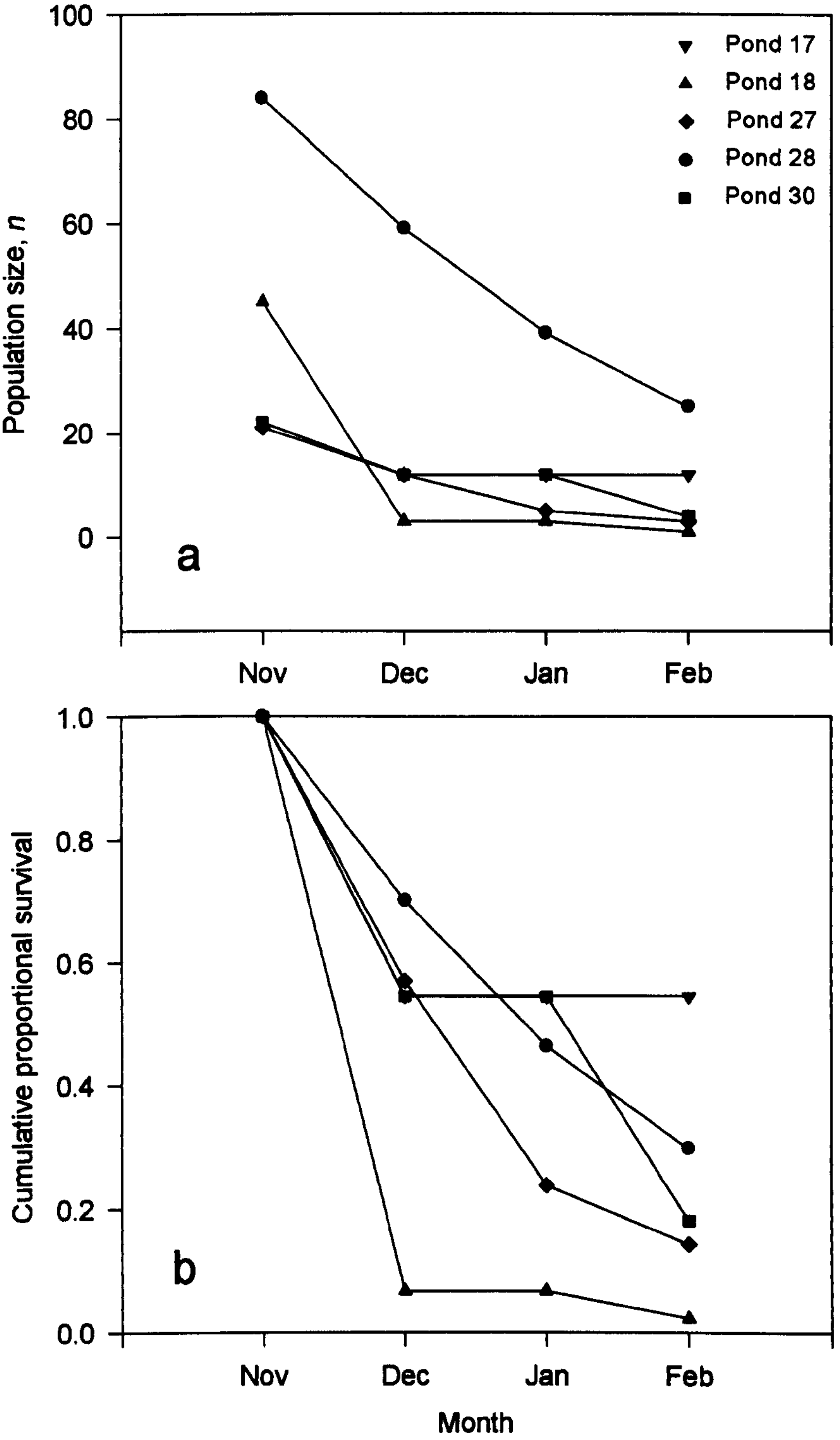

Figure 4.9 Decline in overwintering populations in five dewponds, Winter 1997-1998. a) numerical decline in population size, b) same data plotted as cumulative proportional survival, legend as for a). The population in pond 18 showed a significantly higher decline in survival over the survey period; see text for details.

curve (figure 4.10). This survivorship curve can be used to estimate the minimum population size required to successfully overwinter and maintain a viable population in the spring. In order to do this, a survival distribution model must be fitted to the observed survival data. The common survival distribution functions that can be fitted are the exponential distribution, the Weibull distribution, the lognormal distribution and the gamma distribution (Miller 1981, Cox and Oakes 1984, Pyke and Thompson 1986). Each of these models were fitted to the data using a iterative non-linear least squares regression procedure and the goodness of fit (as indicated by non-linear R^2) assessed. A simple two parameter negative exponential function had the best overall fit to the data ($R^2 = 0.911$) and hence this model was used to describe the combined survivorship curve (figure 4.10), which is linear if a $\log_{10}$ dependent axis is used. From this relationship, predictions of spring population size can be made from known autumn population sizes, assuming that the winter 1997/8 was a 'typical' winter (see Discussion).

Table 4.4 Bonferroni corrected significance from logrank (Mantel-Cox) test of survival for pairwise comparisons between overwintering survival of notonectid populations in dewponds.

	Pond 18	Pond 27	Pond 28	Pond 30
Pond 17	< 0.001	0.054	0.371	0.101
Pond 18		0.002	< 0.001	< 0.001
Pond 27			0.143	0.608
Pond 28				0.895

4.4.4 Discussion.

Annual Survey.

The results of the logistic regression analyses suggest that the probability of local extinction of populations is related to changes in the habitat, which may affect the suitability of the patch for the species concerned. The habitat variables included in the logistic regression models, and their direction of influence, appear to reflect the habitat preferences of

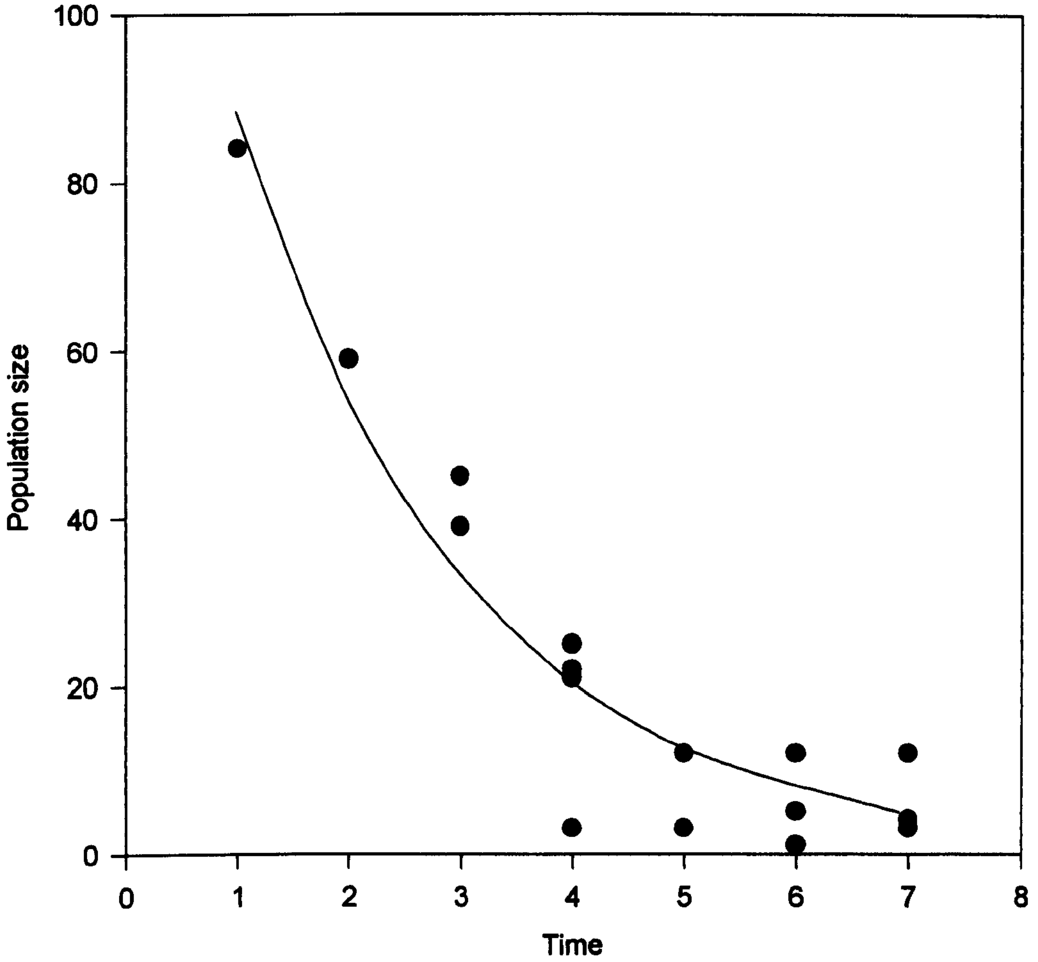

Figure 4.10 Overall survivorship curve for overwintering *Notonecta* derived from combined data across all ponds. Fitted line is an exponential function with parameters estimated by non-linear regression, equation: $y = 142.9\ e^{-0.48x}$. Time units = months.

the two species (Chapter 3). The habitat preferences of the species may reflect a number of factors such as foraging efficiency (Giller and McNeill 1981, Chapter 5), but the habitat variables that were included in the model are consistent with the suggestion that the availability of oviposition sites may be an important factor in habitat preferences and hence habitat driven extinction events.

The oviposition preferences of the two species are well known (Walton 1936, section 3.4). For *N. maculata*, the increase in mud depth between census years is likely to have led to a reduction in the availability of suitable hard substrate for oviposition. Given a thin cover of mud or silt, *N. maculata* can still successfully oviposit, and may clear the silt off the substrate through the action of oviposition (personal observations). However, thicker layers of mud on the substrate may render the surface unusable for this species. *N. obliqua* oviposits almost exclusively by embedding eggs into the stems of water plants. Therefore a lower percentage cover of submerged vegetation equates with fewer oviposition sites which may in turn serve to increase the probability of local extinction. In both cases, the paucity of oviposition sites may lead to smaller local population sizes and hence the probability of extinction via environmental stochasticity or chance demographic effects may increase.

Quantitative survey.

There appears to be no relationship between *N. maculata* population size and pond size in the dewponds, at least over the size range of ponds sampled. The population size of *N. maculata* also appears to be unrelated to habitat variables that influence local population extinction (see *Annual Survey* above), although the small number of samples involved makes the detection of any relationship difficult. Therefore, although it was hypothesised that the habitat related extinction events may be caused through changes in availability of oviposition sites, which in turn affect local population size, there is little supporting evidence from the data here.

Overwintering mortality.

The general decline in population size overwinter suggests that mortality during this period is a potentially important component of local extinction. When the proportional survival rates were examined, there were significant differences in the rate of decline overwinter between ponds, with one pond (pond 18) showing a significantly higher rate of decline than all the other ponds. The period of most rapid decline in this pond occurred between November and December and this coincided with extended ice cover on this pond, which was the only pond to freeze over this period.

There was a significant increase in the thickness of ice cover with altitude (figure 4.11) suggesting that higher ponds are more likely to suffer more severe and extended periods of freezing, which may lead to higher mortality (due to the reduction in dissolved oxygen concentrations in the water). However the fact that altitude does not enter the logistic regression analysis of the annual survey data also suggests that the effects of altitude on the overall rate of extinction are not strong over the range of altitude sampled. The considerable residual variation in this relationship probably indicates the importance of local aspect and exposure. Localised freezing of ponds, such as that of pond 18, may also have a considerable impact on overwintering mortality.

Despite the differences in survival rate detailed above, the overall numerical survivorship curve was well described by a simple negative exponential function. An exponential decline in population size over time suggests that although the proportional decline in survival is constant, larger populations will show a more rapid rate of decline in numerical terms. This is consistent with the numerical decline data (figure 4.9a) which suggests that the ponds with larger starting population sizes (for example pond 28) show a more rapid numerical decline, although the decline in proportional survival (figure 4.9b) is not significantly different from that of ponds with smaller starting population sizes.

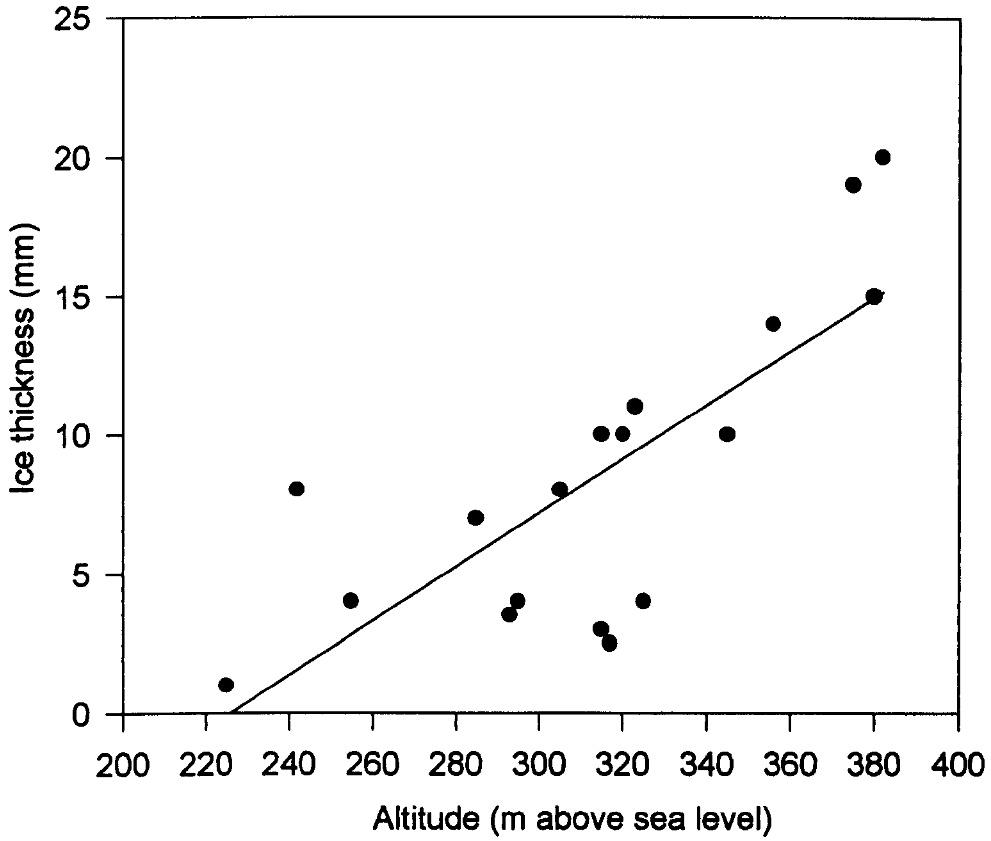

Figure 4.11 The relationship between the thickness of ice cover at one metre from the pond edge and pond altitude. Regression line fitted by linear least squares regression, regression equation is: Ice thickness = -21.4 + 0.0953 altitude, $F_{[1,17]} = 27.7$, $p < 0.001$, $R^2 = 0.597$. The data was collected following a three day period of sub-zero temperatures across the whole of the survey area.

The constant proportional decline in population size implicit in the exponential survivorship curve suggests that small autumn populations may still overwinter successfully and avoid extinction, as numerical decline will be slower. However the small population sizes will still make such populations vulnerable to extinction through demographic stochasticity. For *N. maculata*, mating occurs in the autumn as well as in the spring so it is potentially feasible for a single mated female to produce a population if it overwinters successfully. For *N. obliqua* a minimum of two individuals would be necessary due to the requirement of spring mating. If a more reasonable estimate of minimum spring population size of between 5 and 10 individuals is assumed for both species, then by interpolating from the survivorship curve, this corresponds to a autumn population size of approximately 30-60 individuals. Many of the local breeding populations will maintain populations of this size or greater, but the transitory populations consisting of dispersing individuals, and other populations whose reproductive success is lower, may not be sufficiently large to survive over winter.

Conclusions.

This section aimed to evaluate the relative importance of different factors in determining local extinction of *Notonecta* populations in dewponds. The evidence from the annual pond surveys suggests a clear link between habitat change and the probability of extinction. Therefore deterministic habitat driven extinctions would appear to be of considerable importance in the dewpond system, consistent with the views of Thomas (1994b,c) that deterministic extinction is of major importance in most metapopulations. Habitat change appears to affect the suitability of individual ponds for the species involved and hence recolonisation by the same species is unlikely following extinction until the habitat becomes more suitable again. The two species of *Notonecta* have contrasting habitat preferences (section 3.2 and 3.3) and hence although the patch may become unsuitable for one species it may become more favourable for the other species. The changes in habitat recorded here are over one year census intervals; in a previous study of population turnover of *N. maculata* in 34 dewponds over a four year census interval (Briers 1997), no link between population turnover and changes in habitat was found. However extinction was not analysed separately to colonisation, and changes in the habitat subsequent to those causing extinction may have left patches suitable again, but unoccupied due to the vagaries of colonisation.

The restricted range of data collected in the quantitative survey limits the conclusions regarding relationships between population size and pond area. The assumption of a positive relationship between these two variables underpins the incidence function approach to modelling metapopulations (Hanski 1994a,b, 1997, Eber and Brandl 1996, Hanski, Moilanen, Pakkala and Kuussaari 1996) and the generality of the relationship has been demonstrated for a wide range of organisms (Hanski 1994b, Williamson 1981). There was also no evidence for relationships between population size and habitat variables, despite the link between these variables and extinction probability in the logistic regression analyses.

Stochastic elements of population extinction in the dewpond system are largely represented by environmental stochasticity, in the effects of overwintering mortality. The survivorship curve derived from the data allows predictions of minimum population size required to successfully overwinter. Populations smaller than this may decline to such an extent that demographic stochasticity may begin to play a role in population extinction. The severity of the winter will obviously affect the viability of populations by altering the mortality rate. The conditions experienced by the populations will be broadly correlated due to the scale over which weather conditions act. However local variation in the severity of freezing due to factors such as pond altitude (see figure 4.11) and local aspect or exposure (pond 18, figure 4.9b) significantly affect population survival. Drought may also act as a catastrophic stochastic agent in the dewponds. In the summer of 1996, several ponds dried out completely and most had severely reduced water levels; again the conditions were broadly correlated across all ponds and hence drought acts to increase regional stochasticity (Hanski 1991).

Overall, deterministic extinction resulting from local habitat change appears to play the dominant role in causing local population extinction in the dewponds, and the effects of environmental stochasticity, as represented by overwintering mortality, and catastrophic events, such as drought are of lesser importance. The evidence from the dewpond system supports the contention of Thomas (1994b,c) that deterministic extinction events have greater importance in metapopulation type systems than has been credited in the majority of current metapopulation theory and models.

4.5 Conclusions.

This chapter examined the spatial population dynamics of *Notonecta* in dewponds, in relation to the proposition that regional persistence is the result of a balance of colonisation and extinction in a metapopulation.

The species showed many characteristics of metapopulation dynamics, such as population turnover, but there is evidence that the availability of suitable habitat is an important driving force in regional dynamics, which violates the stochastic turnover assumption of almost all metapopulation models. The availability of suitable habitat across the landscape appears to influence regional occupancy levels. Changes in the habitat of individual patches alter their suitability, which in turn affects the persistence of local populations, through the probability of extinction. There is less evidence of a link between habitat and colonisation of ponds, suggesting that this process may be more stochastic.

These results suggest that the regional population dynamics of *Notonecta* do not strictly conform to the assumptions of current metapopulation models, as regional persistence is more strongly influenced by the availability of suitable habitat across the landscape than a dynamic balance of colonisation and extinction.

5. Competition and coexistence.

5.1 General introduction.

Most metapopulation models consider single species dynamics, but extension of the single species metapopulation model of Levins (1969, 1970) and its derivatives to consider two competing species suggests that, contrary to the competitive exclusion principle (Hardin 1960), two species competing for the same resources can show stable coexistence over a regional area, even if they have an unstable local interaction, through dispersal to competitor-free patches (Levins and Culver 1971, Horn and MacArthur 1972, Slatkin 1974, Hanski 1983, 1995, Lehman and Tilman 1997, Nee, May and Hassell 1997). However in field systems, such fugitive regional coexistence may be relatively rare (Hastings and Harrison 1994, Harrison and Taylor 1997, but see Hanski and Ranta 1983, Bengtsson 1989, 1991). Natural systems of multiple habitat patches are likely to consist of a mosaic of different patch types rather than the homogeneous patches envisaged by metapopulation models (Holt 1997, Wiens 1997). In a landscape where there are qualitative differences between patches, contrasting habitat selection by species at the landscape scale may reduce the likelihood of competitive interactions between them, by reducing distributional overlap (Pimm and Rosenzweig 1981, Hanski 1995), in a similar manner to within-patch habitat partitioning (Schoener 1974). If competition does occur, the outcome of the interactions between the species may be influenced by the habitat type where the species co-occur (Danielson 1991, Hanski 1995)

N. maculata and *N. obliqua* show preferences for different habitat types (sections 3.2 and 3.3), but there is still some degree of overlap in their distributions (sections 3.2 and 4.2.3) and hence competition and other interactions such as mutual predation (Streams 1992) may influence regional distribution patterns. In this chapter I examine the competitive interactions between nymphs of the two species, to determine the extent to which competition where the species co-occur may influence pond occupancy and hence modify regional population dynamics and distribution patterns. I use laboratory and field experiments to investigate competition between the species in different environments, and also examine mutual predation in the laboratory.

5.2 Competition between nymphs.

The following section consists entirely of a paper accepted for publication in *Freshwater Biology*, with the exception that the figure and table legends have been altered and some minor re-formatting has been carried out to be consistent with the rest of the thesis, and the references are included with the other references at the end of the thesis.

Competition between the nymphs of two regionally co-occurring species of *Notonecta* (Hemiptera: Notonectidae).

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Running header: Competition and habitat in co-occurring *Notonecta*.

5.2.1 Summary.

1. Two species of freshwater invertebrate predator, *Notonecta maculata* and *N. obliqua* show a negative association in a series of small man-made ponds in the Peak National Park, Derbyshire, UK. This study examines the potential role of interspecific interactions among nymphs on this regional distribution pattern.

2. Survival, development and feeding efficiency of nymphs were examined in laboratory and field mesocosm experiments with intra- and inter-specific competition and contrasting environmental complexity.

3. Survival to adult and mean lifespan varied significantly in inter-specific competition treatments in both laboratory and field experiments, with *N. maculata* showing higher survival in the simple environment and *N. obliqua* higher survival in the complex environment.

4. Variations in feeding efficiency were consistent with the survival trends; *N. maculata* had a higher efficiency in the simple environment whereas *N. obliqua* had greater efficiency in the complex environment. There was evidence of a developmental response in feeding efficiency, with differences between species increasing with age.

5. These results suggest that the relative competitive abilities of the two species are affected by habitat complexity, and that competition between species may modify the species distribution where they co-occur.

5.2.2 Introduction.

Species of backswimmer, *Notonecta*, are important invertebrate predators in small standing freshwater habitats, such as ponds, ditches and pools (Blaustein, Kotler and Ward 1995, Jeffries 1996). Different species of *Notonecta* have broadly similar ecology (Hungerford 1933, Gittleman 1975), and there is the potential for strong competitive interactions between species when they co-occur, due to trophic niche overlap (Streams 1987a,b). Studies of notonectid guilds have shown that although individual species often show overlap in their geographical distribution, some combinations of species rarely co-occur and there is evidence for species segregation by habitat type (Taylor 1968, Streams and Newfield 1972).

Such partitioning of available habitats may be indicative of competitive, or other interactions between species (Gilpin and Diamond 1982, Connor and Simberloff 1983), but other factors influencing habitat selection in *Notonecta*, such as foraging efficiency in different environments (Giller and McNeill 1981), physical habitat characteristics such as pH, and preferences for different types of oviposition substrate (Hungerford 1933, Walton 1936) may also be important in influencing distribution patterns.

Most previous studies of competition in *Notonecta* have relied on comparative studies of foraging efficiency, activity patterns and body size to infer the likelihood of competition between species, or the relative competitive abilities of species in different environments (Taylor 1968, Streams and Newfield 1972, Gittleman 1975, Giller and McNeill 1981, Streams 1987a). There is some evidence that the type of habitat occupied is correlated with foraging strategy, and differences in habitat use may reduce the likelihood of inter-specific competition (Giller and McNeill 1981, Streams 1987b).

With the exception of Streams (1987b), these studies have been based on observations of adults. However in small habitats, nymph populations are often strongly food limited (Fox

1975a,b). Fox (1975b) found that in a series of small stream pools, an average of only four percent of *N. hoffmani* nymph populations successfully matured as adults, and Streams (1987b) cites between two and five percent survival to maturity of *N. insulata* in a 0.2ha pond. This would suggest that competition, and other interactions such as mutual predation (Streams 1987b, 1992) between the developmental stages of notonectids may also play an important role in determining patterns of distribution.

In the present study, we examined the competitive interactions between the nymphal stages of two notonectid species, *Notonecta maculata* Fabricius and *N. obliqua* Gallen, which co-occur regionally in the study area, but appear to have a negative association in their distributions. Previous studies of the adults of these species have shown an effect of environmental complexity on predation efficiency and habitat occupancy (Giller and McNeill 1981), which may influence the outcome of competition between the species. In a combination of laboratory and field mesocosm experiments we tested the influence of habitat complexity on the outcome of nymphal competition.

5.2.3 Study system.

The two species of *Notonecta* considered in this study regionally co-occur in 'dewponds' in the Peak National Park, Derbyshire, UK and are the dominant top predators in this system. The dewponds are small (4-12m in diameter), shallow (less than 1m deep) and generally saucer-shaped. The ponds, which occur at relatively high densities across the study area, are all man-made for the purpose of supplying water to stock in limestone areas, which have little or no natural standing water. Many ponds have no macrophytic vegetation, but a minority have extensive growth of submerged species such as water crowfoot (*Ranunculus* spp.) and pondweeds (*Potamogeton* spp.). They are generally circumneutral (median pH = 7.1, range = 6.4-8.6) and all ponds are fishless.

The two species are widely distributed in the dewponds, although *N. maculata* has a higher frequency of occurrence. Adult *Notonecta* have good dispersal mechanisms, being strong fliers, and pond occupancy is not constant over time; both species showing periodic local extinctions and colonisations. A survey of 68 dewponds over an area of 380km^2 carried out in July and August 1996, found that the occurrence of breeding populations of the two species showed a negative association ($\chi^2_{[2]} = 6.62, p < 0.05$). There is some evidence from these data that the negative association between the species may be partly related to submerged vegetation cover (figure 5.1): *N. maculata* is found largely in ponds with little or no submerged vegetation whereas *N. obliqua* is found over a much wider range of vegetation cover. This pattern of distribution is consistent with the differences in adult predation strategy and feeding efficiency demonstrated by Giller and McNeill (1981). Based on laboratory examination of predation efficiency, *N. maculata* was expected to be a better competitor in a simple environment, whereas *N. obliqua* had a predation strategy that enabled it to exploit a wide range of environments, and hence it was expected to out-compete *N. maculata* in more complex environments (Giller and McNeill 1981).

5.2.4 Materials and methods.

Laboratory experiments.

The laboratory experiments examined the survival and development of pairs of nymphs, either two conspecifics or one of each species, under conditions of differing environmental complexity and with increasing food limitation over time.

Experiments were carried out in clear plastic cups containing 200ml of dechlorinated tapwater. Two levels of environmental complexity were used: complex, with two 8cm segments of artificial aquarium weed, and simple, with no artificial weed. Each replicate contained two instar II *Notonecta* nymphs, all of which were reared from eggs laid in

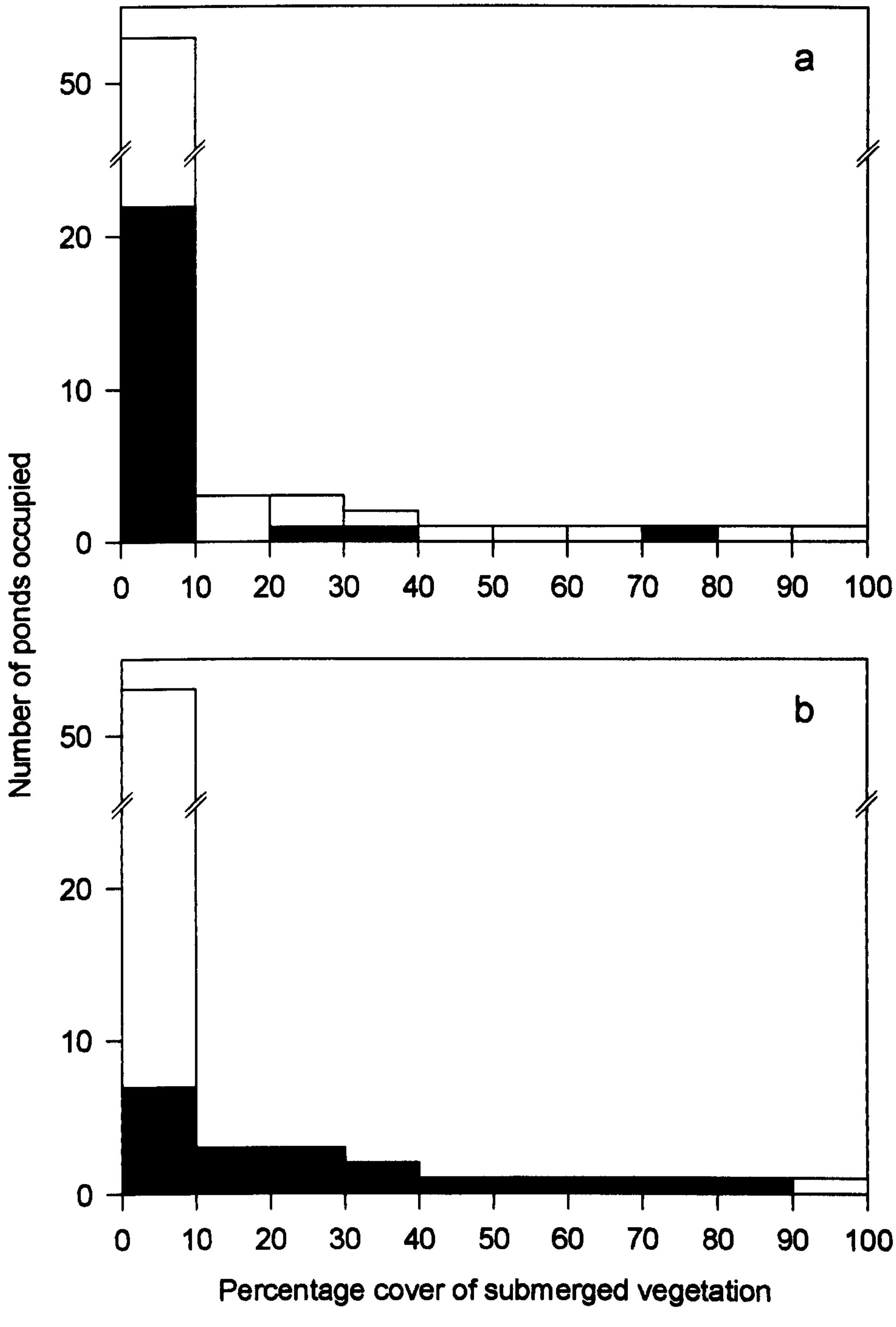

Figure 5.1 Number of ponds occupied by species of *Notonecta* in relation to percentage cover of submerged vegetation, a) *N. maculata*, b) *N. obliqua*. Solid bars indicate number of ponds occupied, open bars indicate unoccupied ponds. Data derived from survey of 68 dewponds in the Peak National Park in 1996. Mean cover for ponds occupied by *N. maculata* = 4.8%, by *N. obliqua* = 23.0%.

laboratory aquaria by adults obtained from dewpond sites, and which had been fed on *Daphnia magna* Straus.

Two competitor combination treatments were used for each species: conspecific, where each replicate contained two nymphs of the same species, and heterospecific, where one individual of each species was used. Experiments were initiated when the nymphs moulted into instar II due to high and unpredictable mortality of instar I. All experiments were carried out at 15^{0}C under a 12h light: 12h dark lighting regime. The number of replicates in each treatment varied between 11 and 15.

Food supply to each pair of nymphs was kept constant, at 25 *D. magna* every two days. The prey were graded with a series of sieves in order to present a consistent size of prey to the nymphs. Random subsamples of prey were taken, preserved in 70% alcohol and their lengths measured under a binocular microscope at × 20. The mean length of the prey was 2.27mm (SE = 0.03). In pilot experiments this feeding level was found to be sufficient to maintain two instar II nymphs or 1 adult. Therefore food limitation increased as the instars developed and their energy requirements increased. This mirrors natural conditions that may be experienced in field populations of *Notonecta* in small habitats (Fox 1975a,b). Dead *D. magna* were removed weekly and half of the water was replaced every two weeks.

All replicates were censused daily. The lifespan of individual nymphs was measured as the number of days from the beginning of instar II to death. In addition the instar that the nymph had reached at death was recorded based on the head widths of the nymphs. Results of the conspecific treatments were based on the first nymph to die of the pair in each replicate. In the heterospecific treatments lifespan data was based on the nymphs which died. Once one nymph had died, the replicate was censored in terms of lifespan data for the surviving nymph, but this nymph provided data on survival to adult.

Mesocosm experiments.

The purpose of the mesocosm experiments was to examine the outcome of competitive interactions between the nymphs, in terms of survival to adult, among larger groups of individuals in a habitat that more closely resembled the natural field conditions found in the dewponds.

Mesocosm construction. Experiments were carried out in square green plastic tanks (50x50x30cm) containing approximately 60 litres of water, located in part of the University of Sheffield Experimental Gardens. The tanks contained a one centimetre layer of washed horticultural sand as a substratum. Twenty tanks were used, giving five replicates of four treatments. Three of these treatments contained just the sand substratum (simple environment) and the fourth had a more complex environment with the complexity provided by five equally spaced bunches of water crowfoot, *Ranunculus* sp. (each bunch containing approximately 20 stems of weed between 20 and 25cm in length) which were weighted down and placed in each tank. The weed was collected from one of the field sites and thoroughly washed and carefully examined before use to prevent uncontrolled colonisation.

The 'simple' treatments contained either 16 *N. maculata*, 16 *N. obliqua*, or a mixture (8:8) of both species. The 'complex' environment treatment contained 8 nymphs of each species. The density used was within the range observed in the field. Practical constraints precluded the establishment of a full factorial design so there were no single species 'complex' treatments. All nymphs used were instar III, collected from dewpond sites known to contain single species populations. No attempt was made to control the age of nymphs other than to instar.

Inoculation. Prior to the start of the experiments, the mesocosms were inoculated with samples of water, detritus and organisms collected from five dewpond sites to provide a prey assemblage similar to that found in the dewponds. The material was collected in the field and brought back to the laboratory, where it was examined briefly on a light table and potential predators of *Notonecta* nymphs, mainly larvae of dytiscid beetles (*Agabus* spp.), removed. Following examination the material was placed in a large tank, mixed thoroughly and 500ml samples removed and added to the mesocosms. Equal amounts were added to each mesocosm until all the material was used up. This process was repeated weekly for four weeks and the mesocosms were then left undisturbed for another four weeks before the nymphs were introduced. During this time, and throughout the course of the experiments, the mesocosms were covered with fine white mosquito netting to prevent further uncontrolled colonisation and a layer of greenhouse shade netting to reduce light levels and prevent excess algal growth and overheating. Previous experiments using the same containers show that mesocosms set up in this way can support communities of invertebrates over periods well in excess of those used in this experiment (Warren and Spencer 1996, P.H.Warren, personal observations).

A secondary inoculation of prey organisms was carried out approximately one month after the start of the experiment which gave some opportunity for new species to colonise, or species that had gone extinct to re-colonise. This second inoculation consisted of two 500ml samples of material added to each mesocosm, which did not substantially augment prey abundance. Prey abundance declined over time, mirroring natural food limitation which is common for notonectids inhabiting small pond or pool habitats (Fox 1975a,b).

Sampling. Once the mesocosms had been stocked with notonectids, they were examined at two week intervals to check on the development of the nymphs. To maintain similarity between mesocosms, growth of duckweed, *Lemna minor* L. was removed during these inspections where extensive cover had developed. Frequency of examination increased to every two or three days as the nymphs reached instar V and each replicate was sampled when visual inspection showed that all the surviving nymphs in that replicate had become adults. All notonectids were removed using a hand net, identified to species in the field by their hemielytral patterns (Savage 1989) and replaced. The experiment was then continued until the last nymph across all the replicates had become adult and the number surviving in each replicate was recorded again. The result of analysis of data from the first and second samples were very similar and hence only the results from the first sample of each replicate are given here.

Feeding efficiency.

These experiments were designed to test whether the feeding efficiency of notonectid nymphs was affected by environmental complexity in a similar way as it is in adults of the same species (Giller and McNeill 1981).

The laboratory arenas and prey used were exactly the same as for the laboratory competition experiments. The use of standard prey size may increase variation in attack rate and handling time between instars (McArdle and Lawton 1979, Streams 1994) but the primary interest here was comparison of feeding rate within instars in arenas of different environmental complexity.

Notonecta nymphs came from the same stock as used in the previous laboratory experiments, and prior to the experiments were fed *ad libitum* on *D. magna*. Nymphs that were near to moult were not used as they tend to have lower feeding rates (Fox and Murdoch 1978). Each trial was set up by introducing a single nymph to each container and keeping it for 24hr under a 12hr light: 12hr dark regime at 15°C without food to standardise hunger levels. Then 40 *D. magna* were added to each container and the number remaining alive counted after 2hr. All experiments were carried out in the light at 15°C. Dead *D. magna* were examined to confirm that all mortality was due to predation, by their crumpled and ragged appearance. The experiments were carried out for instars I to V of both species, in the simple and complex environments. Eight replicates were performed for each species/instar/complexity combination.

5.2.5 Results.

Laboratory experiments.

Survivorship and mean lifespan. All replicates for the conspecific treatments are uncensored (i.e. all replicates were followed until death of one of the pair) and the mean lifespan (time from start of instar II until death) of the first nymph to die in different environments was analysed using a two-way ANOVA, with species and environment as fixed effects. Neither the fixed effects, or the interaction between them, was significant (species $F_{[1,44]} = 0.26, p = 0.609$, environment $F_{[1,44]} = 0.78, p = 0.381$, and interaction $F_{[1,44]} = 0.09, p = 0.767$). Data from the heterospecific treatments, based on the survival of both nymphs, were censored, as once one nymph had died, no further lifespan information could be obtained for the other nymph. No *a priori* assumptions were made concerning survival distributions (Cox and Oakes 1984) and therefore the logrank (Mantel-Cox) test (Pyke and Thompson 1986) was used to compare the lifespan of nymphs in these treatments, taking into account the censoring of replicates.

There was a significant difference between the average lifespan attained by nymphs in the different treatments ($Z_{[3]} = 14.51, p = 0.002$, see figure 5.2). Therefore pairwise comparisons of the survivorship curves were carried out, using a Bonferroni correction to allow for the number of comparisons being carried out (Norusis 1993) (see table 5.1). There was no significant difference between survival of *N. maculata* in the different environments, whereas *N. obliqua* had significantly higher survival in the complex environment compared to its survival in the simple environment and that of *N. maculata* in the complex environment (see figure 5.2).

Instar at death. In order to test whether the proportion of individuals reaching a given instar varied between treatments a three-way contingency table (variables = instar at death [*I*], environmental complexity [*E*] and species combination [*S*]) was constructed. This was

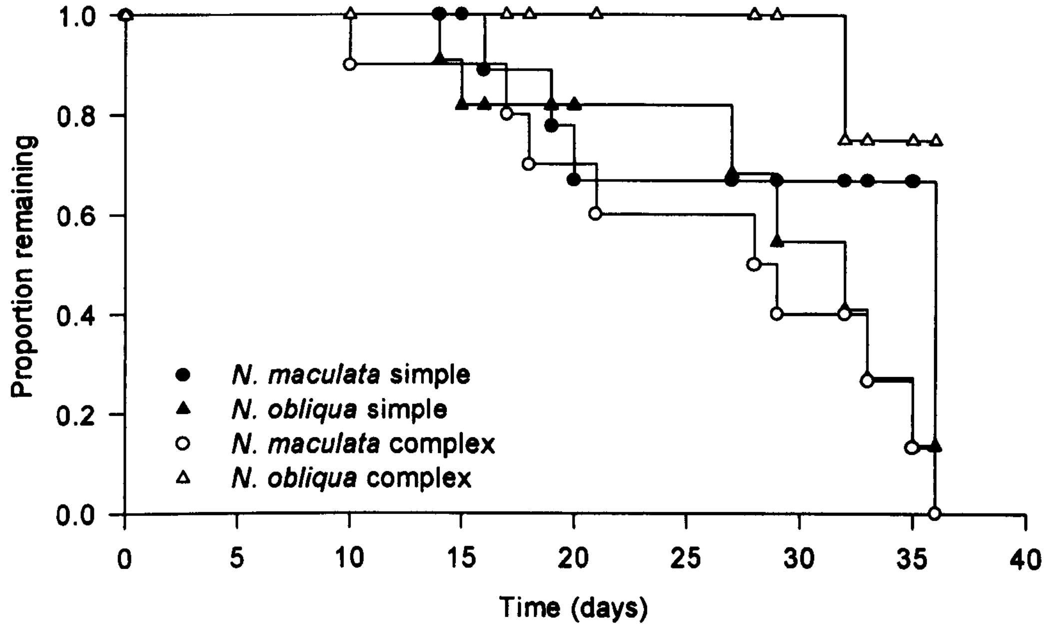

Figure 5.2 Survivorship curves showing proportional survival across all replicates for *Notonecta* nymphs in heterospecific treatment. Data points indicate where proportional survival changed (i.e. a nymph died) or where a replicate was censored (no 'step' in line).

analysed using a logit loglinear model (Wrigley 1985, Tabachnick and Fidell 1996) implemented in SPSS (Norusis 1993) with [*I*] as the dependent variable. In the heterospecific treatments, only the nymphs that died were included, the censored replicates being analysed separately (see *Survival to adult with heterospecific competitors*). Only three nymphs out of 77 which died reached instar IV and hence for the purposes of analysis Instars III and IV were collapsed into category Instar III+ to minimise structural zeros which influence expected cell values and may affect the fit of the model (Fienberg 1970, 1977).

Initially a saturated model, containing all possible effects and interactions, was fitted and then interactions and effects removed by backwards deletion based on the change in the likelihood ratio G^2, in order to obtain the best fit to the observed frequencies. The model with best overall fit to the data (likelihood ratio $G^2_{[6]} = 5.56, p = 0.475$) contained no significant associations between the instar at death and species combination or environment.

Table 5.1 Bonferroni corrected significance from logrank (Mantel-Cox) test for pairwise comparisons between nymph lifespans in heterospecific treatment.

Environment		Simple		Complex	
	Species	*N. maculata*	*N. obliqua*	*N. maculata*	*N. obliqua*
Simple	*N. maculata*	-	0.365	0.140	0.189
	N. obliqua		-	0.607	0.035
Complex	*N. maculata*			-	0.011
	N. obliqua				-

Developmental response. Although the effects of environmental complexity and competitors on lifespan and instar at death have been considered above, these analyses do not account for the fact that nymphs may show overall slower development when experiencing competition. Nymphs may have a long lifespan, but not develop beyond the instar at which the experiment was started. It was therefore necessary to factor out the variation in lifespan due to slow development within instars. A three-way ANOVA was carried out on the lifespan data, with instar at death, species and environment as fixed effects. The heterospecific treatments were excluded due to the large number of censored replicates and hence the analysis only considered the effects of environmental complexity on intraspecific competition. There were no significant interactions between effects and the only significant main effect was that of instar at death ($F_{[1,33]} = 20.9$, $p < 0.001$). Not unexpectedly, the mean lifespan of instar III nymphs was longer than that of nymphs which only reached instar II.

Survival to adult with heterospecific competitors. In the heterospecific treatments, once one nymph of the pair died, the replicate was censored with respect to lifespan data. However the surviving nymph of the pair was maintained under experimental conditions and was identified to species on reaching instar V by the colouration of the hind tarsi. Therefore the numbers of individuals reaching maturity (all surviving nymphs subsequently became adults) could be compared. *N. obliqua* had higher survival to adult than *N. maculata* in the complex environment and a reverse and slightly weaker trend was evident in the simple environment (table 5.2).

Table 5.2 Survival to adult of *Notonecta* species with heterospecific competitors in environments of differing complexity. Frequency of survival varied significantly with environment (Fishers Exact test, $p = 0.017$).

Environment	Species	
	N. maculata	*N. obliqua*
Simple	7	4
Complex	1	9

Mesocosm experiments.

Proportional survival to adult (S_a) was calculated for each species as the number of adults remaining at the end of the experiment divided by the number present at the start (16 in single species treatments or 8 in the treatments containing both species). For analysis, the proportions were transformed using the arcsine square root transformation.

Simple environment survival. There were significant differences in the survival of nymphs in different species combinations in the simple environment (one-way ANOVA, $F_{[3, 16]} = 8.45$, $p = 0.001$). Taking each species separately, survival of *N. obliqua* was significantly lower with heterospecific competitors than with conspecifics (Tukey test, $p < 0.05$, figure 5.3) but there was no significant difference in survival of *N. maculata* with either competitor combination.

Simple-complex comparison. Survival of each species in the presence of heterospecific competitors was compared in different environmental complexities using a two-way ANOVA. There was a significant interaction between species and environment ($F_{[1, 16]} = 14.52$, $p = 0.002$), but the main effects were only borderline significance (both $F_{[1, 16]} = 4.08$, $p = 0.06$). *N. maculata* showed significantly lower survival in the complex environment (Tukey test, $p < 0.05$), whereas there was no significant difference between environments in the survival of *N. obliqua* (Tukey test, $p > 0.05$, figure 5.4).

Feeding efficiency.

For each species, the mean number of *D. magna* eaten was analysed in a two-way ANOVA, with instar and environment as fixed effects. For both *N. maculata* and *N. obliqua* there were significant effects of instar ($F_{[4, 70]} = 279$, $p < 0.001$ and $F_{[4, 70]} = 370$, $p < 0.001$ respectively), environment ($F_{[1, 70]} = 17.1$, $p < 0.001$ and $F_{[1, 70]} = 27.0$, $p < 0.001$) and the interaction ($F_{[4, 70]} = 5.4$, $p = 0.001$ and $F_{[4, 70]} = 8.7$, $p < 0.001$) (figure 5.5).

Considering only the within-instar comparisons, instars I and II of both species showed no effects of environmental complexity on predation rate. However later instars demonstrated a divergence in predation rate in different environments. Instar III and IV *N. maculata* had a significantly higher predation rate in the simple environment, and instar IV and V *N. obliqua* had a significantly higher predation rate in the complex environment.

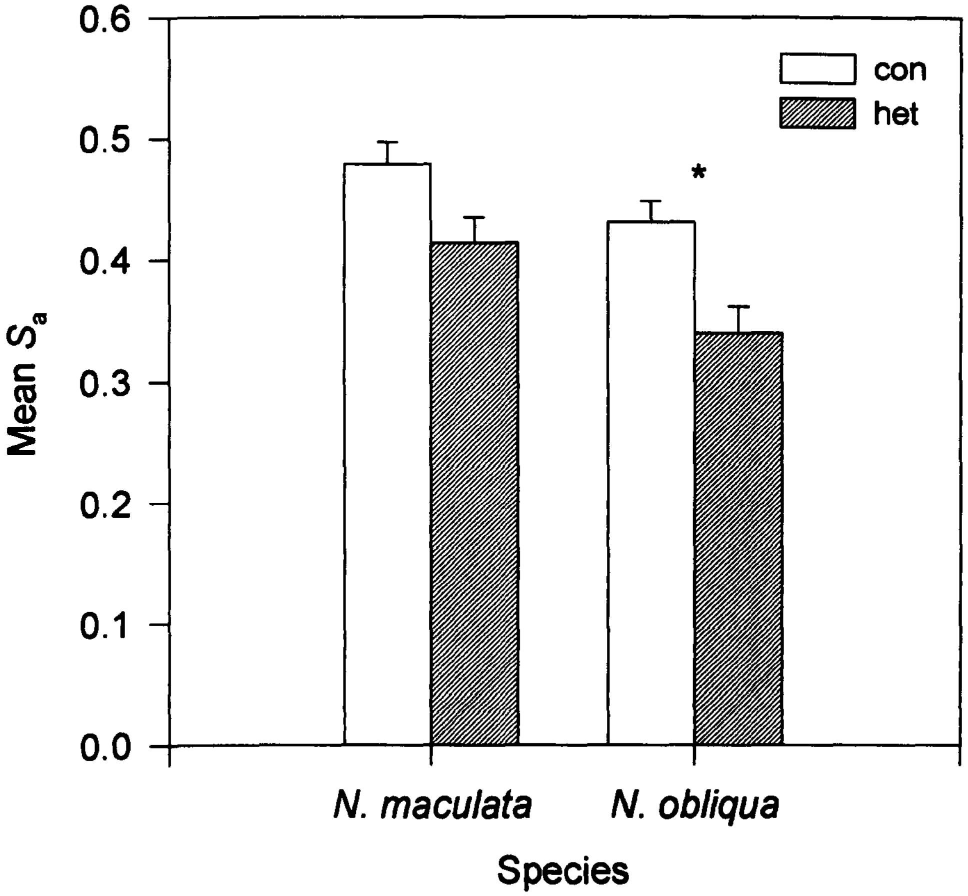

Figure 5.3 Mean proportional survival to adult (S_a) for *Notonecta* nymphs in simple environment mesocosms with different competitor combinations. Legend codes as follows: con = conspecific competitors, het = heterospecific competitors. Error bars = 1 standard error. Means and standard errors are arcsine square root transformed. * = indicates where means differ significantly within species at $p < 0.05$ (Tukey test).

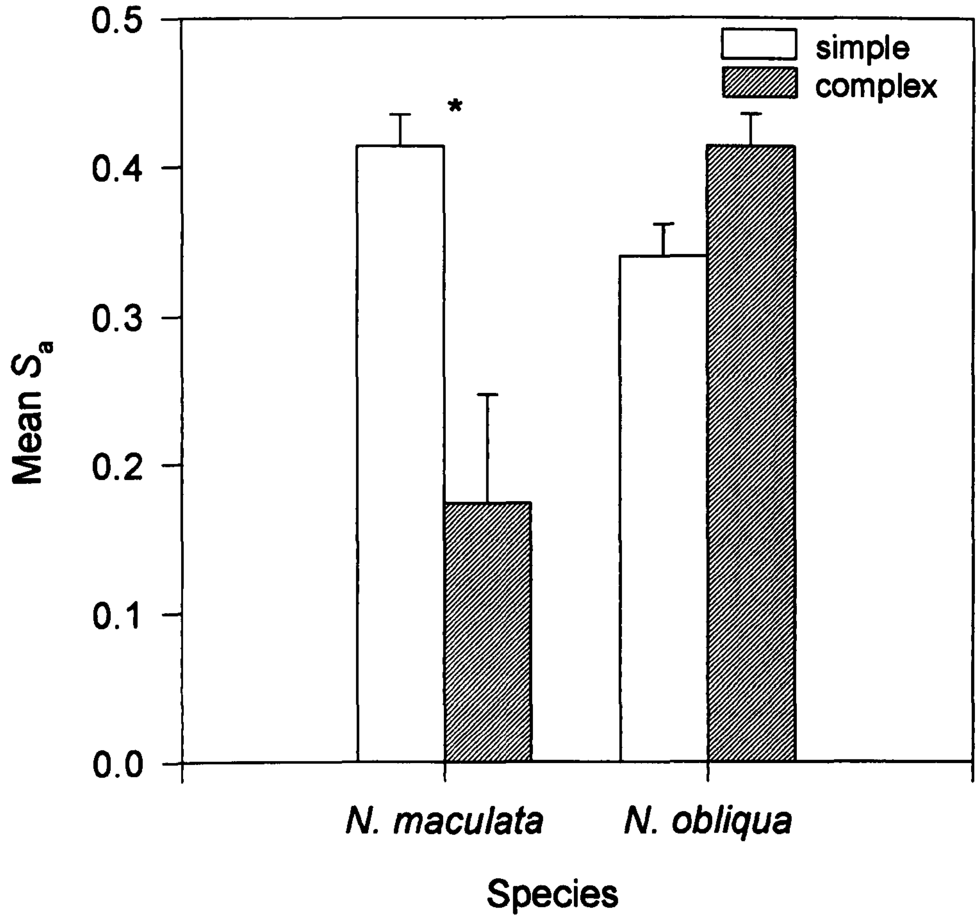

Figure 5.4 Mean proportional survival to adult (S_a) of *Notonecta* species with heterospecific competitors in mesocosms of different environmental complexity. Error bars = 1 standard error. Means and standard errors are arcsine square root transformed. * = indicates where means differ significantly within species at $p < 0.05$ (Tukey test).

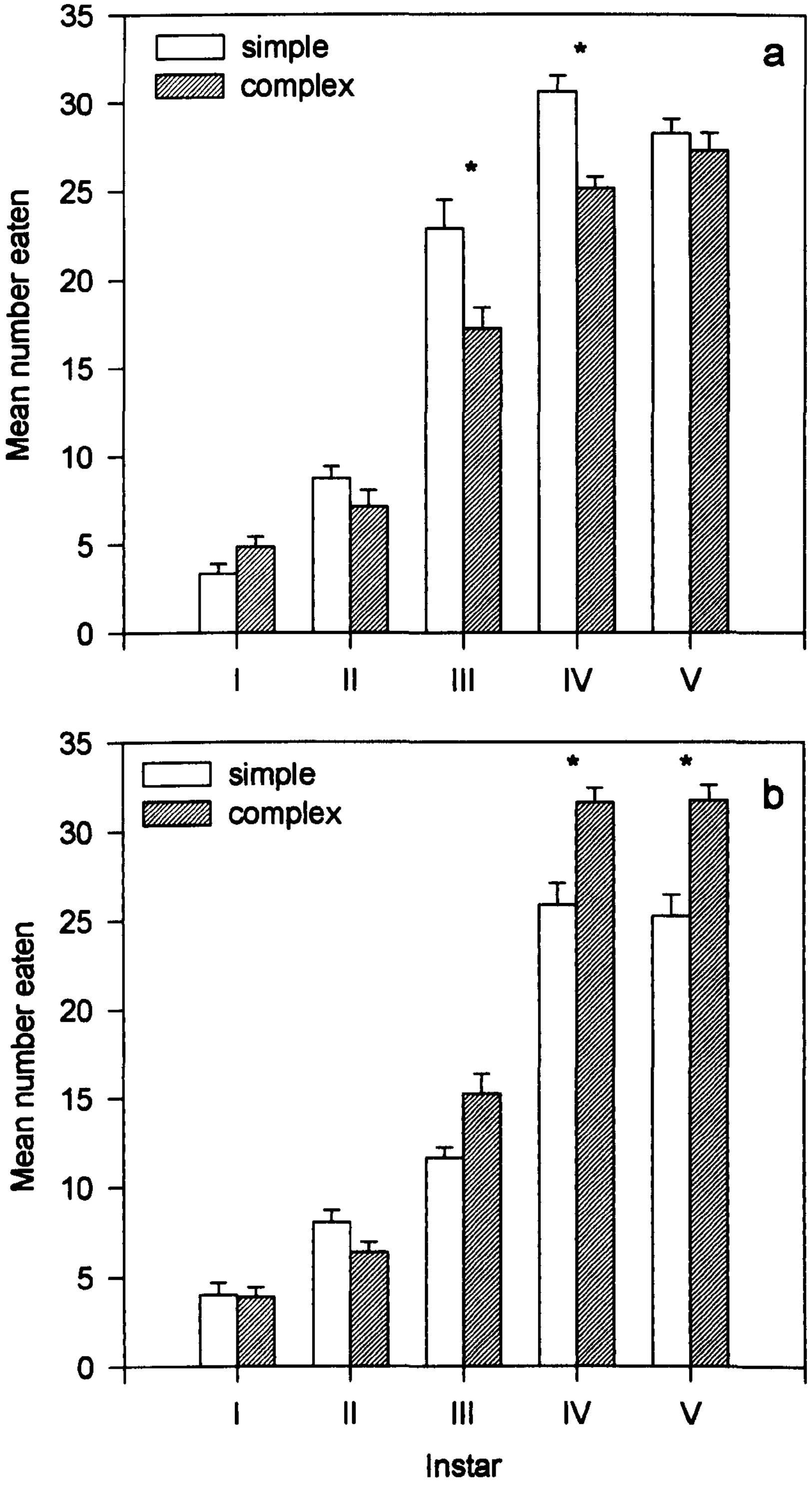

Figure 5.5 Mean number of *D. magna* eaten by nymphs of a) *N. maculata*, b) *N. obliqua* in two hours in different environmental complexities. Error bars = 1 standard error. * = indicates where means differ significantly within instars at $p < 0.05$ (Tukey test).

5.2.6 Discussion.

The results presented here indicate that differences in environmental complexity can alter the outcome of competitive interactions between the two species of *Notonecta*.

In the laboratory experiments, there was no effect of environment on mean lifespan in the conspecific treatments and a similar lack of effect was evident in the analysis of developmental response. In the heterospecific treatments, environmental complexity significantly affected the mean lifespan of nymphs. *N. obliqua* showed significantly higher mean lifespan in the complex environment. Similar patterns were evident in survival to adult, except that *N. maculata* showed a more pronounced difference in survival between environments than *N. obliqua*. There was no effect of environment or competitor species on the instar reached before death, but the small cell totals in the heterospecific treatments due to high censoring may have affected the analysis.

Survival to adult in the mesocosm experiments showed slightly different patterns to the laboratory results. There was significant effect of competitor species on the survival of *N. obliqua* in the simple environment, but the censoring of the heterospecific treatments in the laboratory experiments prevents direct comparison of survival of this species with different competitors in the simple environment. Contrary to the laboratory experiments, with heterospecifics *N. maculata* had significantly lower survival in the complex environment, whereas *N. obliqua* showed no difference.

The feeding experiments suggest that the predation efficiencies of the nymphs of both species vary between different habitat types, with *N. maculata* showing significantly higher efficiency in the simple environment and *N. obliqua* higher efficiency in the complex environment. The exception to this is *N. maculata* instar V which showed no significant difference in feeding efficiency between environments. This may be due to the small size of the experimental arenas relative to the nymphs in instar V, which may have limited the efficiency of predation (Fox and Murdoch 1978). The difference in efficiency between environments increases with instar number in both species. This suggests there is a developmental response in feeding efficiency in habitats of differing complexity, with increasing habitat specialisation with age. These results further confirm the conclusions based on survival trends in both laboratory and field mesocosm experiments, and point to feeding efficiency being a factor in competition between the species in the nymphal stages.

Although the details of the trends found in the laboratory and mesocosm experiments show some variation, the overall pattern is that nymphs of *N. maculata* are superior competitors in a simple environment, while *N. obliqua* nymphs are better able to exploit complex environments. The strongest effects are seen in survival to adult in heterospecific treatments, and the developmental response in feeding efficiency suggests that competition between the species in a given environment may become increasingly asymmetric as the nymphs develop. This is a possible reason why effects of competition were non-significant in early instars (see *Instar at death* and *Developmental response*). The young instars demonstrated no effect of environmental complexity on feeding efficiency and hence inter- and intra-specific effects of competition for food would be similar.

In the presence of conspecific competitors, the effect of environment on survival is much less marked, despite the differences in feeding efficiency. Therefore in the field, in the absence of heterospecific competitors, the species may successfully occupy habitats in which they do not have a high feeding efficiency. However if both species occur together, competitive interactions, mediated by habitat complexity, may lead to the exclusion of the subordinate competitor. A similar effect was demonstrated in species of water strider (Heteroptera: Gerridae) by Spence (1981, 1983).

The results of this study are consistent with observations on adult foraging strategies and field distribution in different environments (Giller and McNeill 1981) and the observed pattern of pond occupancy in the Peak District dewponds (figure 5.1). However the importance of competition between the two species depends upon the frequency of overlap in terms of field distribution. Differences in preferences for oviposition substrates (Walton 1936) and other habitat characteristics (Giller and McNeill 1981) may reduce the potential for competition by allowing partitioning of pond occupancy over a regional area (Taylor 1968, Streams and Newfield 1972) or partitioning of habitat within individual ponds (Giller and McNeill 1981, Streams 1987a,b). For example Streams (1987b) showed that two species of *Notonecta* coexisting in a pond partitioned habitat space and hence avoided potential competition, and that the habitat partitioning was a reflection of fundamental niche differences. In the dewponds, the ponds with high vegetation cover that are occupied by *N. maculata* are also occupied by *N. obliqua* and tend to have well defined areas that are free of submerged vegetation, which may allow habitat partitioning within ponds.

However dispersal and colonisation of ponds by adults is liable to lead to some overlap in distribution and if the two species occur in the same pond by chance, the small size of the ponds and potential food limitation makes competition between nymphs likely. In this situation, competitive superiority will be mediated by habitat complexity. Therefore the observed distribution patterns in the dewponds are likely to be the result of habitat selection, modified by competitive interactions where the two species co-occur.

5.2.7 Acknowledgements.

We would like to thank John Brewington and John Shutt for help with various aspects of the laboratory experiments, Matt Spencer for statistical advice and two anonymous referees for their comments on the manuscript. RAB was supported by an Alfred Denny studentship from the University of Sheffield.

5.3 Mutual predation.

5.3.1 Introduction.

Cannibalism is an common interaction between notonectids, which can have important effects on nymphal survival rates, and the demography of populations of *Notonecta*, through changes in population age structure (Fox 1975a,b), as well as effects on nymphal behaviour (Sih 1981, 1982). However predation is not limited to the same species; one *Notonecta* species will also prey upon the nymphs of other congeneric species (Streams 1992). If species co-occur in the same habitats, mutual predation may be an important factor in determining the overall survival of a species population. These experiments examine mutual predation of *N. maculata* and *N. obliqua* in the laboratory, to determine whether there is any evidence of differential rates of predation of conspecific and heterospecific nymphs of different instars.

5.3.2 Methods.

Experiments were carried out in simple laboratory arenas, as described in the laboratory competition experiments (section 5.2); each experimental arena contained two nymphs, either two conspecifics or one nymph of each species. All nymphs were fed *ad libitum* with *D. magna* prior to use and kept individually. As with the feeding efficiency experiments (section 5.2), nymphs near to moult were not used in experiments. Moulting nymphs are vulnerable to mortality unrelated to predation (Sih 1982) as well as having lower feeding rates. Due to difficulties in identifying the nymphs to species, one of the pair was chosen at random and marked with a permanent marker pen on the thorax. The nymph was blotted dry on tissue paper before the mark was applied and then returned to its container. The unmarked nymph was handled in a similar manner apart from the application of a mark to control for any effects of handling. The marks were retained by the nymphs for the duration of the experiment but faded after three or four days.

The nymphs were left for 48hr in the experimental arenas without additional food, at 15°C under constant dim lighting to avoid any diel periodicity in feeding (Streams 1982) and any incidence of predation noted after this time, along with the species and instar of the survivor and prey nymphs. Every combination of instars III to V was tested and ten replicates were carried out for each combination of species and instar. These stages were used for two reasons. Firstly, although intrageneric predation may occur throughout nymph development (Giller 1979), it is later instars that demonstrate the highest rates, particularly in food limited conditions (Fox 1975a). Second, nymphs in this size range are known to overlap in the field (section 2.7), whereas more extreme combinations (such as instar I and V) are unlikely to occur. Therefore it is the interactions between these combinations which are of most relevance to the dewpond system.

5.3.3 Results.

A three-way contingency table was constructed from the counts of predation events, with variables [*S*] - species combination, [*P*] - 'prey' instar and [*Pr*] - 'predator' instar (where 'predator' was the survivor and 'prey' the nymph that was killed). There were no instances of predation of a larger instar by a smaller instar, hence these totals were zero. However because this interaction was possible, these cells were defined as sampling zeros for the purposes of analysis, rather than structural or logical zeros, which would indicate that the combination was not possible (Fienberg 1970).

The incidence of intrageneric predation in the different species-instar combinations was analysed using a loglinear model, implemented in SPSS. Initially a saturated model was fitted containing all possible effects and interactions, and then terms were removed hierarchically by backwards elimination (Benedetti and Brown 1978) using the likelihood ratio G^2 statistic (p for removal = 0.05) to obtain the model with the best fit to the observed frequencies. The model with best overall fit to the data (likelihood ratio $G^2_{[27]} = 3.52$, $p = 1.00$) contained the term [$P*Pr$], the interaction between predator and prey instar (significance of term: likelihood ratio $G^2_{[4]} = 19.3, p = 0.007$). There was no significant effect of species combination on the incidence of predation. The incidence of predation increased with increasing difference in instar between the nymphs (figure 5.6).

5.3.4 Discussion.

The results of these experiments show that incidence of intrageneric predation between notonectid nymphs in the laboratory increases with the size difference between the interacting nymphs. This result is broadly consistent with other investigations of intrageneric predation in species of *Notonecta* (Sih 1982, Streams 1992) and other predatory species of Hemiptera such as Gerridae (Jamieson and Scudder 1977). The increased risk of predation with increasing size difference between interacting individuals has also been shown to have other effects on the foraging behaviour and feeding rate of smaller instars of *Notonecta* in the presence of adults (Murdoch and Sih 1978, Sih 1982). However, Sih (1982) found that the predation risk from adult *N. hoffmani* on instars IV and V was minimal in the laboratory and this was reflected in the lack of avoidance behaviour in field populations. In this study the rate of predation in the laboratory for instar V preying on instar IV was still quite high, but the rates of predation recorded may not reflect the predation experienced in the field. Streams (1992) found no evidence of size dependent predation rates in field enclosures, although there was strong evidence of such interactions in laboratory experiments. Changes in the encounter rate in the larger field enclosures and possible avoidance effects (Sih 1982) may affect intrageneric predation rates in the field, suggesting that although the laboratory experiments may provide information on the relative predation rates of different instar combinations, the observed rates in the field are likely to be much lower (Sih 1982, Streams 1992).

The lack of any significant effect of species combination in the analysis suggests that the rate of predation is not affected by whether the prey is a conspecific or heterospecific nymph.

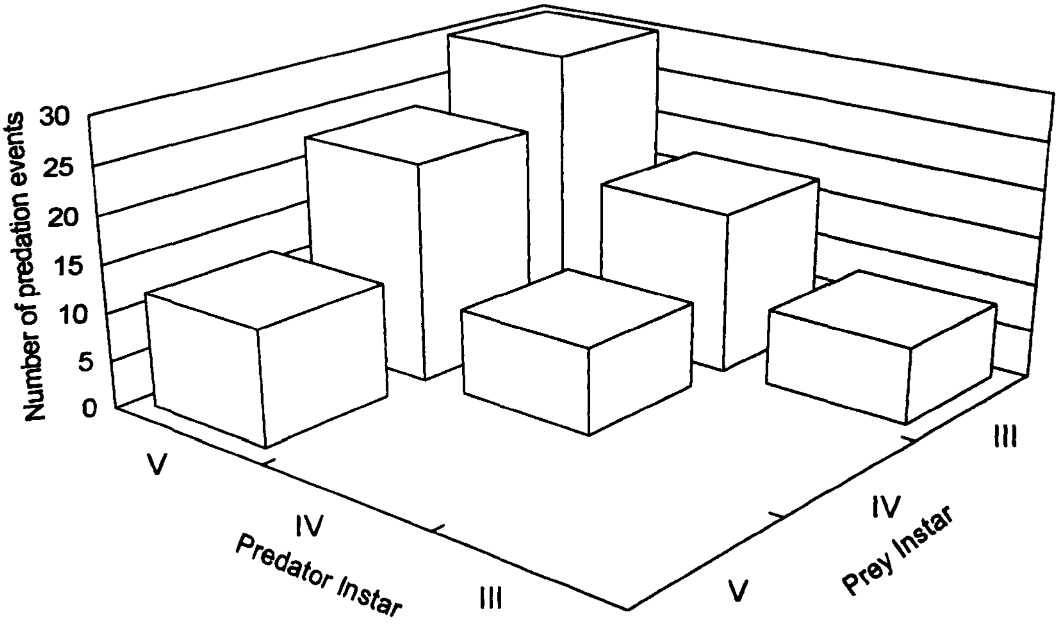

Figure 5.6 Number of predation events occurring between pairs of *Notonecta* nymphs of differing size combinations, totalled across all species combinations.

Streams (1992) also found no evidence for any discrimination between species in terms of incidence of predation and similar lack of discrimination between species had been demonstrated in Gerridae (Spence and Cárcamo 1991). This points to size differences being the main factor in determining the rate of intrageneric predation. In the case of the two species under consideration in this study, there is a consistent size difference between the species throughout development, with *N. obliqua* being larger in all instars (figure 2.3) suggesting that if the two species develop at the same rate, *N. obliqua* may have a predatory advantage. However if the analysis is repeated on only the same instar combinations, there is still no significant effect of species combination ($\chi^2_{[3]} = 2.31, p = 0.511$), suggesting that the size difference is insufficient to generate any strong selective effects.

In terms of the impact of intrageneric predation on species coexistence, rather than there being any effects via selective predation on heterospecifics, the timing of oviposition, hatching and subsequent development of the nymphs may be more important. If one species hatches before another species or has a faster rate of development, the size difference generated may lead to a higher rate of predation on the heterospecific nymphs, potentially affecting the species composition of the habitat (Morin 1984, Spence and Cárcamo 1991, Streams 1992). This priority effect may have significant impact on the survival of the species with smaller nymphs at any given time, and the effect will be magnified with increasing size difference between the nymphs. Life history variation, such as timing of oviposition (see figure 1.5), will have an important influence in terms of restricting the potential overlap of nymphal instars, but annual variation in the environment, which will affect subsequent nymph survival and development rates is likely to lead to a dynamic interaction between the two species over time.

5.4 Conclusions.

This chapter examined competitive interactions between *Notonecta* species with respect to the impact of competition on regional population dynamics and distribution. The outcome of competition between the two species in the nymphal stages is influenced by habitat complexity in a manner consistent with the differences in foraging strategy demonstrated for the adults (Giller and McNeill 1981) and feeding efficiencies of the nymphs (section 5.2). Mutual predation would also appear to be a potentially important interaction between the species, which may influence the survival of individual populations. However there is no evidence for selection of heterospecifics over conspecifics; the likelihood of predation appears to be governed by the relative size of the individuals (Streams 1992). Therefore the importance of mutual predation in species coexistence is dependent on the timing of oviposition and rate of development of the two interacting species.

The importance of all these interactions in regional population dynamics depends on the amount of overlap in species distributions. The contrasting habitat preferences (sections 3.2 and 3.3) will tend to reduce the overlap of breeding populations and hence fugitive coexistence via metapopulation dynamics is likely to be of limited importance in this system. However where they do co-occur, competitive and predatory interactions between the two species will modify the distribution patterns generated by habitat selection at the landscape scale.

6. Patterns in the dewpond metacommunity.

6.1 Introduction.

The majority of the work so far in this thesis has been focused on the spatial population dynamics and interactions between two species of *Notonecta* in the dewpond system. The dynamics of one, or two interacting species, has been the main area of development for theory and models of spatially structured population systems (Hastings and Harrison 1994, Hanski and Simberloff 1997, Nee, May and Hassell 1997, Hanski 1998) and this is also where empirical research has been concentrated (e.g. Harrison, Murphy and Ehrlich 1988, Sjögren Gulve 1994, Thomas and Hanski 1997). However these species do not (usually) occur in isolation and are likely to interact with the other species in the community. Together, these species make up a metacommunity, which can be defined simply as local communities linked by dispersal by one or more of their member species (Holt 1997).

Many of the other species in the dewponds, and similar pond systems, are capable of dispersing between ponds, and show similar patterns of local population turnover as those demonstrated for the species of *Notonecta* (Macan 1939, Popham 1951, Fernando 1958, 1959, Jeffries 1989, 1994, Briers 1997). Therefore pond invertebrate communities may be good examples of field metacommunities, although the spatial scale of metapopulation dynamics and temporal rates of population turnover of member species are likely to vary depending on species life history traits such as dispersal ability (Harrison and Taylor 1997).

Here I examine some aspects of structure in the dewpond metacommunity, and focus in particular on the evidence of links between patterns in *Notonecta* distribution and putative prey species. *Notonecta* is the top predator in the dewponds; it is widely distributed and may reach high local abundances. Previous studies have demonstrated that *Notonecta* can severely reduce the local abundance of prey organisms, and may cause local extinctions (Murdoch, Scott and Ebsworth 1984, Jeffries 1996), and that these impacts may be reflected in changes at other levels in the food web (Blaustein, Kotler and Ward 1995, Arnér, Koivisto, Norberg and Kautsky 1998, Blaustein 1998). Such unstable local interactions between predator and prey can be stabilised over a regional area as a result of metapopulation dynamics (Hastings 1977, A.D.Taylor 1991, Nee, May and Hassell 1997), where the prey species has a spatial refuge from predation via dispersal to predator-free patches. Therefore *Notonecta* may be negatively associated with prey species at the landscape scale. This type of interaction is the most thoroughly examined theoretically, but is only one of a range of potential interactions between the distribution and abundance of predator and prey at the landscape scale (Holt 1997). In a metacommunity, the distribution of a predator such as *Notonecta* may be nested within the distribution of its prey species, as a result of sequential trophic dependency (Holt 1993, 1995, 1997). Therefore the predator may exist as a metapopulation with respect to the prey species. In this situation prey abundance is synonymous with patch quality, and hence distribution patterns may be influenced by donor control (Pimm 1982, DeAngelis 1992, Polis and Strong 1996) acting at the landscape scale (Holt 1997), with the predator positively associated with the prey, with respect to patch occupancy and local abundance.

6.2 Methods.

Field sampling.

A semi-quantitative sample of the invertebrate population was taken from 28 dewponds in July and August 1996. The sample consisted of three 1m sweeps through the middle of the water column, and a 30cm benthic trawl, both collected with a standard pond net. All collected material was preserved in 70% alcohol in the field. Each sample was sorted at a later date in the laboratory. Large particles of substrate and debris were removed using a series of sieves of varying mesh size. The remainder of the material was examined on a light table and all invertebrates removed and re-preserved. Super-abundant taxa (Chironomidae and *Helophorus* spp.) were enumerated using a sub-sampling technique similar to that described in Wrona, Culp and Davies (1982). Each sample was made up to two litres with water and mixed thoroughly by bubbling compressed air through it. Six 50ml subsamples were taken from the sample, and all the organisms in each subsample counted. These counts were summed and the invertebrate count scaled up to the total volume of sample. These samples were used to give an estimate of the relative abundance of taxa. Most of the invertebrates were identified to species or genus, with the exception of Chironomidae.

Data analysis.

Many species were found in a limited number of ponds (often only one or two) and only reached very low abundances in these ponds. The data were grouped into broader taxonomic categories (see table 6.1) and taxa recorded from less than five ponds were excluded from the analysis. The inclusion of these species would degrade the analysis, as measures of association or correlations between variables are unlikely to be reliable given the small number of non-zero values (Tabachnick and Fidell 1996) and hence any patterns of association, either in terms of pond occupancy or abundance, between these species would be difficult to assess.

The association between taxonomic groups was measured using the Phi coefficient (Yule 1912, Jackson, Somers and Harvey 1989), which has a range of -1 to +1, indicating positive or negative associations. The group *Helophorus* was excluded from the group association analysis as it was present at all sites and hence measures of association cannot be calculated. The similarity of invertebrate community composition at different sites was measured using a similarity coefficient based on presence/absence data. Both the Jaccard index (C_j) and the Sørensen index (C_s) (Southwood 1978, Pielou 1984) were calculated, but in all analyses performed, the different indices gave similar results in terms of final clustering and only differed in the levels of similarity at which the clusters were divided. Therefore only the Jaccard index results are given.

Dendrograms of group associations and similarity of community composition were constructed using the unweighted average linkage method of clustering. Similarity and association coefficients are known to be affected by the relative occupancy of species (the size effect, Jackson, Somers and Harvey 1989), but the removal of species that have low occupancy should have reduced the influence of this effect, and there was little evidence for a strong effect of the number of sites occupied on the results of the analysis of group associations or community composition.

Table 6.1 Taxonomic groupings of prey organisms used in analysis.

Taxonomic grouping	Species included in group
Notonecta	*N. maculata* *N. obliqua* (adults and nymphs)
Corixa	*Corixa punctata*, adults and nymphs
Sigara	All *Sigara* spp. adults and nymphs
Dytiscidae	*Acilius sulcatus* *Agabus bipustulatus* *Agabus nebulosus* *Agabus* spp. larvae
Chironomidae	Chironomidae larvae and pupae
Helophorus	All *Helophorus* spp.
Lymnaea	*Lymnaea peregra*
Helobdella	*Helobdella stagnalis*
Excluded (low abundance and small number of ponds occupied)	*Cloeon dipterum* Culicidae *Erpobdella* spp. *Gyrinus substriatus* *Haliplus* spp. *Hydrobius fuscipes* *Hydroporus* spp. *Laccophilus* spp. *Nymphula* spp. *Planorbis* spp.

6.3 Results.

6.3.1 Association between taxonomic groups.

The patterns of association summarised by the dendrogram (figure 6.1) show that the groups Dytiscidae and *Sigara* are not strongly associated with the other groups in either a positive or negative direction. The positive association between Dytiscidae and *Sigara* appears to be due to a bias in Phi, which overestimates the association between species when the distribution of one species is nested within that of another (Jackson, Somers and Harvey 1989). There are only two sites where Dytiscidae are present and *Sigara* are absent, leading to an inflated association coefficient. Examination of the distributions of other taxa showed that none of the other associations suffered from this problem. The associations between Dytiscidae and the other groups (apart from *Sigara*) are all negative, but because average linkage takes into account the associations between *Sigara* and the other groups as well, these groups separate from the others with an average association of 0.023. All the other groups have positive values of Phi, indicating positive association to some extent, but this may be partly a result of the grouping of species into higher taxonomic groups, which will tend to lead to greater association between taxa than if individual species had been used to construct the dendrogram. The group *Helobdella* separates from the other groups at a fairly low positive Phi, and is not strongly associated with other taxa. The strongest positive associations are between *Notonecta* and *Corixa*, and Chironomidae and *Lymnaea*.

6.3.2 Community composition.

Five fairly distinct clusters, labelled A-E (see figure 6.2), with between two and nine sites in each cluster, were identified by the cluster analysis. Cluster E contains only one taxon and hence the clustering of sites into this grouping may be influenced by the size effect, but as the same taxon is found in all sites within this group, its separation is determined as much by the

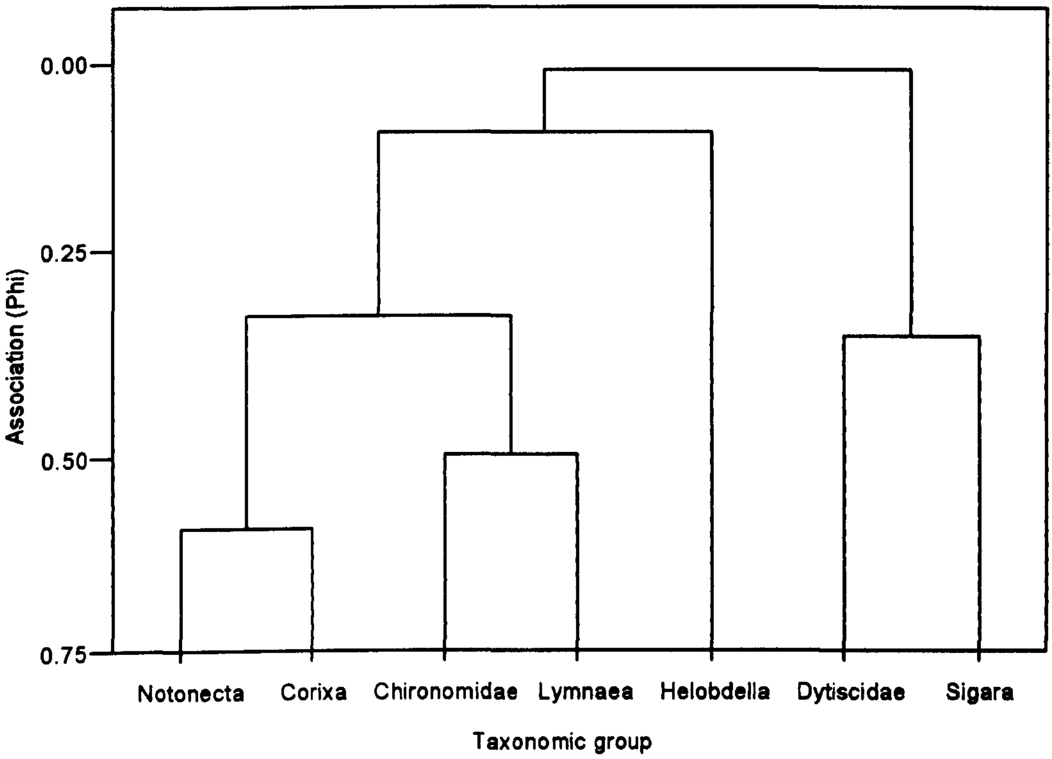

Figure 6.1 Cluster dendrogram of association (Phi) between taxonomic groups, constructed using unweighted average linkage clustering.

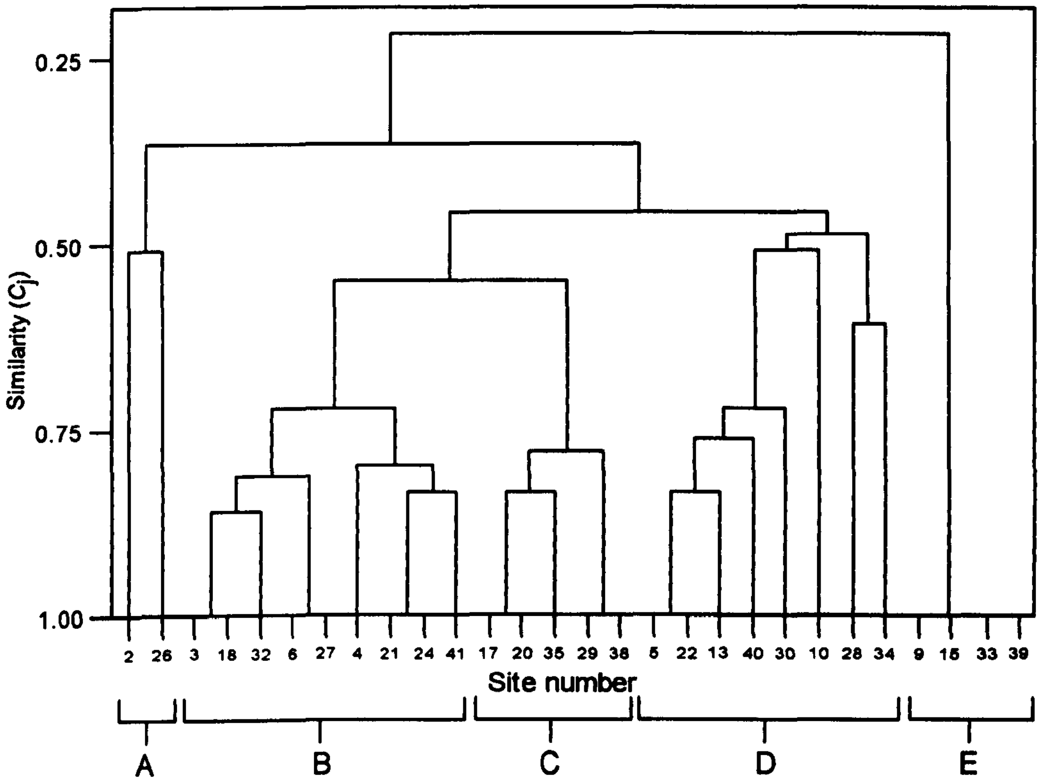

Figure 6.2 Cluster dendrogram of community similarity (C_j) based on unweighted average linkage clustering of taxonomic groups present. Letters indicate resultant clusters (see text for details).

absence of other taxa as the presence of the one taxon found. On this basis it would appear to be a reasonable ecological grouping.

Following analysis of dewpond community composition using a binary presence/absence similarity measure, variation in the abundance of the different taxonomic groups across all ponds was summarised using PCA to assess whether patterns in abundance reflected the differences in community composition indicated by the cluster analysis. The abundances of all the organisms were transformed to normality using a natural log +1 transformation. Figure 6.3 shows the first two components derived from the PCA, with datapoints labelled according to the clusters based on group presence and absence, and table 6.2 gives summary statistics and component loadings for the first two components.

Table 6.2. Summary statistics for principal components analysis of grouped abundance data, a) cumulative percentage variance explained by each component, b) component loadings for taxonomic groups included in the analysis. All variables ln +1 transformed.

	Component 1	Component 2
a) Cumulative % variance	30.4	54.0
b) Taxonomic group		
Chironomidae	-0.389	0.064
Corixa	-0.371	-0.445
Dytiscidae	0.398	-0.268
Helobdella	-0.239	-0.422
Helophorus	0.348	-0.431
Lymnaea	-0.246	0.008
Notonecta	-0.555	0.048
Sigara	-0.074	-0.599

Examination of the loadings of the different taxonomic groups shows that the first component clearly separates the ponds with high abundance of Coleoptera from all others; the two coleopteran groups are the only groups to have positive loadings on component 1, all other groups having fairly high negative loadings. Most taxonomic groups have negative loadings on the second component, and hence this component describes a general decline in

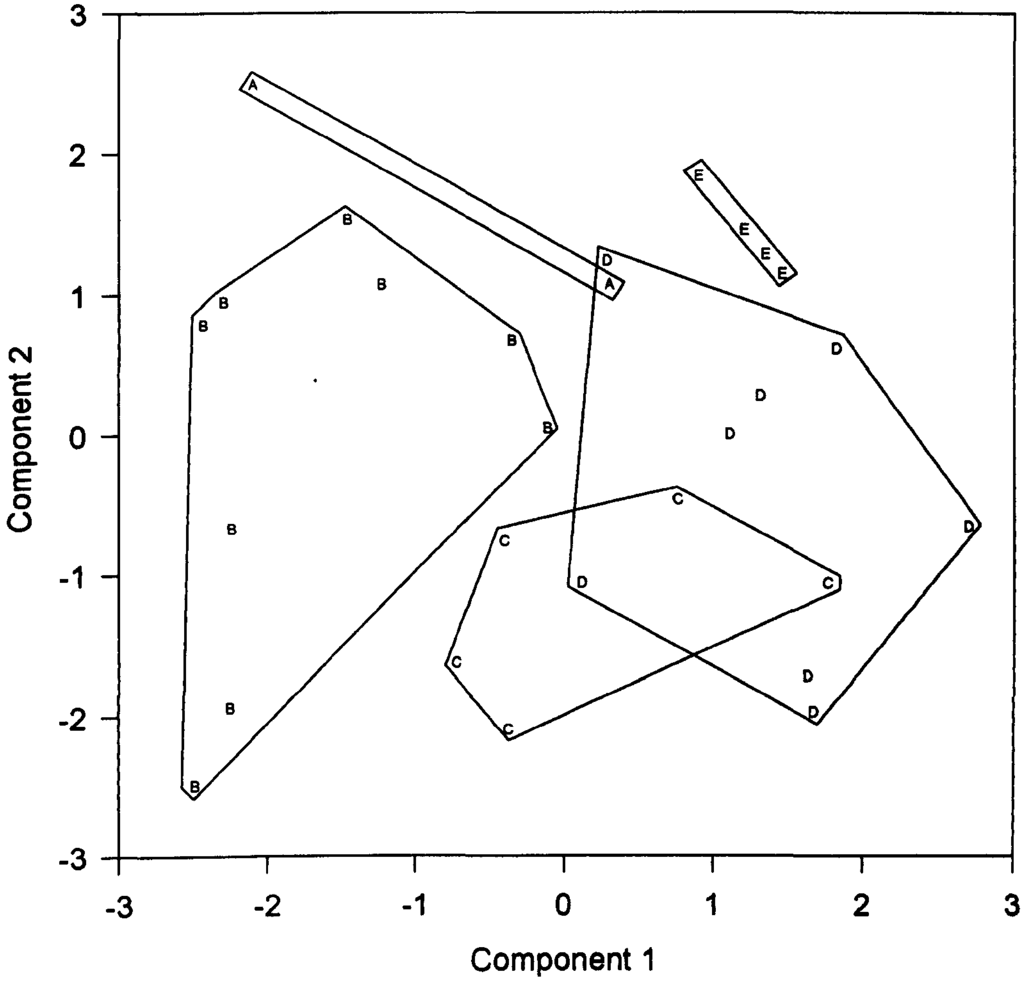

Figure 6.3 Plot of the first two components from principal components analysis of taxonomic group abundance. Datapoints labelled according to community types defined by cluster analysis of taxon presence-absence (see figure 6.2).

abundance. Exceptions to this are the abundance of the groups Chironomidae, *Lymnaea* and *Notonecta*, which have very weak positive loadings on this component. The subsequent components of the PCA were examined but they were not well defined in terms of group loadings.

The clusters defined on the basis of presence-absence data are also fairly well separated on the PCA analysis, suggesting that the use of binary similarity indices does not result in the loss of significant information in highly heterogeneous communities (Pielou 1984). The different clusters can be described in terms of the groups present and their relative abundance, as detailed in table 6.3.

Table 6.3. Description of clusters according to the presence and relative abundance of the groups present in the sites.

Cluster	Sites included	Description
A	2, 26	Species poor, high chironomid abundance.
B	3,4,6,18,21,24,27,32,41	High abundance of Hemiptera and chironomids.
C	17,20,29,35,38	Low chironomid abundance, dytiscids abundant, *Lymnaea* absent.
D	5,10,13,22,28,30,34,40	High abundance of both *Helophorus* and dytiscids, Hemiptera poor.
E	9,15,33,39	Only *Helophorus* present.

The two clusters A and E are very distinct from the others. This is largely a result of their low taxonomic richness, E only containing one group, and A three groups. Sites within cluster A also have very high abundance of Chironomidae. The clusters B-D appear to represent a succession from Hemiptera dominated communities, to communities dominated by Coleoptera, both in terms of the number of ponds occupied by the two groups, and their numerical abundance, although the presence of other taxa is also important in defining the clusters (for example the absence of *Lymnaea* in cluster C). The main separation of clusters is on the first component of the PCA, which appears to reflect the shift in community dominance from Hemiptera (B) to Coleoptera (D). The low taxon richness/high dominance clusters (A and E) also form distinct groups.

Parametric correlation coefficients (Pearson product-moment) were calculated between the first two principal components and the habitat variables recorded from the sites (section 2.6). Percentage cover variables were converted to proportions and transformed using the arcsine square root transformation prior to calculation of correlations; all other variables were not transformed. The table of correlations is shown in table 6.4.

Table 6.4. Correlation coefficients of habitat variables and scores of sites from principal components analysis of group abundance, df of all variables = 28. $^{\phi}$ = variable transformed using the arcsine square root transformation.

Habitat variable	Component 1	Component 2
Altitude	0.149	-0.194
Conductivity	0.156	-0.460*
Emergent vegetation$^{\phi}$	0.395*	-0.105
Mud percentage cover$^{\phi}$	-0.221	-0.479*
Mud depth	0.022	-0.253
Pond width	-0.114	0.102
Submerged vegetation$^{\phi}$	0.052	-0.171
Water clarity	-0.062	0.342
Water depth	0.073	0.232

* $p < 0.05$

Component 1 of the PCA is significantly positively correlated with cover of emergent vegetation. This component describes the shift in dominance from Hemiptera to Coleoptera, and the correlation of this axis with emergent vegetation cover suggests that the change in community composition may be influenced by changing habitat conditions, with increasing cover of emergent vegetation correlated with increasing dominance by Coleoptera. Component 2 has significant negative correlations with percentage mud cover and conductivity. The separation of clusters is less clear on this component, With the exception of the taxon poor clusters A and E which are associated with low mud cover and conductivity, the component loadings suggesting a general increase in abundance with increasing mud cover and conductivity.

6.3.4. Community composition and *Notonecta.*

The analyses carried out in section 6.3.1-3 demonstrated that some taxa (for example the group *Corixa*) show positive associations with *Notonecta*, both in terms of co-occurrence and abundance. The purpose of this section is to further investigate the associations between *Notonecta* and other taxa, in relation to interactions between occupancy and abundance of *Notonecta* and its potential prey species, given the potential importance of *Notonecta* as the most abundant large predator in the dewponds.

For the purposes of these analyses, only taxa that are known from the literature or from personal observations to be preyed upon by *Notonecta* were included (the 'prey community'). Therefore groups *Helobdella* and *Lymnaea* were excluded from the analysis as these items have not been recorded as taken in any study of the diet or feeding preferences of *Notonecta* species (Jeffries 1984, Giller 1986 and references therein, P.H.Warren, unpublished data, R.A.Briers, personal observations). PCA was used to summarise the variation in the abundance of the prey groups and explore whether the abundance of *Notonecta* was correlated with overall changes in the prey community. The results of the PCA are given in table 6.5, and figure 6.4 shows the first two components derived from the PCA with datapoints labelled according to the untransformed abundance of *Notonecta*.

Examination of the plot of the first two components of the PCA suggests that there may be some changes in the abundance of the different groups within the prey community, with changes in *Notonecta* abundance. The first component of the PCA reflects an overall decline in the abundance of three of the prey groups included in the analysis: *Helophorus*, *Sigara* and Dytiscidae. Component 2 reflects increases in the abundance of three of the prey groups:

Corixa, *Sigara* and Chironomidae. It can be seen from figure 6.4 that ponds with high abundance of *Notonecta* are generally in the top right corner of the ordination, whereas the ponds with low numbers or no *Notonecta* are largely in the bottom left corner of the plot. Therefore there would appear to be some changes in the prey community with increasing *Notonecta* abundance that are evident as a diagonal shift in prey community structure with respect to components 1 and 2 of the PCA. Subsequent components of the PCA were examined but no evidence of any pattern in relation to the abundance of *Notonecta* was observed.

Table 6.5. Summary statistics for principal components analysis of prey abundance data, a) cumulative percentage variance explained by each component, b) component loadings for variables included in the analysis. All variables ln +1 transformed.

	Component 1	Component 2
a) Cumulative % variance	35.0	65.3
b) Variable		
Corixa	-0.172	0.665
Helophorus	-0.609	-0.118
Sigara	-0.470	0.484
Chironomidae	0.250	0.493
Dysticidae	-0.562	-0.261

6.3.4 *Notonecta* and prey group abundance.

The pattern of change in the abundance of individual groups with the abundance of *Notonecta* was assessed by calculating simple parametric correlations. The total abundance of the groups classified as potential prey was not correlated with the abundance of *Notonecta*. The abundance of four of the prey groups were significantly correlated with notonectid abundance; two groups were negatively correlated (*Helophorus* and Dytiscidae) and two were positively correlated (*Corixa* and Chironomidae) (see figure 6.5). The two numerically dominant prey groups (*Helophorus* and Chironomidae) are correlated with the abundance of

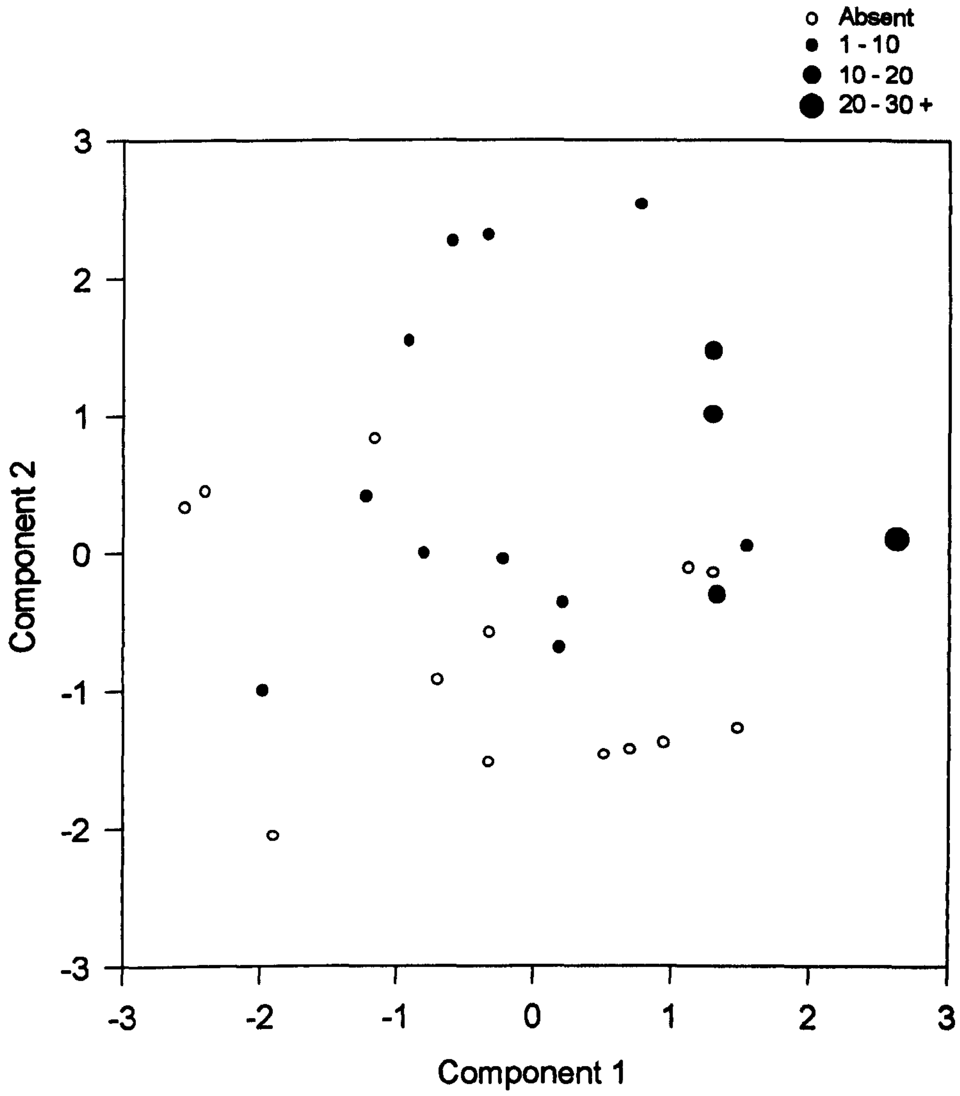

Figure 6.4 Plot of the first two components from principal components analysis of prey abundance data. For details of the PCA see table 6.5. Datapoints are labelled according to the untransformed abundance of *Notonecta*.

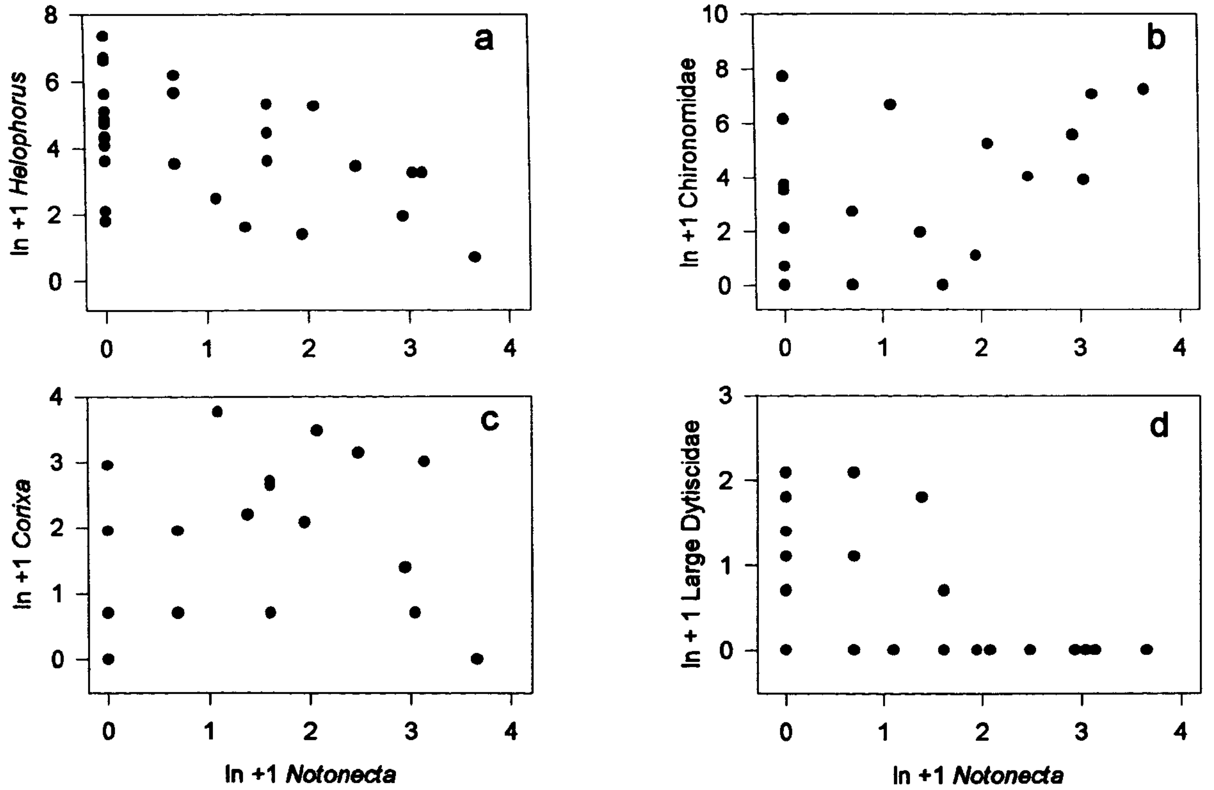

Figure 6.5 Correlation of abundance of prey organisms with abundance of *Notonecta*. Only prey groups with significant correlations are included All data are ln +1 transformed. a) *Helophorus*, $r_{[26]} = -0.504$, $p = 0.006$, b) Chironomidae, $r_{[26]} = 0.460$, $p = 0.014$ c) *Corixa*, $r_{[26]} = 0.403$, $p = 0.034$ d) Large Dytiscidae, $r_{[28]} = -0.396$, $p = 0.037$.

Notonecta in opposite directions and hence any potential effect on overall abundance is likely to be cancelled out by these contrasting correlations.

Since the earlier analyses in this chapter suggest that there are links between habitat variables and changes in community composition, the interpretation of the variation in the prey community in relation to *Notonecta* is not straightforward. In order to assess the effects of *Notonecta* on the prey community, it is necessary to take account, as far as possible, of the possible confounding role of habitat variation. In order to do this, correlations between the abundance of prey groups and habitat variables (see section 2.6) were calculated for the sites where *Notonecta* was absent. Variables that were significantly correlated ($p < 0.05$) with the abundance of prey groups were subsequently included in a multiple regression of all sites, with abundance of the prey group as the dependent variable. The habitat variables were forced to enter the regression model and then abundance of *Notonecta* was entered into the model by a forward stepwise procedure (p for entry = 0.05) to test whether entry into the regression model led to a significant increase in the F ratio, when the habitat factors affecting the abundance of the prey group were already entered. Following the multiple regression, the standardised multiple regression coefficients or beta weights (b') were examined to assess the relative magnitude of the effects of the independent variables included (Sokal and Rohlf 1981). This procedure was carried out for the four prey groups that showed significant correlations with *Notonecta* abundance.

Helophorus *prey group.*

There was a significant positive correlation between *Helophorus* abundance and two of the habitat variables: emergent vegetation cover (arcsine square root transformed) and conductivity, in the absence of *Notonecta* ($r_{[13]} = 0.56, p = 0.048$, and $r_{[12]} = 0.58, p = 0.05$ respectively). Therefore these variables were forced to enter the multiple regression before attempting to enter *Notonecta*. However *Notonecta* still entered the model (using stepwise entry) with a negative coefficient, indicating that abundance of *Helophorus* declines with increasing abundance of *Notonecta*, and the final regression model was highly significant ($F_{[3,22]} = 7.52, p = 0.0012$, see table 6.6). From examination of the b' values, it would appear that conductivity has the strongest influence on the abundance of *Helophorus*, followed by *Notonecta* and then emergent vegetation cover.

Table 6.6. Results of multiple regression of *Helophorus* abundance with habitat variables and abundance of *Notonecta*.

Variable	Coefficient (β)	SE of β	b'	t-value	Significance of t
Constant	2.69	0.69	-	3.90	0.001
Conductivity	0.004	0.001	0.43	2.84	0.009
Emergent vegetation cover	7.40	3.73	0.31	1.98	0.059
Notonecta	-0.50	0.69	-0.34	-2.20	0.039

Corixa *prey group.*

In the absence of *Notonecta*, there is a significant positive correlation between the abundance of *Corixa* and proportion of mud cover on the substrate (arcsine square root transformed), ($r_{[13]} = 0.58, p = 0.037$). Therefore transformed proportion mud cover was forced to enter the multiple regression before attempting to enter *Notonecta*. However *Notonecta* still entered the model (using stepwise entry), with a positive coefficient, and the final regression model was highly significant ($F_{[2,25]} = 5.43, p = 0.011$, see table 6.7). From examination of the b' values, it would appear that mud cover and *Notonecta* abundance have approximately equal magnitudes of influence on the abundance of *Corixa*, and in this case high abundance of *Notonecta* is associated with high abundance of the group *Corixa*.

Table 6.7. Results of multiple regression of *Corixa* abundance with habitat variables and abundance of *Notonecta*.

Variable	Coefficient (β)	SE of β	*b'*	*t*-value	Significance of *t*
Constant	-0.36	0.62	-	-0.57	0.571
Mud depth	1.25	0.56	0.38	2.24	0.034
Notonecta	0.40	0.18	0.38	2.26	0.033

Chironomidae prey group.

There were no significant correlations between the abundance of Chironomidae and the habitat variables recorded in the absence of *Notonecta*. Therefore the positive correlation between Chironomidae and *Notonecta* would appear to be unaffected by any effects of the habitat variables recorded. As there were no habitat effects, multiple regression analysis was not carried out.

Dytiscidae prey group.

As for the prey group Chironomidae, in the absence of *Notonecta* there were no significant correlations between the habitat variables and the abundance of Dytiscidae. No further regression analysis was carried out.

6.4 Discussion.

Group associations and community composition.

The most consistent pattern in the results of the taxonomic group association analysis is the negative association between the Dytiscidae and other taxa. Only *Sigara* is positively associated with this group and this association is artificially high as a result of bias in the coefficient when distribution patterns are nested. However a nested distribution pattern may be of ecological significance if it is indicative of trophic dependency. Although Dytiscidae will feed on *Sigara* species, the rate of predation in the laboratory is not high (P.H.Warren, unpublished data, R.A.Briers, personal observations), and dipteran groups such as Culicidae and Chironomidae make up the majority of the diet of most species in this group (Nilsson and Svensson 1994, 1995). Therefore this pattern of distribution is unlikely to be the result of strong trophic dependence. Apart from the associations with the Dytiscidae, there are no strong negative associations between taxa, with most having positive values of Phi, although again the values are generally not high, with the strongest positive association between *Notonecta* and *Corixa*. This and other associations between *Notonecta* and potential prey taxa are further explored in section 6.4.2.

Analysis of community composition suggests that some of the observed associations are the result of common responses by taxa to variation in habitat characteristics. The main pattern evident in the data is a shift from Hemiptera dominated communities (B) to Coleoptera dominated communities (D), suggesting that the clusters B to D may represent points on a continuum rather than separate and distinct communities. Although sites in cluster D are described as Coleopteran dominated , they are probably more accurately described as *Helophorus* dominated, as this group makes up the majority of the total Coleoptera, with a mean abundance of more than 10 times that of the group Dytiscidae. This shift in community composition from dominance by Hemiptera to Coleoptera is also reflected in the positive association between hemipteran groups, and the negative associations between Dytiscidae and other taxonomic groups (*Helophorus* was not included in the group association analysis as it was present at all sites and hence association measures cannot be calculated).

The correlation between the first component of the PCA and emergent vegetation cover suggests that the changes in community composition described along this axis may be influenced by the habitat conditions within ponds. The shift towards Coleoptera dominance at high cover of emergent vegetation is consistent with the habitat preferences recorded for the species of *Helophorus* (Friday 1988) which make up the majority of the Coleoptera. Warren *et al.* (in press) found a similar negative correlation between the species richness of Hemiptera and Coleoptera in a survey of 40 dewponds in 1992 (including all 28 ponds sampled in this study), which appeared to be linked to the method of pond construction. Species richness of Hemiptera higher in concrete lined ponds, and Coleoptera higher in clay lined ponds. There is no evidence of a similar link to construction method in this study, although the small sample size of clay ponds (n = 6) makes analysis difficult. Re-analysis of the data from Warren *et al.* (in press) shows that emergent vegetation cover, which from this study appears to be correlated with the changes in community composition, was more abundant in clay lined ponds (Mann Whitney *U* test, $U_{[8, 32]} = 56, p = 0.002$, mean cover in concrete ponds = 5.5%, in clay ponds = 13.2%). Therefore the observed patterns in species richness in the study by Warren *et al.* (in press) may be linked to differences in habitat which are correlated with the method of pond construction.

Notonecta and the prey community.

There is no evidence for an overall negative impact on the abundance of the prey community, but individual prey taxa do appear to show some variation in abundance in relation to the abundance of *Notonecta*. Some of this variation is undoubtedly due to the shift in community composition in relation to habitat factors that is discussed above. However, there are still consistent patterns of variation in relation to *Notonecta* abundance when responses to habitat factors are taken into account, and the effects of *Notonecta* are of similar magnitude to the influence of habitat factors. The pattern of variation is not consistent across all taxa; both positive and negative correlations were found, and other taxa showed no response to the abundance of *Notonecta*.

Prey groups Chironomidae and *Corixa* showed positive correlations with *Notonecta*. Both of these groups are known from laboratory and field studies to be prey items for *Notonecta* (Jeffries 1984, Giller 1986, Streams 1992, personal observations), and adult and juvenile *Corixa* spp. have been used in the course of these studies to maintain notonectids in the laboratory (section 2.2). Jeffries (1984) ranked adult *C. punctata* as having low vulnerability to predation by *N. glauca*, but this was based on the interaction between adults. Personal observations in the laboratory have shown that the nymphal stages of *Corixa* species are highly vulnerable to predation by adults and nymphs of *Notonecta*. Therefore the degree of overlap between the different life stages of the two groups may be critical in determining the importance of predation. The strong positive association between the groups at the landscape scale is also suggestive of a link between the two groups potentially as a result of trophic dependency.

Chironomidae are highly vulnerable to predation in the laboratory (Jeffries 1984), but in the field the benthic tube dwelling habit of the larvae act as a refuge from predation, reducing predation rates (Crowder and Cooper 1982, Folsom and Collins 1984, Warren 1988). Other life stages, such as pupae, would appear to be vulnerable to predation. This group often reaches very high abundances in the dewponds, and where *Notonecta* is very abundant, it is only found at high abundances (figure 6.5). Therefore even if only a small percentage of the total suffer predation, they may still act as an important food source for *Notonecta*. The positive correlation between the abundances of the two groups may therefore be the result of donor control, although the association between the two groups at the landscape scale is not as strong as would be expected if there was strong trophic dependence between them (Holt 1995, 1997).

The two groups of Coleoptera, *Helophorus* and Dytiscidae, showed negative correlations with *Notonecta*. In part, these correlations are likely to be related to the overall negative relationship between the abundance of Hemiptera and Coleoptera (section 6.3.3). However the negative correlations are still evident when habitat effects are factored out. A previous study of predation by *N. glauca*, involving field manipulation of notonectid predation in small enclosures (Jeffries 1984), also found that the abundance of species of *Helophorus* was significantly depressed when *Notonecta* was added to the enclosures, and personal observations in the laboratory have shown that *Notonecta* readily prey upon species of *Helophorus*. Therefore it seems quite likely that the negative correlation between *Notonecta* and *Helophorus* is at least partly the result of an impact of predation.

The negative correlation between Dytiscidae and *Notonecta* was not related to the habitat variables that were recorded. *Notonecta* are known to take larvae of large Dytiscidae (Jeffries 1984, Giller 1986) but personal observations suggest that predation on adult Dytiscidae such as *Agabus* spp. is very rare. The Dytiscidae are found over a fairly wide range of abundances where *Notonecta* is absent or at low abundance, which suggests that other factors may be involved in influencing the abundance of Dytiscidae, possibly unmeasured habitat variables. Combined with the relative scarcity of predation, this would suggest that *Notonecta* is unlikely to be a significant determinant of the abundance of this group. The observed response may be related to the overall changes in abundance of Hemiptera and Coleoptera that have been described in the dewponds.

6.5 Conclusions.

Patterns of association between taxa in the dewpond 'metacommunity' appear to some degree to be a reflection of common variation in abundance and likelihood of pond occupancy in response to habitat factors, which leads to overall shifts in community composition. The main variation in community composition is between Hemiptera dominated and Coleoptera dominated communities, which is influenced by the amount of emergent vegetation present in the ponds.

There is some evidence for both positive and negative associations between *Notonecta* and other taxa, both at the landscape scale (pond occupancy) and local scale (abundance within individual sites). These patterns provide conflicting evidence for the role of prey species dynamics in influencing the distribution and dynamics of *Notonecta* populations over a regional area. The degree to which both positive and negative associations between *Notonecta* and prey taxa are likely to be seen over a regional area in the field depends on the strength of the links between the predator and prey species (Holt 1995, 1997). Tightly coupled predator-prey systems are more likely to show strong sequential trophic dependencies, leading to nested distribution patterns (Holt 1997). *Notonecta* is a generalist predator, which is only weakly coupled to the dynamics of a particular prey species (Murdoch and Bence 1987, Murdoch 1993). The generalist nature of *Notonecta* may result in greater local prey instability (Murdoch and Bence 1987) depending on the relative vulnerability of prey taxa (Scott and Murdoch 1983). However over a regional area, this means that the distribution of *Notonecta* is less strongly tied to the distribution of a particular prey taxon and hence the metacommunity dynamics of prey species are more likely to play a modifying rather than a driving role in the spatial dynamics of *Notonecta*.

7. Summary and conclusions.

7.1 The aims reviewed.

In this thesis I aimed to explore the extent to which the spatial population dynamics of *Notonecta* species conformed to standard models of metapopulation dynamics. The focus of metapopulation dynamics is on the persistence of multiple populations scattered across a landscape. A species is seen to persist as a metapopulation if the patterns of occupancy and distribution at this scale are determined primarily by a balance in the rates of regional stochastic extinction and colonisation (Levins 1969, 1970, Hanski 1991, 1994b, Harrison 1994). For the most part, local processes are glossed over; patches are either unoccupied or at carrying capacity and there is no variation in habitat patch isolation or quality. More realistic metapopulation models, such as incidence function models (Hanski 1994a,b, 1997a,b, 1998, see section 1.2) include information on patch locations and sizes, but the emphasis is still on persistence via a regional balance of colonisation and extinction, and other aspects of species ecology, such as changes in habitat or interactions with other species are largely ignored. To what extent is this an appropriate view of the dynamics of *Notonecta* in dewponds?

7.2 Synthesis of results.

Single-species patterns and dynamics.

In ponds, and other isolated waterbodies, the edge of the water forms a clear boundary between habitat and non-habitat for the majority of the pond's inhabitants. Therefore, unlike many other field systems, where patch boundaries are less clearly defined (A.D.Taylor 1991, Wiens 1995, 1997), ponds are a good approximation of the patches envisaged in most metapopulation models. Due to this close similarity, and the relative physical uniformity of the dewponds, from an anthropomorphic point of view it is tempting to view all the ponds as being part of a network of patches. However from the viewpoint of an individual, or population of, *Notonecta*, the ponds are not all of equal suitability. Chapter 3 presents clear evidence that the species have consistent and contrasting habitat preferences, which are likely to be initiated by differences in oviposition substrate selection. However the habitat preferences are not mutually exclusive; there is some degree of overlap in the species distributions and they tend to co-occur in habitats that are intermediate between the species preferences. At the landscape scale, the ponds represent a mosaic of patches of varying quality, rather than the binary patch-matrix landscape envisaged by most metapopulation models (Holt 1997, Wiens 1995, 1997). Therefore the effective patch network for each species, defined by the spatial distribution of suitable habitat (Dunning, Danielson and Pulliam 1992, Harrison and Fahrig 1995, Hanski 1997b), is considerably smaller than the extent of the total pond network.

However the remaining ponds, which do not constitute suitable habitat for breeding populations, do not simply form part of the matrix of non-habitat surrounding patches of suitable habitat (Wiens 1997). They may still play a role in dispersal and colonisation by acting as 'stepping- stones' (Kareiva 1990). Although the species may not be able to reproduce successfully in these ponds, they can survive in the short term and this may enable individuals to disperse further in stages than they could in a single flight. Theoretical studies have also suggested that population may persist in habitats where local reproduction does not balance mortality; 'sink' habitats, through immigration from surrounding 'source' habitats (Pulliam 1988, Howe, Davies and Mosca 1991). The implications of a source-sink population structure for metapopulation dynamics remain largely unexplored (Harrison and Taylor 1997), but the study of a grasshopper metapopulation by Stelter, Reich, Grimm and Wissel (1997) demonstrated that populations which have low reproductive success and do not persist in the long term can nevertheless be important in maintaining overall persistence, if larger source populations are vulnerable to stochastic extinction. Sink populations may also be of significant importance for *Notonecta* dynamics. During dispersal in late summer, numerous transitory populations of *Notonecta* are established, not all of which persist to form breeding populations the following year. However if they are of sufficient size to overwinter successfully (see section 4.4) they may contribute to the persistence of extant breeding populations and the establishment of new populations during the spring dispersal phase (section 4.3). In the case of *N. maculata*, which can mate in the autumn, a single fertile female that overwinters successfully may contribute a propagule of sufficient size to establish a new population in the spring, whereas the spring mating *N. obliqua* would require a minimum of two individuals to potentially establish a new population.

Having taken into account the fact that not all ponds are suitable for occupancy by the species of *Notonecta*, the dewpond system still bears a strong resemblance to a metapopulation. If the spatial population dynamics of *Notonecta* are examined over the survey area (section 4.2), the system displays many of the hallmarks of metapopulation dynamics (Thomas 1996, Hanski, Pakkala, Kuussaari and Lei 1995, Hanski 1997a). Regional levels of occupancy over the survey area are fairly stable, although at smaller survey scales there is greater variation in occupancy. Some of this variation is due to random sampling error, but there is some evidence that habitat affects the number of ponds occupied. Despite frequent population turnover, a good proportion of the populations do persist from year to year, and populations can be maintained for at least three generations (which is the limit of continuous observation in this study), and probably considerably longer. The species have good dispersal abilities, and judging from the patterns of transient pond colonisation during dispersal phases (section 4.3) the ponds are not too isolated to prevent recolonisation via dispersal. The strongly seasonal pattern of dispersal prevents individual populations from becoming demographically united with surrounding patches. Although the high dispersal rates would suggest that the system may resemble a patchy population (Harrison 1991, 1994) rather than a metapopulation, the populations do represent local breeding populations.

However, a more detailed examination of the processes of colonisation and extinction (section 4.3 and 4.4) throws some doubt on the assertion that *Notonecta* in dewponds exist as 'classical' or Levins-type metapopulations. The assumption of metapopulation models is that regional persistence is based on a dynamic balance of stochastic colonisation and extinction, and in this respect *Notonecta* in the dewpond system clearly does not conform to this definition. Local extinction of populations of both species is linked to changes in the habitat of ponds (section 4.4), which appears to affect the suitability of the pond for occupancy. There is limited evidence for a similar link between colonisation and habitat (section 4.3), but problems with the analysis do not allow any firm conclusions to be drawn. If population turnover is driven by local changes in habitat quality, regional levels of occupancy and persistence at the landscape scale will be determined by the availability of suitable habitat, and the ability of species to 'track' its distribution (Thomas 1994b,c, Harrison and Fahrig 1995, Harrison and Taylor 1997). The species will have stable levels of regional occupancy only if the rates of creation and destruction of suitable habitat are equal (Thomas 1994b) and any inequality in the rates will influence persistence at the landscape scale. Changes in the habitat mosaic will alter the spatial distribution of suitable habitat patches, and patches may become more isolated, affecting the ability of a species to track the available habitat (Webb and Thomas 1994, Harrison and Fahrig 1995).

Isolation is unlikely to affect pond occupancy at the scale of this study due to the good dispersal ability of *Notonecta* (section 4.3) and the potential importance of stepping-stone habitats in reducing overall isolation of ponds. However not all suitable habitats are occupied by the species (section 3.2), and therefore there is clearly some stochasticity in the process of colonisation that prevents *Notonecta* from occupying all habitats across a landscape; the habitat tracking by this species is imperfect. Although colonisation and extinction do not determine regional persistence, they are still important in determining the spatial distribution of populations across the landscape (Harrison and Taylor 1997). In common with many, if not most, species that occupy fragmented habitat patches which experience temporal changes in habitat quality (e.g. Stelter, Reich, Grimm and Wissel 1997, Thomas and Hanski 1997), *Notonecta* appears to exist as a metapopulation within a dynamic mosaic of suitable habitat.

Multi-species patterns.

Metapopulation models of competition between two species emphasise fugitive mechanisms of coexistence, based on a trade-off between competitive and dispersal abilities. However in a mosaic landscape such as the dewponds, competition between *Notonecta* species appears to be largely avoided as a result of habitat partitioning at the landscape scale. However there is some overlap between the distribution of the species, mostly in ponds that have habitat characteristics that are intermediate between the preferences of the two species (section 3.2). In the ponds where the two species co-occur, the outcome of competition is dependent on the environment (section 5.2), and appears to be related to variation in foraging efficiencies in habitats of differing complexity, that have been demonstrated for both the nymphs (section 5.2) and the adults (Giller 1979, Giller and McNeill 1981). Although regional coexistence of the two species is largely habitat mediated, fugitive coexistence may play a role in the distribution of populations in the ponds where the species are likely to overlap. Species may occupy habitats that are more suitable for the other species, in the absence of that species, but will be displaced if the patch is colonised by the superior competitor. The number of ponds where the two species co-occurred varied between 6 and 12 in different years of survey, and a small number of ponds contained successful breeding populations of both species in all three years of survey (section 4.2.3). This suggests that coexistence is possible over several generations at least; habitat heterogeneity within an individual pond may allow partitioning of habitats, promoting coexistence (Streams 1987b).

Broadening the view yet further, patterns of association between *Notonecta* and the metacommunity of potential prey, in terms of pond occupancy and local abundance suggest that unlike other studies (Blaustein, Kotler and Ward 1995, Arnér, Koivisto, Norberg and Kautsky 1998, Blaustein 1998), in the dewponds, *Notonecta* does not exert a strong top-down influence on community structure. Dewpond community composition appears to vary largely in response to habitat factors (section 6.3.2). There is some evidence of both positive and negative associations between *Notonecta* and individual prey taxa (section 6.3.4), which suggests that donor control by prey species may have some impact on the abundance of *Notonecta*, but overall links between the dynamics of *Notonecta* and its potential prey at the landscape scale do not appear to be strong.

7.3 Implications for the study system.

Patterns of regional distribution and coexistence.

Regional occupancy and persistence of *Notonecta* species appears to be driven by habitat availability, but colonisation and extinction are important in determining the spatial distribution of populations. Given the importance of habitat conditions in determining occupancy (sections 3.2 and 3.3), changes in the amount of suitable habitat over a regional area will obviously have implications for regional distribution and persistence. If the amount of suitable habitat declines over the landscape, the number of occupied patches will also decline, although the proportion of suitable habitat occupied may stay fairly constant until the patch network reaches the critical size for persistence (Hanski, Moilanen and Gyllenberg 1996). The spatial distribution of habitat change will also affect regional dynamics. If the changes occur randomly across the landscape, then the average isolation of patches will increase. Given the dispersal ability of *Notonecta* and its ability to use other ponds as stepping-stones during dispersal, this is likely to have less effect than it would on species with weaker dispersal powers. Alternatively, if the habitat change is concentrated in one area, the species may become extinct in that area, but it is likely to persist elsewhere in the landscape if sufficient habitat remains.

As a result of the contrasting habitat preferences, changes in habitat conditions across the landscape may have different effects on the two species. For example, as a result of the availability of piped water and modern cattle troughs, the use of dewponds for watering of livestock has declined and many are now neglected. In the absence of regular management, the ponds gradually silt up and become more heavily vegetated through successional processes (Carpenter 1995, Chicken 1996), particularly the clay lined ponds which provide a better rooting medium for plants. Indeed there is evidence that even over the period of study, the Peak District dewponds became on average more heavily silted (figure 2.5), although whether this is indicative of a long-term trend is difficult to establish. The overall change in the habitat across the landscape, particularly the increase in average silt cover and amount of vegetation in the ponds resulting from succession, will increase the amount of suitable habitat for *N. obliqua* and decrease the amount suitable for *N. maculata*.

N. obliqua has a higher foraging efficiency in complex environments (section 5.2) and oviposits in the stems of water plants (section 3.4); it would therefore be better suited to the prevailing habitat conditions. In the survey of 32 ponds between 1992 and 1998, there was a significant correlation between the number of ponds containing submerged vegetation and the number occupied by *N. obliqua* (section 4.2.2), suggesting that at this scale, occupancy was responding to the amount of suitable habitat available. *N. maculata* however, oviposits on solid substrates, which are likely to become increasingly scarce as the siltation of the ponds progresses. Although there is little evidence of a decline in occupancy by *N. maculata*, despite the increase in average silt cover over the same period, it seems reasonable to assume that as oviposition sites become rarer, this species will decline in regional occupancy. Therefore in the absence of any other trends in habitat change, or active management, the natural successional processes within dewponds may lead to a shift in the patterns of regional occupancy exhibited by the species.

Competition between the two species may exacerbate the effects of the habitat change on regional occupancy. Metapopulation models have suggested that reducing the amount of habitat available over a regional area can alter the competitive balance between two species, and lead to an increase in the relative occupancy of an inferior competitor (Nee and May 1992, Moilanen and Hanski 1995, Nee, May and Hassell 1997). In the dewponds, *Notonecta* species are largely separated by habitat preferences, but show some overlap in distribution in patches of intermediate habitat type (section 3.2). Under conditions of habitat change, the species occupying the declining habitat type will tend to show a more rapid decline when a competitor is present than if habitat change alone was influencing distribution (Danielson 1991).

Spatial dynamics and pond communities.

At a more general level, the mesoscale spatial dynamics demonstrated by *Notonecta* in the dewponds have implications for the ecology and conservation of pond communities. Many pond dwelling species show similar patterns of population turnover and dispersal abilities as *Notonecta* (Brown 1951, Popham 1951, 1952, 1953, 1964, Fernando 1958, 1959, Jeffries 1994, Nürnberger 1996, Briers 1997). Studies of pond community structure have generally found that although taxa often show patterns of variation in relation to physico-chemical attributes (Friday 1987, Hecnar and McLoskey 1996) and other habitat variables such as pond area (Möller and Rordam 1983, Bronmark 1985), pond faunas are never entirely predictable (Friday 1987, Jeffries 1997). There is a strong ‘element of chance’ in the assemblage of species that is found in any individual pond within a regional area (Talling 1951, Jeffries 1989, 1994, 1997). This stochastic variation in community structure is likely to be due, at least in part, to the dynamics of colonisation and extinction of species which show metapopulation or similar dynamics. Given the potential importance of mesoscale spatial population dynamics in pond community structure, it is important to move towards conservation of 'pond landscapes'; regional networks of sites which have sufficient connectivity to potentially allow recolonisation if local populations go extinct (Boothby and Hull 1995, Briers 1997, Williams *et al.* 1997).

7.4 Implications for metapopulation theory.

The study system deviates from the strict definition of a metapopulation in so far as population turnover results from changes in local habitat conditions, rather than being primarily stochastic (sections 4.3 and 4.4). Therefore persistence at the metapopulation level is likely to be dependent on the amount of suitable habitat and its distribution across the landscape.

Of the still relatively small number of studies carried out on field metapopulations, only a very small proportion fit within the framework of 'classical' Levins-type metapopulations (Harrison 1991, 1994, Harrison and Taylor 1997, but see Hanski, Pakkala, Kuussaari and Lei 1995). Models with greater realism and field application (e.g. incidence function models) have tended to incorporate more local attributes, such as patch-specific area and isolation measures. No model can satisfy the conflicting needs for generality, precision and realism (Levins 1966). Therefore as ecologists seek to improve the fit of metapopulation models to the observed patterns in real systems, the complexity of the models is likely to show a concomitant increase and the role of local processes will increase in relative importance (Harrison and Taylor 1997). This may reduce the conceptual strength of classical metapopulation dynamics, with the emphasis on regional persistence through balancing colonisation and extinction. Given the current vogue in the use of metapopulation models to address questions in conservation biology (Harrison 1994, Hanski and Simberloff 1997), it is essential that the concepts and models put forward by ecologists deliver the right messages to those who apply them in the field of species conservation, to prevent inappropriate management of habitats or species populations. If there is only limited evidence for regional persistence through colonisation-extinction dynamics then there may be a need to broaden the concept of a metapopulation to include other forms of mesoscale spatial population dynamics (Harrison and Taylor 1997).

The failure to consider changes in the underlying habitat of individual patches within the metapopulation is a serious shortcoming of metapopulation models (Thomas and Hanski 1997). Few species are likely to inhabit an entirely static environment; to a greater or lesser degree all ecosystems show temporal changes in local habitat conditions. Many of the field metapopulation studies that have been undertaken have demonstrated the importance of local habitat conditions, or changes in habitat, on patch occupancy and population turnover (Sjogren 1991, Thomas and Harrison 1992, Sjogren Gulve 1994, Kindvall 1996, Stelter, Reich, Grimm and Wissel 1997, Thomas and Hanski 1997). Gyllenberg and Hanski (1997) examined structured metapopulation models which incorporated variation in habitat quality and found that the patch quality distribution within a metapopulation had important effects on the relationship between the amount of suitable habitat and the proportion occupied at equilibrium. The incidence function model has been further developed by Moilanen and Hasnki (1998) to include the effects of habitat quality and landscape structure. In this model habitat quality modifies the effective area of each patch. However the improvement of the fit of the model with habitat quality included over the standard incidence function model, which only considers patch area and isolation, was not great when it was applied to a butterfly metapopulation. Moilanen and Hanski (1998) therefore suggest that in some systems, metapopulation dynamics may be effectively modelled without further increasing the complexity of the models by including habitat or other effects.

The degree to which habitat change affects the persistence of the species as a metapopulation depends on the relative timescales of the dynamics of the species and of habitat change (Thomas and Hanski 1997). Over the timescales of most ecological studies, species may be seen to persist as metapopulations, but in the long term, regional persistence and levels of occupancy may be determined by trends in habitat conditions (Thomas and Hanski 1997). Butterflies are seen to be prime examples of field metapopulations (Harrison, Murphy and Ehrlich 1988, Thomas and Harrison 1992, Hanski, Pakkala, Kuussaari and Lei 1995, Thomas and Hanski 1997). However in many cases, long term trends in regional occupancy and persistence appear to be driven by changes in the habitat as a result of succession or anthropogenic habitat change (Warren 1993, Thomas 1994b,c). Butterfly population dynamics are fast relative to the speed of habitat change, therefore they still fit the predictions of metapopulation models in the short to medium term (Thomas and Hanski 1997).

Notonecta in dewponds show strong links between habitat change and population turnover on an annual basis (sections 4.3 and 4.4). Although the regional average habitat conditions remain fairly constant over time (see figure 2.5), the habitat conditions within individual ponds often show dramatic changes between years. Therefore the speed of habitat dynamics appears to be similar to that of *Notonecta* and hence habitat tracking is more important than stochastic colonisation and extinction in determining regional persistence. Over the timescales which most studies are carried out, it may be very difficult to assess the relative importance of metapopulation processes and long-term habitat change on overall regional persistence. If long-term habitat change influences regional occupancy, many fragmented population systems may not be at equilibrium, and are likely to exhibit an 'extinction debt' (Tilman, May, Lehman and Nowak 1994), where extinctions occur and the level of occupancy shows a further decline, even if no additional habitat change occurs. This makes application of equilibrial metapopulation models for the purpose of defining the 'minimum viable metapopulation' size (Hanski, Moilanen and Gyllenberg 1996, Hanski 1997a) or other conservation applications very difficult.

Incidence function models and other spatially explicit approaches to the modelling of metapopulation dynamics take account of the area and isolation of patches, which have historical importance in island biogeographical models (MacArthur and Wilson 1967). Incidence functions are easy to apply to a suspected metapopulation, as a result of this, may also be easily misapplied (Thomas 1994a). Given the diversity of 'types' of metapopulation dynamics that have been observed in field systems (Harrison and Taylor 1997), it is important to develop a flexible model framework which can accommodate differences in the importance of stochastic and deterministic factors in different systems. In the future development of metapopulation models, greater attention will have to be given to the dynamic underlying habitat mosaic which the species inhabit (Thomas and Hanski 1997). In order to achieve this, it may be possible to draw on the developments in patch dynamics (Pickett and White 1985, Levin, Powell and Steele 1993) which, by analogy, consider the metapopulation dynamics of the patches themselves, resulting from succession and disturbance. Although regional persistence as a result of metapopulation dynamics may be overemphasised in current theory, the persistence of local populations, and regional distribution patterns may be strongly dependent on the spatial location of habitat patches and dispersal from occupied patches (Harrison and Taylor 1997). Temporal changes in the suitable habitat, through patch dynamics, will alter the distribution of patch sizes and relative isolation, which will in turn influence metapopulation dynamics. In an example of an approach which combines aspects of patch dynamics and metapopulation dynamics, Stelter, Reich, Grimm and Wissel (1997) present a simulation model of grasshopper metapopulation dynamics which incorporates both stochastic and deterministic causes of population turnover. Although such models are much less tractable analytically, the model framework given by Stelter, Reich, Grimm and Wissel (1997) could easily be adapted for application to other species inhabiting dynamic habitat mosaics, including *Notonecta* in dewponds.

Most natural ecosystems are becoming increasing fragmented, largely as a result of the activities of man. Metapopulation theory, with its emphasis on regional species persistence in a network of habitat fragments, is being increasingly used by conservation biologists and others who are concerned with the protection and conservation of species, to inform planning decisions and management regimes for endangered species (Hanski and Gilpin 1991, McKelvey, Noon and Lamberson 1993, Hanski 1994b, Harrison 1994). As such this represents a paradigm shift in conservation biology from island biogeographical approaches (e.g. the SLOSS debate, Soulé and Simberloff [1986]) to metapopulation based conservation strategies (Hanski and Simberloff 1997), although the two approaches are clearly related.

Despite the increasingly widespread use of metapopulation theory in conservation biology, there is still a large mismatch between the development of the theory and empirical studies aiming to test the theoretical predictions. Given that the majority of empirical studies that have been carried out have deviated in some way or other from the theoretical predictions (Harrison and Taylor 1997), it is essential that further empirical work is carried out to assess the applicability of current models to field systems, pinpoint weaknesses in model assumptions, and suggest areas for future development of metapopulation theory. The extensive spatial and temporal scales required to study the dynamics of most field metapopulations makes empirical examination of theoretical predictions difficult. Due to their close resemblance to the habitat patches envisaged by most metapopulation models, and the capacity of many of their inhabitants to disperse between sites, dewponds, and pond systems in general, (e.g. Jeffries 1994, Sjögren 1991, Sjögren Gulve 1994) provide ideal model systems for testing the predictions of metapopulation theory.

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Appendix 1.

Pond locations, construction types and years of survey.

Note: Missing pond numbers are ponds that were recorded, but not sampled.

Pond No.	National Grid Reference Easting	Northing	Construction	Surveyed 1992	1996	1997	1998
01	420400	372700	Concrete	*	*	*	*
02	420500	372800	Concrete	*	*	*	*
03	420200	372300	Concrete	*	*	*	*
04	420300	372700	Concrete	*	*	*	*
05	420200	372700	Concrete	*	*	*	*
06	419800	372800	Concrete	*	*	*	*
07	422000	375400	Concrete	*			
08	422200	375400	Concrete	*			
09	421400	375200	Concrete	*	*	*	*
10	421200	374800	Concrete	*	*	*	*
11	421200	375300	Concrete	*	*	*	*
12	419900	375200	Concrete	*	*	*	*
13	420100	375000	Concrete	*	*	*	*
14	420400	376300	Concrete	*	*	*	*
15	420500	376200	Concrete	*	*	*	*
16	418300	372600	Clay	*			
17	417100	368700	Concrete	*	*	*	*
18	416800	368700	Concrete	*	*	*	*
19	416100	369000	Clay	*	*	*	*
20	417300	369800	Concrete	*	*	*	*
21	417000	369900	Concrete	*	*	*	*
22	417000	369500	Concrete	*	*	*	*
23	417300	369300	Concrete	*			
24	417300	368900	Concrete	*	*	*	*
25	416500	376200	Concrete	*	*	*	*
26	416500	376100	Concrete	*	*	*	*
27	416200	378400	Clay	*	*	*	*
28	416100	378400	Clay	*	*	*	*
29	414500	378200	Clay	*	*	*	*
30	414400	377700	Concrete	*	*	*	*

Pond No.	National Grid Reference Easting	 Northing	Construction	Surveyed 1992	 1996	 1997	 1998
31	413100	377400	Concrete	*	*	*	*
32	412500	378400	Clay	*	*	*	*
33	412600	378400	Clay	*	*	*	*
34	412700	376700	Concrete	*			
35	412200	378400	Concrete	*			
37	412800	377300	Concrete	*			
38	412700	377500	Concrete	*	*	*	*
39	412600	377700	Concrete	*	*	*	*
40	418400	370900	Clay	*	*	*	*
41	418100	371200	Clay	*	*	*	*
42	421830	360550	Concrete		*	*	*
43	421350	360520	Clay		*	*	*
44	421300	360430	Concrete		*	*	*
46	420310	359320	Clay		*	*	*
47	422600	360350	Concrete		*	*	*
48	422300	360270	Concrete		*	*	*
49	422010	360130	Concrete		*	*	*
50	422200	360200	Concrete		*	*	*
51	422100	359950	Clay		*	*	*
52	423300	360400	Concrete		*	*	*
53	421030	360650	Clay		*	*	*
54	421270	360900	Concrete		*	*	*
57	419550	358840	Clay		*	*	*
58	414340	377570	Concrete		*	*	*
59	414000	378400	Clay		*	*	*
60	413560	379210	Clay		*	*	*
61	413260	379190	Clay		*	*	*
62	413390	379030	Concrete		*	*	*
63	416040	377770	Concrete		*	*	*
64	413550	379840	Clay		*	*	*
65	413750	379940	Concrete		*	*	*
66	426850	360270	Concrete		*	*	*
67	426090	357650	Clay		*	*	*

Pond No.	National Grid Reference		Construction	Surveyed			
	Easting	Northing		1992	1996	1997	1998
68	421850	359320	Clay		*	*	*
69	420950	360650	Concrete		*	*	*
70	418730	358710	Clay		*	*	*
71	418780	363980	Concrete		*	*	*
72	418410	363500	Concrete		*	*	*
73	417850	366750	Concrete		*	*	*
74	418270	373140	Concrete		*	*	*
75	418180	371250	Concrete		*	*	*
76	418470	370250	Concrete		*	*	*
77	418440	370300	Concrete		*	*	*

Appendix 2.

Species lists for dewpond sites (1996).

Sites in bold type indicate records from the samples analysed in Chapter 6. Other records of Hemiptera and Coleoptera, excluding *Notonecta*, are from other survey work undertaken in 1996 at all sites. Zooplankton were not identified to species and hence are not included in the table.

Order/Class	Family	Species	Sites present
Clitellata	Erpobdellidae	*Erpobdella octoculata*	**29**
	Glossophonidae	*Helobdella stagnalis*	**3,4,17,18,20,26,29,32,34,38**
Coleoptera	Dytiscidae	*Acilius sulcatus*	**5,22**,49,67
		Agabus bipustulatus	3,4,5,**10,13,20**,26,27,**28**,29,30,**34,35,41**,42,43,44, 47,48, 49,51,52,57,60,61,62,65,66,68,70,71,74,75
		Agabus nebulosus	3,**5**,6,**10**,13,**17**,18,**20**,21,**22**,24,26,27,28,29,**30**,31, **33**,34,35,38,40,**41**,42,49,50,51,52,53,57,59,60,63, 65,67,70,71, 75
		Agabus spp. larvae	**13,17,18,20,26,35**
		Coelambus confluens	5,13,18,22,30,47,49,50,52,53,65,75
		Coelambus impressopunctatus	13
		Colymbetes fuscus	13
		Hydroporus palustris	**34**,67,70
		Hydroporus spp.	**10**,13,**34**,42,44,47,50,52,57,59,67,70
		Hygrotus inaequalis	19,21,34,60,62,67,70
		Ilybius spp.	11,74
		Laccophilus minutus	5,18,**20**,21,26,40,41,42,51,59,63,70, 72
	Gyrinidae	*Gyrinus substriatus*	9,11,20,**24**,41,52
	Haliplidae	*Haliplus confinis*	**5,9**,10,**18,20,22,34**,59,70,73,74
	Hydrophilidae	*Helophorus* spp.	**2,3,4,5,6,9,10,13,15,17,18**,19,**20,21,22,24,26,27,28** **29,30,32,33,34,35,38,39,40,41**,43,47,48,49,50,51, 52,53,57,59, 61,62,63
		Hydrobius fuscipes	5,15,17,19,27,**33,34**,35,40,**41**,44,57, 64,67,70
Diptera	Chironomidae	spp. larvae and pupae combined	**2,3,4,5,6,13,18,21,22,24,26,2730,32, 40,41**
	Culicidae	spp. larvae	**5**
Ephemeroptera	Baetidae	*Cloeon dipterum*	**13**
Gastropoda	Lymnaeidae	*Lymnaea peregra*	**3,4,6,13,18,21,24,27,28,41**
	Planorbidae	*Armiger crista*	**41**
Hemiptera	Corixidae	*Arctocorisa germani*	18
		Callicorixa praeusta	40
		Corixa punctata	1,**2,3,4,5**,9,10,17,18,**20**,21,22,**24**,26,27,28,29,38,**40** **41**
		Hesperocorixa sahlbergi	5,13,20,22,27,40
		Sigara concinna	**5,22**
		Sigara lateralis	1,**3,5,18,22**,24,26,27,28,30,31,**38**,29
		Sigara limitata	13,20,**22**

Order/Class	Family	Species	Sites present
Hemiptera	Corixidae	*Sigara nigrolineata*	1,2,**3,5**,6,13,15,17,**18**,20,**22**,24,**27**,29,30,31,**32**,35, **38,40**, 41
		Sigara spp. nymphs	**5,6,13,17,18,20,24,28,29,30,32,34,35,38**
	Notonectidae	*Notonecta maculata*	**2,3**,5,**6**,9,11,13,**17,18,21,24**,26,**29,41**,47,48,49,52, 63,65,71,73,75,76,77
		Notonecta obliqua	4,9,10,11,**20**,29,**24,29,32,38**,40,42,51,57,59,64,65, 66,72,74,77