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Predation by *Gambusia Holbrooki* (Girard) (Pisces Poeciliidae) on Tadpoles : Feeding Trials and Microhabitat Utilisation in Two Contrasting Wetlands on the Swan Coastal Plain, Western Australia

Beate Sommer
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**PREDATION BY *GAMBUSIA HOLBROOKI* (GIRARD) (PISCES:
POECILIIDAE) ON TADPOLES: FEEDING TRIALS AND
MICROHABITAT UTILISATION IN TWO CONTRASTING
WETLANDS ON THE SWAN COASTAL PLAIN, WESTERN
AUSTRALIA**

by

Bea Sommer

This thesis is submitted in partial fulfilment of the requirements for the Award of Honours in the Bachelor of Science (Environmental Management) at the Faculty of Science, Technology and Engineering, Edith Cowan University.

Date of submission: 24 April 1997

USE OF THESIS

The Use of Thesis statement is not included in this version of the thesis.

ABSTRACT

Predation by non-native *Gambusia* spp. (somewhat inappropriately referred to as "Mosquitofish") has been implicated in the decline of some frog populations overseas and in eastern Australia. Originally introduced to control mosquito larvae, *Gambusia holbrooki* are now widely distributed and abundant in wetlands of the Swan Coastal Plain (Western Australia). Anecdotal evidence suggests that some frog populations on the Swan Coastal Plain may be declining. Through a series of laboratory feeding trials and a field survey conducted in a permanent and a seasonal wetland on the Swan Coastal Plain, this study investigated whether predation by *G. holbrooki* has the potential to impact local frog populations.

Laboratory feeding trials were carried out with tadpoles/eggs of five local frog species. Larval developmental stages were classed into four broad groups. One experiment involving 20 single predator:prey treatments and 20 controls (prey only) was conducted with each developmental stage group of each tadpole species. All tadpole species with which feeding trials were conducted were either consumed or injured by *G. holbrooki*. Hierarchical log-linear analysis revealed that there were significant associations between larval developmental stage and survival, and between tadpole species and survival. However, there was no association between tadpole species and the number of tadpoles consumed by *G. holbrooki*. The smallest tadpoles (hatchlings) had the highest mortality and consumption rate, indicating gape-limited predation by *G. holbrooki*. It was therefore concluded that differences in survival and consumption rate between species and between larval developmental stages are more likely to be related to tadpole size than to palatability.

The field survey examined temporal and spatial associations in microhabitat use by *G. holbrooki* and local tadpole species. A total of 103 4x4m quadrats were sampled at Lake Jandabup and Lake Gwelup on three sampling occasions. Major habitat types, characterised by vegetation community structure, were identified using UPGMA classification, and faunal abundances within each habitat type and each sampling occasion were compared. Sites were then classified and ordinated based on faunal assemblages in order to find patterns in their spatial and temporal

distribution. Principal axis correlation was used to find the best linear correlation of various environmental variables with the ordination of sites. The results of these analyses indicate considerable microhabitat overlap, and thus a potential for interactions to occur, between *G. holbrooki* and some local tadpole species.

Scenarios of potential interactions in the field are discussed in view of the combined results of both research components, as well as in consideration of other influencing factors which were not directly investigated as part of this study. It was concluded that there is a potential for the direct and/or indirect effects of predation by *G. holbrooki* on tadpoles to impact local frog populations.

Declaration

I certify that this thesis does not incorporate without acknowledgement any material previously submitted for a degree or diploma in any institution of higher education; and that to the best of my knowledge and belief it does not contain any material previously published or written by another person except where due reference is made in the text.

Signed: _

Date: 22-8-1997

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1. Introduction

1.1 Background

Frogs are a valuable asset to the environment. They have complex life cycles (Wilbur, 1980), that is, they are typically aquatic herbivores as tadpoles and terrestrial carnivores as adults. They are thus important links in the food chain of fresh aquatic ecosystems, and potentially reflect environmental effects at all trophic levels (Rowe and Dunson, 1994). Amphibians have permeable eggs, gills and/or skin which are in intimate contact with water or soil increasing the chances of uptake of pollutants. These properties make amphibians sensitive to subtle changes in the environment, and potentially excellent indicators of wetland, and general environmental, health (Heyer *et al.*, 1994; Rowe and Dunson, 1994).

Unfortunately, it appears that amphibian populations are declining in many parts of the world (Barinaga, 1990; Blaustein and Wake, 1990; Phillips, 1990; Wyman, 1990), and Australia is no exception (Czechura and Ingram, 1990; Ferraro and Burgin, 1993a & b; Gillespie and Hollis, 1996; Hero, 1991; Ingram and McDonald, 1993; Laurance, 1996; Tyler, 1991a, 1991b & 1993). Habitat destruction by humans is given as the primary cause of the declines and extinctions. However, this does not explain the disappearance of frogs from seemingly pristine areas (Blaustein and Wake, 1990). Pechmann *et al.* (1991) discuss the problem of separating human impacts from natural population fluctuations and stress the need for long-term studies, particularly as there is a paucity of historical data on the size of amphibian populations. As Blaustein and Wake (1990) point out, natural population fluctuations are difficult to invoke as explanations for the world-wide decline of an entire class of animals, which in many places seems to have begun in the early to mid 1970s.

Most scientists now agree that there is not a single cause for the loss of amphibians, but a number of individual factors. Some of the factors that have been implicated in the decline of Australian frogs were reviewed by Ferraro and Burgin (1993a). These include: the susceptibility of frogs to pollution, habitat destruction, pH stress, heavy, and other metals, pesticides and

herbicides, increased radiation, salinity, elevated temperatures, competition with, and predation by, introduced species, disease and collection by humans. Many of these factors interact to produce synergistic effects and potentially exacerbate predation levels (Bradford 1991; Ferraro and Burgin, 1993a). The presence of introduced predators, in addition to other influencing factors, may often be the final stroke for many frog populations.

It has been claimed that, unlike in eastern Australia, few frog species in south-western Australia seem to be in decline (Roberts, 1996). However, since commencement of the FROGWATCH program, the Western Australian Museum has been receiving numerous queries and reports about frogs disappearing from where they were once common (K. Aplin, pers. comm.). Many of these apparent declines appear to be unrelated to habitat loss. On the Swan Coastal Plain, it is estimated that approximately 80% of wetlands have been lost since European settlement either by clearing of vegetation, landfill or drainage (Godfrey, 1989, cited in Balla and Davis, 1993). The majority of wetlands that remain are modified to some extent, and most of these support large populations of the introduced fish, *Gambusia holbrooki* (Balla and Davis, 1993).

1.2 Introduced aquatic organisms and amphibian declines

There is growing world-wide concern that introduced aquatic organisms may play a role in the decline of amphibian populations. Introduced salmonid fish have been implicated in the serious decline of *Rana muscosa* populations in Nevada (USA) (Bradford, 1989; Panik, 1995). The direct and indirect impacts of fish introductions have been linked to the decline of frog populations in mid-western United States (Lannoo, 1996). The micropredatory fish, *Gambusia affinis*, along with bullfrogs, are regarded as the principal causal agents of declines of *Rana aurora* and *Bufo boreas* in the Great Central Valley of California (Fisher and Shaffer, 1996). Lardner and Sidenmark (1996) reviewed the effects of introduced fish on amphibian populations. The literature cited shows that fish introductions often adversely affect amphibian populations.

In eastern Australia, laboratory and field experiments indicate that *Gambusia holbrooki* prey on a number of local tadpole species (Daly, 1995; Harris, 1995; Morgan and Buttemer, 1996; Webb, 1994). Harris (1995) demonstrated a negative relationship between the abundance of *G. holbrooki* and tadpoles. In another example, a population of the endangered green and golden bell frog, *Litoria aurea*, has been discovered at a degraded sand-mining pit in Sydney (Wright, 1996). The species, which is closely related to *Litoria moorei* found in south-western Australia, seems to thrive i.e. places where *G. holbrooki* are absent (Daly, 1995).

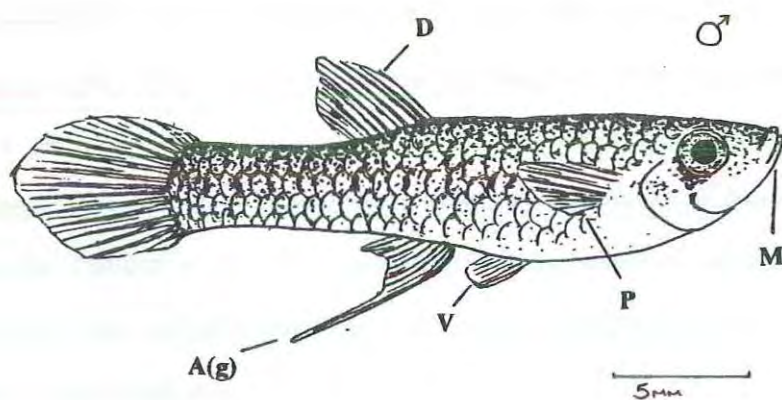
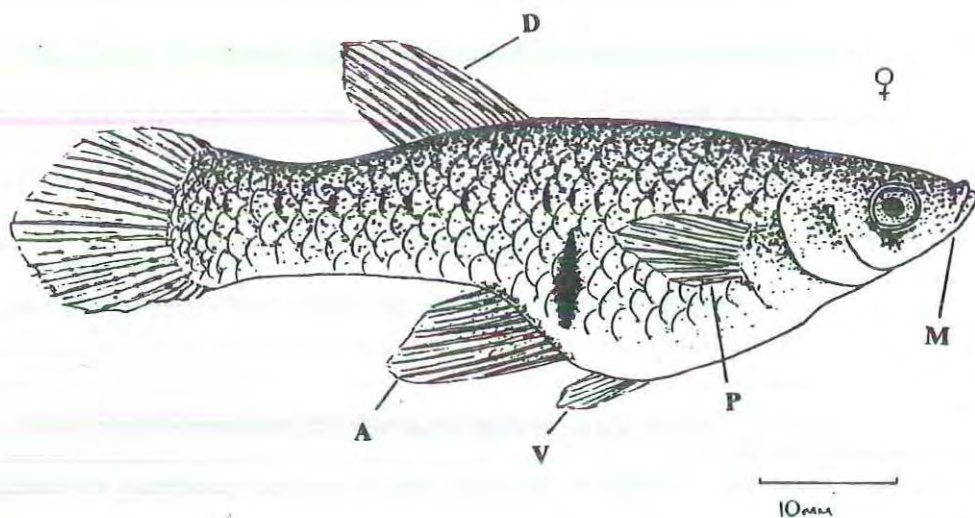
Reynolds (1995) found that under laboratory conditions *G. holbrooki* preyed on a number of tadpoles of frog species occurring on the Swan Coastal Plain (Western Australia). It was nevertheless concluded that the impact of potential predation by *G. holbrooki* on tadpoles in south-western Australia would be minimal as the breeding periods of most of the local frog species did not coincide with peaks of *G. holbrooki* abundance. In eastern Australia, there is a more or less regular rainfall pattern throughout the year and the majority of frog species breed in the warmer seasons, that is, during late spring and into summer (Harris, 1995). In summer, *G. holbrooki* abundance is high (eg. Trendall, 1983), and the risk of tadpoles being preyed upon by this fish is greater than during other seasons. By contrast, south-western Australia is characterised by winter rainfall, and the majority of frog species breed during this time, while *G. holbrooki* breed in the warmer spring and summer months. In another study carried out in south-western Australia, Blyth (1994) compared the survival of *Crinia* spp. and *Heleioporus eyrei* tadpoles in experimental enclosures with and without *G. holbrooki*. Significantly more tadpoles survived in the enclosures without *G. holbrooki*, and therefore it was concluded that *G. holbrooki* may have a negative impact on the recruitment of local frog species. However, up to date, the extent of spatial and temporal overlap in microhabitat utilisation between *G. holbrooki* and local tadpoles in wetlands on the Swan Coastal Plain has not been determined, and therefore, the potential impact of predation by this fish on local tadpoles in a natural situation could thus far not be realistically evaluated.

1.3 The introduced 'mosquitofish', *Gambusia holbrooki*

'Mosquitofish' originally entered Australia in the 1920's as an aquarium species and were subsequently widely released to control mosquito larvae (Arthington and Lloyd, 1989; Lloyd, 1986). It has been established that all of the feral 'mosquitofish' present in Australia belong to the species *Gambusia holbrooki* (Hutchison, 1991; Lloyd and Tomasov, 1985), and previous reports about *Gambusia affinis* in Australia, by default, refer to *G. holbrooki*. The distinguishing features of *G. holbrooki* are shown in Figure 1.1. *G. holbrooki* are native to south-eastern United States (Arthington and Lloyd, 1989). Unfortunately, early warnings (Sweetman, 1936) with regards to the ineffectiveness of *Gambusia* to control mosquitoes, as well as their potential to cause environmental damage, did not become generally known until much later. As a result, *Gambusia* are now considered to be the most widely distributed freshwater fish in the world (Service, 1996). They are widespread throughout Australia (Lloyd *et al.*, 1986), and in south-western Australia, they are the dominant fish species in the streams and lakes of the northern Swan Coastal Plain, common in the Canning River and North Dandalup River systems, and are abundant in the Collie and Murray Rivers (Mees, 1977; Merrick and Schmida, 1984; Pen and Potter, 1991; Trendall, 1982 & 1983).

'Mosquitofish' display the typical traits of aggressive and successful invaders (Arthington and Mitchell, 1986; Fox and Adamson, 1986; Lloyd *et al.*, 1986; Myers, 1965). Behavioural and genetic flexibility (Trendall, 1982 & 1983) makes them tolerant of a wide range of environmental conditions (Arthington and Lloyd, 1989; Hutchison, 1991; Lloyd *et al.*, 1986; Sterba, 1962). Habitat preference is for shallow, calm water, dark-coloured substrates and subsurface vegetation providing lateral concealment (Casterlin & Reynolds, 1977). Arthington *et al.* (1983) found that in the Brisbane region (Queensland), *Gambusia* preferred edge areas with exotic grasses and mixed weed beds, while open water was largely avoided. In temperate areas there are marked seasonal fluctuations in abundance of *Gambusia* (Krumholz, 1948; Pen and Potter, 1991). In the Perth region, there is high mortality of *G. holbrooki* in winter. Breeding usually begins in early spring, and populations increase dramatically over summer (Lloyd *et al.*, 1986; Trendall, 1982), placing an increasing demand on aquatic resources.

Figure 1.1: *Gambusia holbrooki* (Baird and Girard), Family Poeciliidae, Order Cyprinodontiformes (drawn by N. Guthrie from preserved fish collected from Lake Jandabup; labelling adapted from Scott *et al.*, 1973)



- M - Mouth, dorsal configuration
- D - Dorsal fin, single, soft-rayed, behind mid-body
- P - Pectoral fin, paired, short, rounded
- V - Ventral fin, paired, very small, close together
- A - Anal fin, ventrally located, behind mid-body
- A(g) - Extended anal fin in males (gonopodium)

Gambusia are omnivorous (with a preference for animal foods) and opportunistic feeders (Arthington, 1989; Arthington and Mitchell, 1986; Lloyd *et al.*, 1986), consuming large quantities of drifting terrestrial invertebrates and zooplankton (Hurlbert *et al.*, 1972; Hurlbert and Mulla, 1981; Pen and Potter, 1991). In the Collie River (south-western Australia), *G. holbrooki* were found to be feeding at the water surface and throughout the water column (Pen and Potter, 1991). The failure of dietary studies to provide evidence of *Gambusia* having consumed tadpoles is probably due to the standard methods of gut analysis employed, which tend to be inefficient at detecting rapidly digested foods (Arthington, 1991). For instance, Reynolds (1995) examined the gut contents of *G. holbrooki* directly after they had consumed anuran hatchlings, finding that the tadpoles were macerated and very difficult to discern.

Rupp (1996) recently reviewed the literature relating to the adverse impacts resulting from the introduction of *Gambusia* for the control of larval mosquitoes. He found that the principal opposition to the introduction of *Gambusia* comes from ichthyologists, although some mosquito researchers have expressed concerns about the environmental impact of placing the fish in habitats to which it is not native. Native fish populations have been negatively affected by *Gambusia* overseas (Belk and Lydeard, 1994; Lydeard and Belk, 1993; Myers, 1965), as well as in Australia (Arthington, 1991; Courtenay, 1990a & b; Fletcher, 1986). This is thought to be a consequence of predation, competition and/or aggressive behaviour. *Gambusia* can also significantly impact aquatic community structure (Horwitz, 1994). Based on trials carried out in experimental ponds, Hurlbert *et al.* (1972) concluded that the selective planktonic feeding of *Gambusia affinis* may have considerable impact on aquatic invertebrate communities and may result in increased algal densities.

1.4 Breeding biology of local frogs

Seven frog species occur on the Swan Coastal Plain in south-western Australia. All of them are endemic to Western Australia (Tyler *et al.*, 1984). One species, *Myobatrachus gouldii*, has tadpoles which are not aquatic, and will not be dealt with in this thesis. Of the six remaining species, two belong to the Family Hylidae (*Litoria adelaidensis* and *Litoria moorei*), and four

belong to the Family Myobatrachidae (*Crinia glauerti*, *Crinia insignifera*, *Heleioporus eyrei*, and *Limnodynastes dorsalis*). With the exception of *L. moorei*, spawning usually occurs during the wettest part of the year (Main, 1965). 'Spawn' refers to anuran eggs and the jelly that surrounds them (Tyler, 1989). Fertilisation of the eggs is external, and the eggs develop into free-swimming aquatic larvae ('tadpoles'). The method of ovipositing and the characteristics of the egg mass varies considerably between different species. The breeding biology of the local frogs investigated in this study is presented in Table 1.1.

Table 1.1: Breeding biology of frog species found on the Swan Coastal Plain. (Data adapted from Bush *et al.* (1995), Main (1965), Tyler (1989), Tyler *et al.* (1984), and W.A. Museum (1995), and personal observations).

Species	Breeding Season	Spawn	no. of eggs per clutch	Length of larval period (days)
<i>Litoria adelaidensis</i>	late winter spring	small clumps attached to submerged vegetation	2 - 25	≈ 75 - 170
<i>Litoria moorei</i>	late winter spring summer	transparent jelly clump attached to floating or slightly submerged vegetation	600 -1000	>120
<i>Crinia glauerti</i>	after rain throughout the year except in middle summer	eggs laid singly in shallow water where they sink to bottom	<50	>100
<i>Crinia insignifera</i>	winter	eggs laid singly in shallow water where they sink to bottom	>50	≈ 60 - 120
<i>Limnodynastes dorsalis</i>	winter spring	floating foamy mass hidden beneath overhanging vegetation	>500	>120
<i>Heleioporus eyrei</i>	autumn	foamy mass in burrow	≈ 300	≈ 120 - 150

1.5 The role of predation in pre-metamorphic tadpoles

Predation can determine the presence or absence of a frog species in a given pond (Bradford, 1989; Catef, 1973; Wilbur, 1980). The larval stage of frogs is characterised by a pulse of

hatching followed by a decline in numbers as individuals are eaten by predators, successfully metamorphose, or are killed by desiccation as the wetland dries. It is not unusual for tadpole mortality to exceed 95% (K. Aplin, pers. comm.; Calef, 1973; Roberts, 1993; Wilbur, 1980). Calef (1973) and Cecil and Just (1979) attribute tadpole mortality primarily to predation, rather than to food availability or desiccation. Predation also influences competitive interactions among tadpoles. A number of studies (for example, Anholt and Werner, 1995; Brockelman, 1969; Gascon and Travis, 1992; Wilbur, 1980) have demonstrated that tadpole growth and survival are density dependent, and that there is an interplay between prey density and predation (Brodie and Formanowicz, 1983; Morin, 1986 & 1987; Werner and Mcpeek, 1994).

Some stages in the development of tadpoles are more susceptible to predation than others. Late metamorphic stages are more vulnerable to predators than intermediate developmental stages because of reduced swimming ability (Arnold and Wassersug, 1978; Huey, 1980; Wassersug and Sperry, 1977). Newly hatched individuals are also less able to escape by swimming (Brodie and Formanowicz, 1987), apart from being more prone to predation by virtue of their small size (Brodie and Formanowicz, 1983; Heyer *et al.*, 1975; Richards and Bull, 1990).

Amphibian larvae have evolved a diverse array of anti-predator mechanisms. These include camouflage (Caldwell, 1982; Lawler, 1989), distastefulness and unpalatability (Blouin, 1990; Brodie and Formanowicz, 1987; Formanowicz and Brodie, 1982; Fritts, 1966; Grubb, 1972; Holomuzki, 1995; Kats *et al.*, 1988; Walters, 1975; Werschkul and Christensen, 1977), aggregation (Brodie and Formanowicz, 1987; Formanowicz and Brodie, 1982; O'Hara and Blaustein, 1985), chemical alarm response which alarms conspecifics of a predatory attack (Hews, 1988; Hokit and Blaustein, 1995; Petranka, 1989; Petranka *et al.*, 1987), the ability to detect predators from non-visual cues (Feminella and Hawkins, 1994; Kats *et al.*, 1988; Petranka, 1989), rapid growth which allows tadpoles to quickly outgrow their predators, swim faster or leave predator-rich waters sooner (Brodie and Formanowicz, 1983; Crump, 1984; Heyer *et al.*, 1975; Richards and Bull, 1990; Semlitsch, 1990 & 1993; Wilbur, 1980), and reduced mobility which decreases the visual stimulus of movement (Horat and Semlitsch,

1994; Skelly, 1994; Skelly and Werner, 1990; Werschul and Christensen, 1977). The effectiveness of these evasive strategies in combatting vertebrate and invertebrate predation, will determine a tadpole's survival.

1.6 The influence of predation on habitat utilisation by prey

Apart from the direct effects of predation which numerically reduce prey populations, predators can also have indirect effects in communities (Semlitsch, 1993; Werner and Anholt, 1996). Tadpoles which otherwise lack defenses to counteract predation may respond by hiding, or altering patterns in microhabitat use in order to avoid the risk of predation (Werner and Anholt, 1996). Such predator induced behaviour can come at a cost: because less time is spent foraging for food, the tadpole may die of starvation, or the growth rate may be slowed, which in turn increases the risk of mortality from predation and desiccation. It is assumed that prey attempt to balance the conflicting demands of acquiring adequate resources while minimising predation risk (Feminella and Hawkins, 1994).

Benthic refugia and habitat complexity are all-important in the stabilisation of predator-prey systems (Dionne *et al.*, 1990; Feminella and Hawkins, 1994; Hews, 1988; Petranka *et al.*, 1987; Sredl and Collins, 1992). In a laboratory study, Hews (1995) established that predator feeding rates and susceptibility of tadpoles to fish predation was related to microhabitat. In another study, Morin (1986) discovered that tadpoles of *Hyla crucifer* alter their microhabitat use when exposed to predatory salamanders by spending greater amounts of time in leaf litter.

Another strategy that allows prey to survive in predator-rich waters is timing diel activity differently from that of predators (Holomuzki, 1986; Stangel and Semlitsch, 1987). If the active foraging period is adjusted to night, there will be less light for visual detection by predators (Caldwell *et al.*, 1980). However, habitats used by predators may be avoided outright (Bradford, 1989; Holomuzki, 1995; Resetarits and Wilbur, 1989 & 1991). Resetarits and Wilbur (1989 & 1991) suggest that adult frogs may alter habitat selection by not calling or ovipositing in water bodies that contain predatory fish. Petranka (1983) reported that salamander larvae were

restricted to the upper portions of breeding streams in eastern USA because of fish predation. Similarly, Pen and Potter (1991) found that coexistence of indigenous fish with *Gambusia holbrooki* in the Collie River (Western Australia) was possible due to differential temporal and spatial habitat utilisation.

1.7 Objectives and significance of the study

Anecdotal evidence appears to suggest that frog populations on the Swan Coastal Plain are declining, and that these declines are independent of habitat loss. The introduced fish, *G. holbrooki*, is abundant in the majority of wetlands on the Swan Coastal Plain. In eastern Australia, predation by *G. holbrooki* has been implicated in the decline of some frog species. This research was designed to contribute to this debate, viz. whether there is a potential for *G. holbrooki* to have a similar impact on local frog species.

It is very difficult to make direct observations of predatory acts on anuran larvae in the field (Hayes, 1983), and therefore predator-prey interactions are commonly investigated through controlled laboratory or field-based experiments. In a local study, Reynolds (1995) determined that *G. holbrooki* prey on a number of tadpoles under experimental conditions. The present study aimed to extend Reynolds' work by testing whether the results of that study could be repeated by applying an altered experimental design, as well as by including species and/or larval developmental stages which were not covered by his work.

The relevance of laboratory feeding trials in determining the potential impact of predation by *G. holbrooki* on the recruitment of local frog species depends on a number of factors (see Section 2.1). Primarily, however, it is essential to know whether microhabitat utilisation of predator and prey is over-lapping so that interactions between them are possible. Through a relatively extensive field survey conducted between September 1996 and January 1997, this study aimed to investigate the spatial and temporal microhabitat utilisation of *G. holbrooki* and local tadpoles. In order to be able to cover as wide a range of factors which might potentially influence interactions between *G. holbrooki* and local tadpoles as possible, two wetlands that

differed in a number of environmental attributes were chosen for this study. These were Lake Jandabup and Lake Gwelup, both situated on the northern Swan Coastal Plain.

The overall objective of this study was to establish whether predation by *G. holbrooki* has the potential to impact local frog populations, as it has done in eastern Australia and overseas. The significance of this research is that it might contribute to the control of this potential threat, before perceived declines on the Swan Coastal Plain are established as scientific fact. As very little is known about the microhabitat distribution of local tadpoles (K. Aplin pers. comm.), it has the added benefit of contributing information which can be used in other areas of local frog conservation (for example, the effects of weed control in wetlands).

2. Feeding Trials

2.1 Introduction

As discussed in Section 1.5, tadpoles are equipped with a number of defense mechanisms to counter predation. Predator pressure in permanent and temporary wetlands differ due to the paucity of predators in at least the initial stages of the development of a temporary pond (Grubb, 1972). In permanent water bodies, fish are likely to be the most important predators (Kats *et al.*, 1988; Petranka *et al.*, 1987). Inadequate anti-predator defenses are considered to be an important reason why temporary pond amphibian species cannot coexist with predatory fish in permanent water habitats (Kats *et al.*, 1988). Tadpoles in fish-filled waters display unique behaviours for hiding or escaping from fish (Kats *et al.*, 1988). However, one of the most effective antipredation defense mechanisms in tadpoles that co-exist with fish is the development of unpalatability. Kats *et al.* (1988) determined that tadpoles of temporary pond *Rana sylvatica* were more palatable to Green Sunfish (*Lepomis cyanellus*) than permanent pond congeners. Unpalatability, resulting from chemicals secreted from granular glands, can develop at critical stages of tadpole development (Formanowicz and Brodie, 1982). Newly hatched tadpoles are slow swimmers compared to larger individuals, while late stage tadpoles have reduced swimming ability due to the development of legs. Brodie and Formanowicz (1987) found that newly hatched and metamorphic climax stages of *Bufo americanus* are unpalatable to vertebrate and invertebrate predators, but intermediate tadpole stages are palatable. These intermediate stages were found to be protected through predator acquired avoidance of the unpalatable conspecifics (Brodie and Formanowicz, 1987).

The eggs of permanent water breeding frogs may also be equipped with predator defense characteristics which eggs of temporary water breeding frogs lack. Grubb (1972) demonstrated that *Gambusia affinis* ate a significantly larger number and volume of eggs of those species which usually breed in temporary, as opposed to permanent, water. This differential predation appeared to result from the larger, firmer egg capsule of the permanent water breeders acting

as a mechanical defense mechanism, rather than from chemical repellents or toxicity in the eggs.

The effectiveness of unpalatability as a predator defense mechanism, however, depends on the availability of alternative prey, the predator's ability to taste the prey and the predator's ability to retain learned information (Brodie and Formanowicz, 1987; Formanowicz and Brodie, 1982). Invertebrate predators, which have piercing and sucking mouthparts, for example, are rarely deterred by skin chemicals (Beebee, 1996). Furthermore, Beebee (1996) explains that having toxic or unpalatable tadpoles does not always improve survival rates to metamorphosis such that overall population dynamics might be impacted, as this adaptation usually just means that different niches can be exploited (such as ponds containing predatory fish). The concept of prey palatability is thus useful only in a relative sense.

Fish are generally gape-limited predators and as such exhibit size preferences among their prey (Zaret, 1980). Based on 'optimal diet theory' gape-limited predators select the largest prey they can profitably handle, thus optimising the benefits obtained from a prey item (Brodie and Formanowicz, 1983). In American rice fields, Farley (1980) and Wurtsbaugh *et al.* (1980) found that *Gambusia affinis* selected the largest prey they could successfully capture, but that prey movement, visibility and palatability affected prey choice in aquarium experiments. By contrast, Arthington (1989) in eastern Australia, and Bence and Murdoch (1986) in New York, discovered that when given the choice, *Gambusia* preferred smaller prey, as this proved to be more profitable. Arthington (1989) further showed that small prey were consumed in greater proportion than their relative abundance in the environment, indicating that the apparent selection of small prey was not a direct result of prey abundance (and encounter rate).

Potential predation by *G. holbrooki* on palatable tadpoles may therefore depend on the availability of alternative, smaller prey. Important invertebrate predators such as dragonfly naiads and adults and larvae of predatory diving beetles were also found to prefer smaller tadpoles (Brodie and Formanowicz, 1983 & 1987; Richards and Bull, 1990). Rapid growth is therefore clearly advantageous for a tadpole, not only as a tactic for escaping predation early in

the larval period, but also as a tactic for escaping a drying wetland later in the season (Wilbur, 1980).

The palatability of *Crinia insignifera*, *C. glauerti*, *Litoria adelaidensis* and *L. moorei* tadpoles to *Gambusia holbrooki* was determined by Reynolds (1995), although some of the results appear to have been based on preliminary trials only, or on very low numbers of experimental animals. The feeding trials carried out in this study were designed to extend the work carried out by Reynolds (1995) by applying an experimental design which allowed comparisons to be made between different developmental stages of different tadpole species (as Formanowicz and Brodie, 1982, have shown that unpalatability can develop at different stages in tadpole development), and to include *Limnodynastes dorsalis* which was not covered by Reynolds' (1995) study. The aim of the feeding trials carried out in this study was to determine whether tadpole mortality in the presence of *G. holbrooki* differs between different developmental stages of different tadpole species. This information can then be related to the periodicity of breeding activity of *G. holbrooki* and the various frog species, as well as to their microhabitat distribution within the wetlands in which they co-occur.

2.2 Materials and methods

Anuran larval developmental stages were grouped into four broad classes (based on Gosner, 1960):

<u>Larval developmental stage Group No.</u>	<u>Larval developmental stage</u>	<u>Description</u>
1	1 - 20	egg
2	21 - 24	hatchling
3	25 - 34	intermediate
4	> 35	late stage

Feeding trials were carried out with the following tadpole species:

<u>Species</u>	<u>Dev. stage group</u>
<i>Crinia insignifera</i>	4
<i>Crinia glauerti</i>	2,3,4
<i>Limnodynastes dorsalis</i>	1,2,3,4
<i>Litoria adelaidensis</i>	1,2,3,4
<i>Litoria moorei</i>	1

2.2.1 Licences and permits

Approval to carry out experiments involving *Gambusia holbrooki* and tadpoles was granted by Edith Cowan University's Animal Experimentation Ethics Committee, and in accordance with the Prevention of Cruelty to Animals Act - Control of Vivisection and Experiments Regulations 1959, by the Health Department of Western Australia.

2.2.2 Source and maintenance of experimental animals

Gambusia holbrooki

All fish used in the experiments were collected from Lake Jandabup. These were housed in an aerated glass aquarium (90 x 45 x 50cm), containing 50% lake water and 50% well-cured tap water (see plate 2.1). The fish were fed commercial fish food (Wardley's 'Cichlid T.E.N.' floating pellets) and invertebrates when available. The water was changed three times between July and December 1996.



Plate 2.1: Aerated glass aquarium housing *G. holbrooki* which were used for feeding trials.

Crinia insignifera and *C. glauerti*

Crinia eggs are deposited singly or in small clumps which sink to the bottom (Main, 1965), making them very difficult to locate. Three amplexant *Crinia insignifera* pairs were therefore collected from Perry Lakes with the help of Dr. Ken Aplin (WA Museum) on the evening of 5th July, 1996. Two individual males, and two individual females were also collected. Each amplexed pair was put into a separate translucent plastic take-away container, the single males and females were put together into one container. The containers were kept indoors at room temperature. The following morning all containers contained eggs (two of the *Crinia* pairs were still in amplexus). The frogs were returned to Perry Lakes the next day. The eggs hatched between 9th and 13th July. Unfortunately, the experimental design had not yet been finalised at this time, and therefore only late stage *C. insignifera* were included in the experiments.

A large number of what were presumed to be *C. glauerti* hatchlings (as *C. glauerti* frogs were calling from near-by vegetation at the time) were located in a small puddle of water (0 - 2 cm deep) on a sand track on the eastern side of Lake Jandabup on 17th August. It is very difficult to differentiate between *C. insignifera* and *C. glauerti* tadpoles, and although all of the frogs that emerged from these clutches after experimentation were *C. glauerti*, it cannot be ruled out that some of the deceased tadpoles were *C. insignifera*.

Limnodynastes dorsalis

A clutch of *L. dorsalis* eggs was collected from the south-eastern side of Lake Jandabup on 22nd August. The foam nest was found on the surface of the water in a stand of *Baumea articulata*. Experiments were conducted with the eggs and tadpoles from this clutch.

Litoria adelaidensis

L. adelaidensis eggs were collected from the southern part of Lake Jandabup on 10th September. Small clusters of between 2 and 20 eggs were found attached to the stems of *Baumea arthropphylla* approx. 15 cm below the water surface. These were abundant at this location.

Litoria moorei

Despite extensive searching for *L. moorei* eggs since September 1996 it was only possible to locate two clutches on the south-eastern side of Lake Jandabup. These were collected on 19th November from inundated introduced grasses and *B. articulata*. The eggs were kept cool in a refrigerator (at 5°C) to slow development. Unfortunately, a fault in the refrigerator resulted in the eggs freezing and both clutches were lost. One experiment was nevertheless carried out with the dead eggs.

Heleioporus eyrei

Experiments were not carried out with *H. eyrei* as this species had finished breeding before commencement of this study.

Tadpoles of all species (as above) were housed and raised in aerated plastic buckets (55 x 30 x 20cm) with at least 50% strained lake water, the remainder being well-cured tap water (see plate 2.2). Water was strained (mesh size 250 μ) so as to exclude invertebrate predators or parasites of tadpoles. Aquatic vegetation (mainly *Villarsia* sp.) was placed into these buckets and the tadpoles were fed boiled lettuce and fish flakes (*Wardley's 'tropical food flakes'*). Apart from topping up, it was not found necessary to change the tadpole water. This is probably a reflection of the efficacy of tadpoles in consuming algae, and perhaps also evidence for coprophagy (Beebee, 1996).

Fish and tadpole water was kept at room temperature ($20^{\circ}\text{C} \pm 3^{\circ}\text{C}$) in an air-conditioned building with an ambient light cycle.

2.2.3 Procedure

The experiments involved a 1:1 predator-prey ratio, eliminating other influencing factors such as predator and prey density effects and habitat complexity. This allowed the experimental results to be related to two main functions: tadpole palatability and tadpole size. The benefit of this approach was that it allowed for good replication while requiring a minimal number of



Plate 2.2: Aerated plastic buckets housing tadpoles used in palatability trials.



Plate 2.3: Layout of experimental and control containers used for feeding trials.

experimental animals. It must be acknowledged, however, that the palatability of a tadpole does not necessarily mean it will be preyed upon in the wild, but it does indicate a potential to be eaten.

For each developmental stage group of each species there were 20 treatments, ie. 20 ice-cream containers with one *G. holbrooki* and one tadpole each, and 20 controls consisting of 20 ice-cream containers with tadpoles/eggs only, and no *G. holbrooki*. Plate 2.3 shows the layout of this experimental design. Each experiment involved randomly assigning one *Gambusia* to a two-litre white plastic ice-cream container, filled with a mixture of 500 ml strained (250 μ mesh size) lake water and 500 ml cured tap water*, where it was not fed and allowed to acclimatise for 3 days. A 3 to 4 day starvation period appears to be the norm in order to encourage feeding behaviour in experiments involving *Gambusia*, and also in other fish (for example Fritts, 1966; Grubb, 1972; Blouin, 1990). Grubb (1972) found that *Gambusia* starved for four days consumed substantially more anuran eggs than those starved for one day. In order to minimise the effect of fish size on the results (it is assumed that small fish are less effective predators of tadpoles due to their small gape widths), juveniles (SL < 18 mm) were not used in these experiments.

On the fourth day, one tadpole/egg was dropped into each of the experimental and control containers. This generally initially caused a fright response from the fish, rather than an attack. Tadpole and fish behaviour was observed for the first 30 minutes of each experiment. The experiments were allowed to run for 24 hours, after which time the number of tadpole fatalities, the number of tadpoles/eggs consumed and the number and types of injuries incurred by the tadpoles were noted. For the anuran eggs, hatching success between control and surviving experimental eggs were compared.

In an attempt to control for satiation, fish were fed alternative food (Wardley's 'Cichlid T.E.N.' floating pellets or fish flakes) once the tadpoles/eggs had been removed. This was, however, found to be problematic, as most of the fish were reluctant to feed straight away, probably as a

*Lake water was used because pure tap water seemed to cause high mortality with the fish. It was strained so as to exclude alternative food sources

result of being observed. Generally, fish that consumed eggs/tadpoles were first to consume the pellets or flakes, while most of the others would consume little or nothing within the first half hour. This was therefore considered an inadequate method to test for satiation when fish are kept in isolation. It is very likely that feeding of live and moving invertebrates would have been more useful, however, time did not allow for this. Nevertheless, it can be assumed that fish which have been accustomed to daily feeds, and have subsequently been starved for four days, should be hungry.

After completion of the experiments (in order to minimise the trauma of handling before the experiments) each fish was measured (in a petri dish using callipers) and sexed (simply by locating the extended anal rays in the males). A note of pregnant females was also made. Each fish was used only once, and all fish used in the experiments were kept for one week following experimentation to check for survival.

2.2.4 Data Analysis

As the data consist of frequencies and are nominal, chi-square analysis was carried out for each individual experiment in order to test whether there was an association between the presence of *G. holbrooki* and the number of surviving tadpoles/eggs. The variables analysed were Treatment (*G. holbrooki* present) / Control (*G. holbrooki* absent), and Survival (tadpole dead / tadpole alive).

A hierarchical three-way frequency analysis was performed to develop a saturated (that is, all effects included) loglinear model (Knoke and Burke, 1980; Tabachnick and Fidell, 1996) to test for associations between species, stage group and survival. The research questions asked were (1) whether survival of tadpoles was associated with tadpole developmental stage, (2) whether survival of tadpoles was associated with tadpole species, and (3) whether there was an association between the survival of tadpoles and the joint effects of developmental stage and species. There were thus seven potential associations: three one-way associations, Species, Stage and Survival (main effects), and the following interactions: Species X Survival, Stage X

Survival, Species X Stage and Species X Stage X Survival. Associations resulting from loglinear analysis give no indication as to which particular component of the association contributes most to a significant result (Tabachnick and Fidell, 1996). One- and two-way frequency analyses were therefore performed in order to find the significant components of the associations.

Further frequency analyses were carried out to determine:

- size-frequency distribution of fish used in the experiments (in order to determine whether there was an association between fish size and the number of surviving tadpoles);
- the proportion of male and female fish used in the experiments (in order to determine whether there was an association between fish sex and tadpole survival);
- the number of tadpoles consumed, and
- the number of tadpoles injured.

2.3 Results

The data obtained from the thirteen palatability trials using *G. holbrooki* and various developmental stage groupings of five local tadpole species are presented in Table 2.1. Mean fish lengths and results of the chi square analyses are also listed. Two of the chi square analyses (*L. dorsalis* eggs and *L. adelaidensis* intermediate stage) contained expected cell frequencies of less than five and should therefore be treated with caution. Details of Table 2.1 are discussed below.

2.3.1 Feeding trials with frog eggs

Only two valid experiments (*L. dorsalis* and *L. adelaidensis*) involving frog eggs were carried out (*L. moorei* eggs were dead, as mentioned in Section 2.2.2). For *L. adelaidensis*, significantly more eggs ($\chi^2(1 \text{ d.f.}, n=40) = 19.26, p<0.0001$) remained in the control buckets

Table 2.1: Number of dead and alive tadpoles/eggs in experimental (*G. holbrooki* present) and control (*G. holbrooki* absent) containers for four tadpole development stage groupings. Chi square significance is indicated for each experiment. Mean fish lengths (\pm SD) are also given.

Species	Dev. Stage	Exp. No.	Date	Mean fish length (mm)	Experiment (No. of tadpoles)		Control (No. of tadpoles)		χ^2
					Dead	Alive	Dead	Alive	
<i>Crinia glauerti</i>	Hatchling	1	14.8.96	29.23 \pm 5.35	12	8	2	18	(1 d.f.,n=40) = 10.99, p < .001
<i>Crinia glauerti</i>	Intermediate	5	31.8.96	24.1 \pm 3.54	16	4	4	16	(1 d.f.,n=40) = 14.4, p < .001
<i>Crinia glauerti</i>	Late stage	10	21.10.96	25.8 \pm 4.34	11	9	0	20	(1 d.f.,n=40) = 15.17, p < .001
<i>Crinia insignifera</i>	Late stage	4	31.8.96	24.05 \pm 3.64	17	3	0	20	(1 d.f.,n=40) = 29.57, p < .00001
<i>Limnodynastes dorsalis</i>	Egg*	2	19.8.96	25.1 \pm 4.38	3	17	0	20	(1 d.f.,n=40) = 3.24, p > .05 (NS) Exp. Freq. < 5 !
<i>Limnodynastes dorsalis</i>	Hatchling	3	27.8.96	25.9 \pm 2.85	20	0	0	20	(1 d.f.,n=40) = 40.0, p < .00001
<i>Limnodynastes dorsalis</i>	Intermediate	9	30.9.96	24.05 \pm 3.07	17	3	0	20	(1 d.f.,n=40) = 29.57, p < .00001
<i>Limnodynastes dorsalis</i>	Late stage	11	18.12.96	29.30 \pm 4.05	14	6	4	16	(1 d.f.,n=40) = 10.10, p < .01
<i>Litoria adelaidensis</i>	Egg*	7	11.9.96	25.92 \pm 5.15	13	7	0	20	(1 d.f.,n=40) = 19.26, p < .0001
<i>Litoria adelaidensis</i>	Hatchling	6	11.9.96	24.85 \pm 3.09	18	2	0	20	(1 d.f.,n=40) = 32.73, p < .00001
<i>Litoria adelaidensis</i>	Intermediate	8	30.9.96	24.18 \pm 2.63	7	13	0	20	(1 d.f.,n=40) = 8.48, p < .01 Exp. Freq. < 5 !
<i>Litoria adelaidensis</i>	Late stage	12	10.12.96	25.58 \pm 4.58	0	20	0	20	χ^2 test not performed
<i>Litoria moorei</i>	Egg*	13	21.10.96	not measured	0	20	0	20	χ^2 test not performed

- (For eggs, numbers indicated are number 'consumed' and number 'not consumed' rather than 'alive' and 'dead')

(*G. holbrooki* absent) than in the experimental buckets (*G. holbrooki* present). It would appear, therefore, that *L. adelaidensis* eggs are palatable to *G. holbrooki*. However, of the seven eggs that remained in the experimental buckets, none hatched. Of the 20 eggs remaining in the control buckets, only three hatched (=15%). It is not possible to say whether this poor hatching success was due to stress, in the case of the experimental eggs due to manipulation by the fish, or due to some other laboratory handling factor. *L. adelaidensis* eggs kept in the aerated buckets (see Plate 2.2) had a much higher hatching success rate, producing sufficient tadpoles to carry out three more feeding trials (>120 tadpoles). All thirteen fish that consumed *L. adelaidensis* eggs were still alive after one week, indicating that the eggs lacked toxic properties which might have been lethal to the fish.

Very few of the *L. dorsalis* eggs (3 out of 20) were consumed by the fish ($\chi^2(1 \text{ d.f.}, n=40) = 3.24$, $p>0.05$). Of the seventeen remaining experimental eggs, 16 hatched (= 94.1%), and of the 20 remaining control eggs, 19 hatched (=95.0%). The three fish that consumed eggs showed no ill effects after one week. Interestingly, a foamy clump of five *L. dorsalis* eggs which was placed into an ice-cream container containing 7 spare fish (also starved) was initially ignored by the fish, but was found to be completely consumed the following morning. One of the fish died, but the remaining six survived.

None of the dead *L. moorei* eggs were consumed by *G. holbrooki*.

2.3.2 Feeding trials with tadpoles

Table 2.1 shows that, apart from the late stage *L. adelaidensis* in which all of the tadpoles in both the experimental and the control containers survived, all experiments carried out with the tadpoles produced significant results. However, as mentioned earlier, the chi square analysis carried out with *L. adelaidensis* intermediate stage contained expected cell frequencies of less than 5 and should therefore be treated with caution. In this case, seven out of twenty experimental tadpoles died compared to zero out of twenty control tadpoles.

Apart from late stage *L. adelaidensis*, and possibly intermediate stage *L. adelaidensis*, all of the control containers had significantly more surviving tadpoles than experimental containers. None of the fish which consumed or injured tadpoles died within 7 days of having done so. It should be noted that with the late stage *L. dorsalis*, all of which were substantially larger than the fish (mean tadpole size: 53mm, mean fish size: 29.3mm), four of the fourteen dead (experimental) tadpoles had no apparent injuries, while the remaining ten had minor injuries (nipped tail tips). Four of the control tadpoles died for no apparent reason. All of the ice-cream containers had a comparatively large amount of tadpole faeces after 24 hours. It is therefore possible that the relatively high mortality of the late-stage *L. dorsalis* may not be solely due to the presence of *G. holbrooki*, although the presence of *G. holbrooki* clearly exacerbated their difficulties.

2.3.3 Results of the Log-linear analysis

Because of the need to have an equal number of developmental stage groups for each frog species tested, the egg stage (3 experiments) and the late stage *Crinia insignifera* (one experiment) were not included in this analysis. The hierarchical three-way frequency analysis was therefore performed with three frog species (*Crinia glauerti*, *Limnodynastes dorsalis* and *Litoria adelaidensis*) and three developmental stage groups ('hatchling', 'intermediate' and 'late stage'). Starting at the lowest level association, the test of the one-way effect of overall survival demonstrates that there was a significant difference between the number of dead and alive tadpoles in the presence of *G. holbrooki* ($\chi^2(1 \text{ d.f.}, n=180) = 14.07, p < 0.001$). Table 2.2 shows that of 180 tadpoles tested, there were 115 (=63.9%) that did not survive, compared to 65 (=36.1%) that did.

Table 2.2: Overall tadpole survival of three frog species (*C. glauerti*, *L. dorsalis* and *L. adelaidensis*) in the presence of *G. holbrooki*

Survival	No. of Tadpoles	Percentage
Dead	115	63.9
Alive	65	36.1
Total	180	100

Statistical significance for individual experiments are shown in Table 2.1.

There was a highly significant two-way effect between tadpole developmental stage and tadpole survival ($\chi^2(2 \text{ d.f., } n=180)= 27.76, p<0.0001$). This suggests that tadpole survival depends on developmental stage. Table 2.3 shows that hatchlings had the lowest survival rate in the presence of *G. holbrooki* (16.67%), followed by the intermediate stage (33.33%), while late stage tadpoles had the highest survival rate (58.33%).

Table 2.3: Frequency distribution of tadpole survival for three developmental stage groups ('hatchling', 'intermediate' and 'late stage') of three frog species (*C. glauerti*, *L. dorsalis* and *L. adelaidensis*) in the presence of *G. holbrooki*

Stage	No. of dead tadpoles	No. of alive tadpoles	Total
Hatchling	50 (83.33%)	10 (16.67%)	60
Intermediate	40 (66.67%)	20 (33.33%)	60
Late stage	25 (41.67%)	35 (58.33%)	60
Total	115	65	180

There was also a highly significant two-way association between tadpole species and tadpole survival ($\chi^2(2 \text{ d.f., } n=180)= 29.79, p<0.0001$), indicating that tadpole survival is dependent on species. The number of dead and alive tadpoles for each species is presented in Table 2.4.

Table 2.4: Frequency distribution of tadpole survival for three frog species (*C. glauerti*, *L. dorsalis* and *L. adelaidensis*) in the presence of *G. holbrooki*

Species	No. of dead tadpoles	No. of alive tadpoles	Total
<i>L. dorsalis</i>	51 (85%)	9 (15%)	60
<i>C. glauerti</i>	39 (65%)	21 (35%)	60
<i>L. adelaidensis</i>	25 (41.67%)	35 (58.33%)	60
Total	115	65	180

Table 2.4 shows that *L. dorsalis* tadpoles had the lowest overall survival rate (15%) in the presence of *G. holbrooki*. More than twice as many *C. glauerti* tadpoles survived than did *L. dorsalis* (35%), while *L. adelaidensis* tadpoles had the highest survival rate (58.33%).

The log-linear model produced also showed that there was a highly significant three-way association between species, stage and survival ($\chi^2(4 \text{ d.f., } n=180)= 25.96, p<0.0001$),

indicating that tadpole survival in the presence of *G. holbrooki* depends on the combined effects of tadpole species and stage .

2.3.4 Consumed and injured tadpoles

The flow diagram in Figure 2.1 shows the fate of 180 tadpoles used in the feeding trials with *G. holbrooki*.

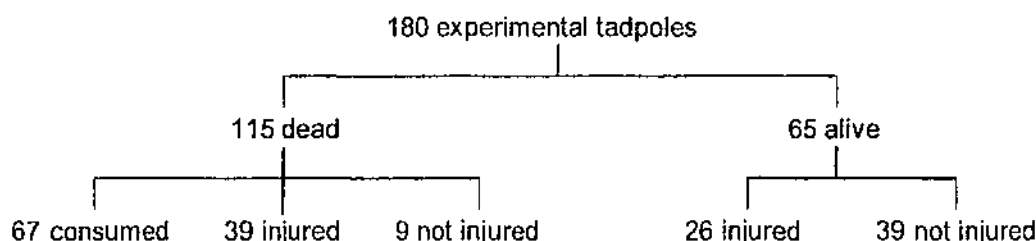


Figure 2.1: The fate of 180 tadpoles used in the feeding trials with *G. holbrooki*. Total number of dead, alive, consumed and injured tadpoles are given.

Figure 2.1 shows that, of the 115 tadpoles that did not survive the palatability trials, 67 were consumed (= 58.26%). Of the remainder (48 tadpoles), 39 (81.25%) were injured and 9 were not injured. Twenty-six tadpoles (40% of all injured tadpoles) recovered from their injuries. The most commonly encountered injury was nipped tail fin, or partial loss of the tail fin. Head and body damage was also observed, but only rarely. In the experiment involving late stage *C. insignifera* (experiment no. 4), eight tadpoles (all of which did not have completely developed legs) appeared to have been ripped apart by *G. holbrooki*. A large proportion of the tadpole tissue which was removed was consumed by the fish. This 'ripping apart' of entire tadpoles (most of which were larger than the fish which inflicted the injuries) was only observed in this particular experiment. Although the tadpoles in this experiment were relatively immobile during the 30 minutes observation period after commencement of the feeding trial (and only 3 attacks were observed), after one hour it was discovered that 15 out of 20 tadpoles had nipped tails. It would appear, therefore, that for some reason late stage *C. insignifera* tadpoles are particularly vulnerable to predation by *G. holbrooki*. With the late stage *Crinia* tadpoles damage or loss of limbs was the most commonly observed injury. One *Crinia glauerti* tadpole successfully

metamorphosed (in the laboratory) into a three-legged frog, after losing one of its legs to a fish during experimentation.

Table 2.5 shows the break up of consumed, injured and uninjured tadpoles into tadpole species and developmental stage. In contrast to survival, the number of injured and consumed tadpoles did not differ markedly between the different species tested. Chi square analysis revealed that there was no significant association between tadpole species and the number of injured tadpoles ($\chi^2(2 \text{ d.f.}, n=113)= 2.83, p>0.05$), nor between tadpole species and the number of consumed tadpoles ($\chi^2(2 \text{ d.f.}, n=180)= 2.33, p>0.05$). However, the association between tadpole developmental stage group and the number of consumed tadpoles was highly significant ($\chi^2(2 \text{ d.f.}, n=180)= 61.39, p<0.0001$). Table 2.5 reveals that 41, or 61.2% of all tadpoles consumed, were hatchlings (group 2). Twenty-six, or 38.8%, were intermediate stage tadpoles (group 3), while no late stage (group 4) tadpoles were consumed (but see comments for *C. insignifera* above).

Likewise, developmental stage group and the number of injured tadpoles were associated, although not as strongly as the association with consumed tadpoles ($\chi^2(2 \text{ d.f.}, n=113)= 6.31, p<0.05$). Table 2.5 shows that late stage tadpoles (group 4) had the highest rate of injury (65, or 57.5%) of all injured tadpoles (including those that survived). This is, of course, because more of these tadpoles survived, and none were consumed, and therefore more were 'available to injure'. The relationship between dead, consumed and injured tadpoles is shown in Figure 2.2.

Table 2.5: Frequency distribution of consumed, injured and not injured tadpoles of three developmental stage groups of three species, in the presence of *G. holbrooki*

	No. of tadpoles consumed				No. of tadpoles injured				No. of tadpoles not injured			
	2	3	4	Total	2	3	4	Total	2	3	4	Total
Developmental Stage group												
Species:												
<i>Limnodynastes dorsalis</i>	18	9	0	27	2	8	13	23	0	3	7	10
<i>Crinia glauerti</i>	8	12	0	20	2	5	14	21	10	3	6	19
<i>Litoria adelaidensis</i>	15	5	0	20	2	8	11	21	3	7	9	19
Total	41	26	0	67	6	21	38	65	13	13	22	48

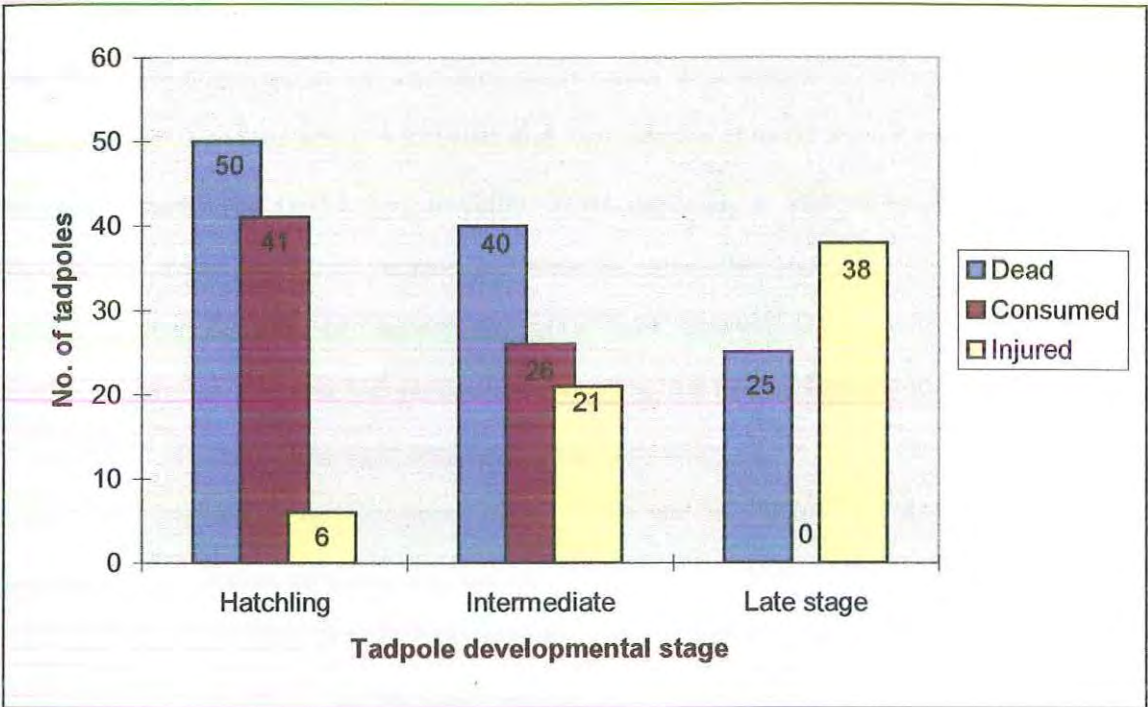


Figure 2.2: The relationship, for three species combined, between dead, consumed and injured tadpoles in the presence of *G. holbrooki*.

2.3.5 Fish size and sex frequency distributions

The fish used in the experiments ranged in size from 18.5 mm - 40 mm. Mean fish size was 25.7mm (± 4.22 SD). Fish length frequency distribution is presented in Figure 2.3.

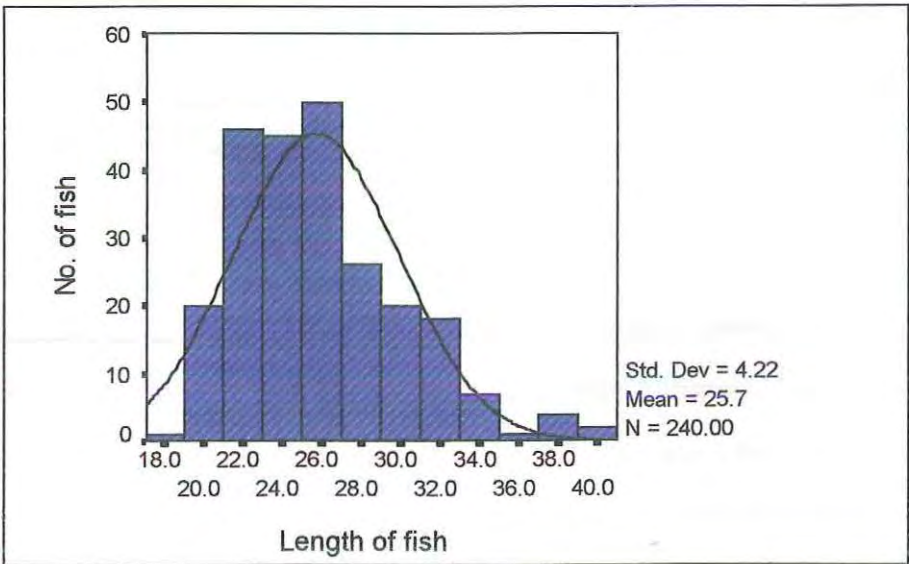


Figure 2.3: Length frequency histogram for fish used in feeding trials

The mean fish size used in the individual experiments is presented in Table 2.1. Although a Kruskal-Wallis one-way ANOVA showed that fish lengths differed significantly between the different experiments ($\chi^2(11 \text{ d.f., } n=230)= 37.81, p<0.05$), a Spearman Rank correlation showed that there was no correlation between the mean fish size per experiment and the number of dead tadpoles per experiment ($r_s(12)=0.21, p>0.05$). Of the total number of fish used, 124 were females and 116 were males, equating to a ratio of females to males of 1.07:1. Overall, 25% of the females were pregnant, pregnancy being much more prevalent in the later experiments (November and December 1996). There was no association between fish sex and the number of tadpoles surviving the feeding trials ($\chi^2(1 \text{ d.f., } n=240)= 1.41, p>0.05$). Fish size frequency and sex ratios in this study are very similar to those reported by Pen and Potter (1991) for the Collie River, and by Balla and Davis (1993) for Lake Jandabup, North Lake and Nowergup Lake (taking into account that juvenile fish were intentionally excluded in this study).

2.4 Discussion

2.4.1 Palatability of frog eggs

None of the *G. holbrooki* that consumed eggs of *L. dorsalis* or *L. adelaidensis* appeared to suffer any ill effects as a consequence. It is, therefore, concluded that the spawn of these two species do not possess chemical defenses which are fatal to *G. holbrooki*. However, significantly more of the eggs of *L. adelaidensis* were consumed, suggesting some preference, or avoidance of the eggs of *L. dorsalis*.

Grubb (1972) suggests that few predators attempt to eat anuran spawn because the jelly is of poor nutritive value, and may have either a bad, or no taste. Therefore, unless the egg capsule is crushed by mastication, allowing access to the nutritious vitellus, a fish might not recognise it as a food item. Thus, these jelly or foam envelopes serve not only as protective supports for the developing embryo, but also protect it from detection by fish predators (Grubb, 1972). Another attribute of the jelly mass is that it holds the eggs together. Grubb (1972) reported

observing that if a fish could not break the adhesion or swallow the entire cluster after several attempts, it often rejected the seized egg. In this study, eggs were offered singly to fish, that is, they had to be separated from each other beforehand (a fiddly task!), although a small amount of jelly still surrounded the individual eggs. *Litoria adelaidensis* eggs appear to have a much looser surrounding jelly mass than *Limnodynastes dorsalis* or *Litoria moorei*. This may be one explanation why *G. holbrooki* consumed more of these eggs than of the other two species. By contrast, in palatability trials carried out by Reynolds (1995) with *G. holbrooki* and *L. adelaidensis* eggs, and in which eggs were also offered singly, but to a group of 15 to 20 *G. holbrooki* at a time, none of the eggs were consumed. *G. holbrooki* are known to show a distinct preference for small and moving prey near the surface of the water (Arthington, 1989; Bence and Murdoch, 1986). It is possible that, in Reynolds' (1995) case, the fish did not detect the egg (lying immotile on the bottom of the container) in amongst their moving conspecifics. Both the *L. adelaidensis* and the *L. dorsalis* eggs used in the current study were approaching hatching. It is possible that embryonic movement may have attracted the fish.

Grubb (1972) concluded that egg size was an important factor influencing predation by *G. holbrooki*. *L. adelaidensis* eggs used in these experiments had an average diameter of around 1 mm, *L. dorsalis* 1.7 mm, and *L. moorei* 1.8 mm. As it happens, *L. adelaidensis* eggs, which had the smallest diameter, had the highest mortality in the presence of *G. holbrooki*. However, all of the eggs used (including *L. moorei*) were within the size range that Grubb (1972) classed as 'small' (< 3mm diameter), and therefore, no conclusions can be drawn concerning egg diameter based on these feeding trials.

From these experiments, it can be concluded that *L. adelaidensis* eggs are palatable to *G. holbrooki*, while *L. dorsalis* eggs, although apparently not noxious to *G. holbrooki*, do not appear to be attractive to them.

2.4.2 Tadpole mortality

The feeding trials with *G. holbrooki* and four local tadpole species carried out in this study have revealed that, in the presence of this fish, the number of surviving tadpoles depends on both tadpole species and tadpole developmental stage. By contrast, the number of consumed tadpoles was only associated with developmental stage and not with tadpole species. Mortality rate of the injured tadpoles (81.25%) was very high. This high mortality may have occurred because of stress resulting from not being able to evade the fish in the confined space of the ice-cream containers. It is questionable whether such high mortality is likely in a natural situation where an unsuccessfully attacked tadpole has the opportunity to flee from fish and seek refuge in the substrate or amongst vegetation. It was found in the laboratory that, under optimal food and low density conditions, tadpoles which survived a fish attack were able to recover from their injuries. On the other hand, however, it is also possible that injured tadpoles may be more vulnerable to predation due to lowered fitness and reduced swimming ability. Cannibalism among conspecifics may further reduce survival of injured tadpoles in a natural situation (Morin, 1985; K. Aplin, pers. comm.).

Morin (1985) found that in artificial pond communities injury frequency in tadpoles was negatively correlated with prey survival. Morin's (1985) research also suggests that tail injury suppresses tadpole growth (although he did not test whether this made them more susceptible to predation). Parichy and Kaplan (1992) established that tail injury not only reduced tadpole survival but also extended the larval period, and decreased larval and metamorphic sizes. Wilbur and Semlitsch (1990), whose experiments also confirmed that tail damage reduced tadpole growth and survival, found that tail injury had only an insignificant effect on a tadpole's ability to avoid predation. It was concluded that tail loss may be an important mechanism to reduce the effect of predation by focusing the attention of predators away from the head and body and towards the less essential tail, which can be quickly regenerated. As different species have different defenses against predation (including different tail shapes, Wilbur and Semlitsch, 1990), it is not possible to determine the ecological consequences of tail injury for the tadpoles used in these feeding trials without carrying out experiments with the individual species concerned.

When considering the palatability of prey, it makes more sense to look at the number of prey consumed by the predator, rather than overall mortality. In this study, the number of consumed tadpoles was very strongly associated with developmental stage, but not with tadpole species. It can therefore be concluded that there are no differences in palatability within the same developmental stage groups of different species. It is, of course, possible that late stage tadpoles, none of which were consumed (apart from *C. insignifera*, but these were not included in this analysis), are unpalatable. However, as the majority of tadpoles (61.2%) consumed were hatchlings, that is small tadpoles, and none of the larger late stage tadpoles were consumed, it can be concluded that tadpole size was the major determinant of whether a tadpole was consumed or not. The palatability or otherwise of tadpoles which are too large for *G. holbrooki* to consume is irrelevant. This accords with Reynolds' (1995) findings that hatchlings of local tadpoles are more susceptible to predation by *G. holbrooki* than other stages, although Reynolds did not differentiate between intermediate (stage 25 -34) and late (\geq stage 35) stage.

As fish in these experiments were not offered a choice of different prey sizes or developmental stages, it cannot be concluded that *G. holbrooki* actually prefer small (as has been shown with invertebrate prey, see Section 2.1) tadpoles. It is more likely that the higher number of small tadpoles consumed is related to the gape size of the fish. Species specific differences (or lack thereof) in the number of tadpoles consumed in the experiments carried out in this study must also be treated with caution. Blouin (1990) established that predation rates in single-species prey treatments do not necessarily predict predation rates in mixed species treatments. He found that Bluegill ate many more *H. gratiosa* than *H. cinerea* tadpoles in single-species trials, but failed to discriminate in mixed-species trials. The relative importance of potential predation by *G. holbrooki* on local tadpoles must therefore be assessed, amongst other criteria, in terms of when which predator and prey species appear in a given wetland, and how quickly a tadpole can outgrow the size threshold which can be successfully manipulated by the predator.

In conclusion, the results of the experiments carried out in this study suggest that all tadpole species with which trials were conducted are palatable to the introduced predator *G. holbrooki*,

but that any differences in consumption rate between species and between developmental stages are not related to differences in palatability, but to tadpole size. However, the relative importance of these findings will depend on a number of factors, in particular the phenology and microhabitat utilisation of the individual tadpole species and *G. holbrooki*.

3. Microhabitat utilisation by *G. holbrooki* and local tadpole species

3.1 Introduction

This research component was designed to examine spatial and temporal associations in microhabitat use by the introduced fish, *Gambusia holbrooki* and local tadpole species. Overlap in microhabitat use by fish and tadpoles would indicate a potential for predator-prey interactions between them to occur. The research was not intended to determine whether such interactions might lead to the exclusion of some species from otherwise suitable habitats, nor to determine whether *G. holbrooki* and certain tadpole species are able to co-exist in the long term. The value of this research is that it can serve as a baseline from which explicit hypotheses about the interactions can be generated and later tested by careful, critical experimentation.

In order to assess the relative importance of *G. holbrooki* as a tadpole predator, the microhabitat distribution of aquatic macroinvertebrates known to prey on anuran tadpoles was also investigated. Invertebrate predation of amphibian tadpoles is rampant in many water bodies, and it has been suggested that this be taken into consideration in any description of pond communities (Beebee, 1996). It has been shown that the presence of aquatic macroinvertebrate predators can have a strong influence on anuran tadpole densities (for example Barrett, 1995; Gascon and Travis, 1992; Morin *et al.*, 1988; Shaffer *et al.*, 1994).

Examination of the effects of predatory fish on amphibian species richness, abundances and distribution in the field is often carried out on a geographic scale (for example Bradford, 1989; Kats *et al.*, 1988; Hecnar and M'Closkey, 1997; Werner and Mcpeek, 1994), where a number of wetlands with and without fish are compared. Another approach, which is well suited to short-term, small-scale, or low-budget projects, is to intensively sample two wetlands and compare species richness, abundances and distribution between different habitat types within the wetlands. Ideally one wetland should be permanent and support fish, the other seasonal and

without fish. In the limited time available for the planning stage of this project, it was not possible to locate a wetland on the northern Swan Coastal Plain within manageable distance from the University that does not support the introduced fish, *G. holbrooki*. The wetlands for this study were therefore chosen on the basis that one be permanent, the other seasonal, but that both support *G. holbrooki* as well as an identical suite of local tadpole species in order to compare abundances of both the fish and tadpoles within different habitat types (characterised by vegetation community structure), as well as within different microhabitats (vegetation community structure plus accompanying environmental attributes).

The extent of seasonal drying in a wetland influences the diversity of aquatic macrophyte vegetation (Froend *et al.*, 1993) which in turn provides habitats for aquatic fauna. There is thus an inter-relationship between the temporal and spatial availability of habitats which can be used by predators and prey. Phenology, or the periodicity of breeding, recruitment etc., of the individual species concerned, and habitat complexity will determine the intensity of interactions between these species. The role of habitat complexity in predator-prey interactions has been reviewed in Section 1.6.

It has been stated that assemblages of larval amphibians differ markedly between permanent and ephemeral wetlands (Kats *et al.*, 1988). Species which breed at permanent sites may be excluded from temporary sites because they have larval periods which exceed the seasonal duration of temporary sites, while on the other hand, species which breed at temporary sites may be excluded from permanent sites because they have not generally evolved adequate anti-predator defenses against fish which often occupy permanent sites (Kats *et al.*, 1988). On the Swan Coastal Plain this segregation between permanent and temporary water anuran species is not so evident. While *Litoria moorei*, for example, is classed as a permanent water species (Main, 1965), its tadpoles are often found in temporary sites (pers. observation). Such species are able to avoid predation by fish in permanent waters by moving to more temporary sites, but risk desiccation during egg and larval development (Hecnar and M'Closkey, 1997). In the wet season, the perimeters of permanent water bodies often provide temporary shallow and well-vegetated nursery refuges for fast-growing anuran species. On the Swan Coastal Plain,

tadpoles of *Crinia* spp. are found in the shallows of both permanent and temporary water bodies (W.A. Museum, 1995). Normally, such species would be separated from fish predators which require deeper water. *G. holbrooki*, however, are micro-predatory fish, and are also known to prefer this habitat type (Casterlin and Reynolds, 1977).

Comparing the abundances and distribution patterns of a micro-predatory fish and an assemblage of tadpole species common to a permanent wetland and a wetland which almost dries (that is, the effects of ephemerality are manifested, but fish are nevertheless able to persist), has not been previously attempted. As it has been amply demonstrated (although not locally) that amphibian species richness and abundance are greater in wetlands without fish than in wetlands with fish (see Section 1.2), the benefit of this approach is that an additional question can be explored. Since it was assumed that *G. holbrooki* would experience greater population crashes in seasonal (due to drying of habitats), than in permanent wetlands, would temporary water tadpole assemblages be affected to a lesser degree by the presence of *G. holbrooki*, than the same tadpole assemblages would be in a permanent wetland? This question has special relevance to the Swan Coastal Plain. Due to urbanization and changes in land management practices, many of the wetlands on the Swan Coastal Plain are now deeper and contain water for a longer period than what would naturally be the case (Balla and Davis, 1993). As a consequence, *G. holbrooki*, which cannot persist in water bodies which completely dry up in summer, is well established in most of these wetlands.

In summary, the aims of this research component were:

- ◊ to identify major habitat types within a seasonal and a permanent wetland in order to be able to compare tadpole and fish abundances within different habitat types;
- ◊ to compare relative abundances of *G. holbrooki* and local tadpole species in a seasonal and a permanent wetland on the Swan Coastal Plain, both spatially and temporally (based on three sampling seasons);
- ◊ to examine spatial and temporal patterns in microhabitat use by *G. holbrooki* and an assemblage of local tadpole species;

3.2 The study areas

Selection criteria for the two wetlands in which the field surveys were conducted are explained in Section 3.1. Lake Gwelup and Lake Jandabup are both situated on the Swan Coastal Plain which extends westwards from the Darling Scarp to the Indian Ocean (see location map in Figure 3.1). The climate on the Swan Coastal Plain is warm Mediterranean with five to six dry months per year. Dry months extend from mid-October to the end of March; winter months are wet. The average rainfall in the Lake Gwelup and Lake Jandabup areas are about 750mm per year. The temperature ranges from an average monthly reading of about 14°C in July to 25°C in summer (Beard, 1979; cited in City of Stirling, 1992). Both lakes contain the introduced fish, *Gambusia holbrooki*, and support good populations of most of the frog species known to occur on the northern Swan Coastal Plain (see in Section 1.4).

Lake Gwelup, located 11 km north-west of Perth, is a small (18.5 ha), permanent and deep (by Swan Coastal Plain standards) wetland, situated within a well-established residential area. Located within the Spearwood dunes system, Lake Gwelup has deposits of peat and peaty sands on predominantly leached sands of the Karrakatta soil association, close to the boundary with the Cottesloe association. The lake is situated 8m AHD, with the lowest point of the lakebed below 4.6m AHD. In dry periods, water levels reflect the water table, while in wet periods the lake levels reflect surface runoff into the drainage network. (City of Stirling, 1992)

Based on OECD and CEPIS water quality criteria, City of Stirling (1992) report the nutrient status of Lake Gwelup as being between mesotrophic and oligotrophic. The littoral zone is relatively narrow and vegetation consists mainly of very dense stands of the rush *Typha orientalis*, in association with *Polygonum salicifolium*, *Elatinaceae* spp. and assorted weed species in shallower areas. Only discrete stands of the original sedge vegetation, mainly consisting of *Baumea articulata*, remain. Some remnant fringing tree vegetation (*Melaleuca raphiophylla* and *Eucalyptus rudis*) is also present. The distribution of vegetation communities at Lake Gwelup is shown in Figure 3.2. Lake Gwelup is reserved for conservation and recreation and is managed by the City of Stirling.

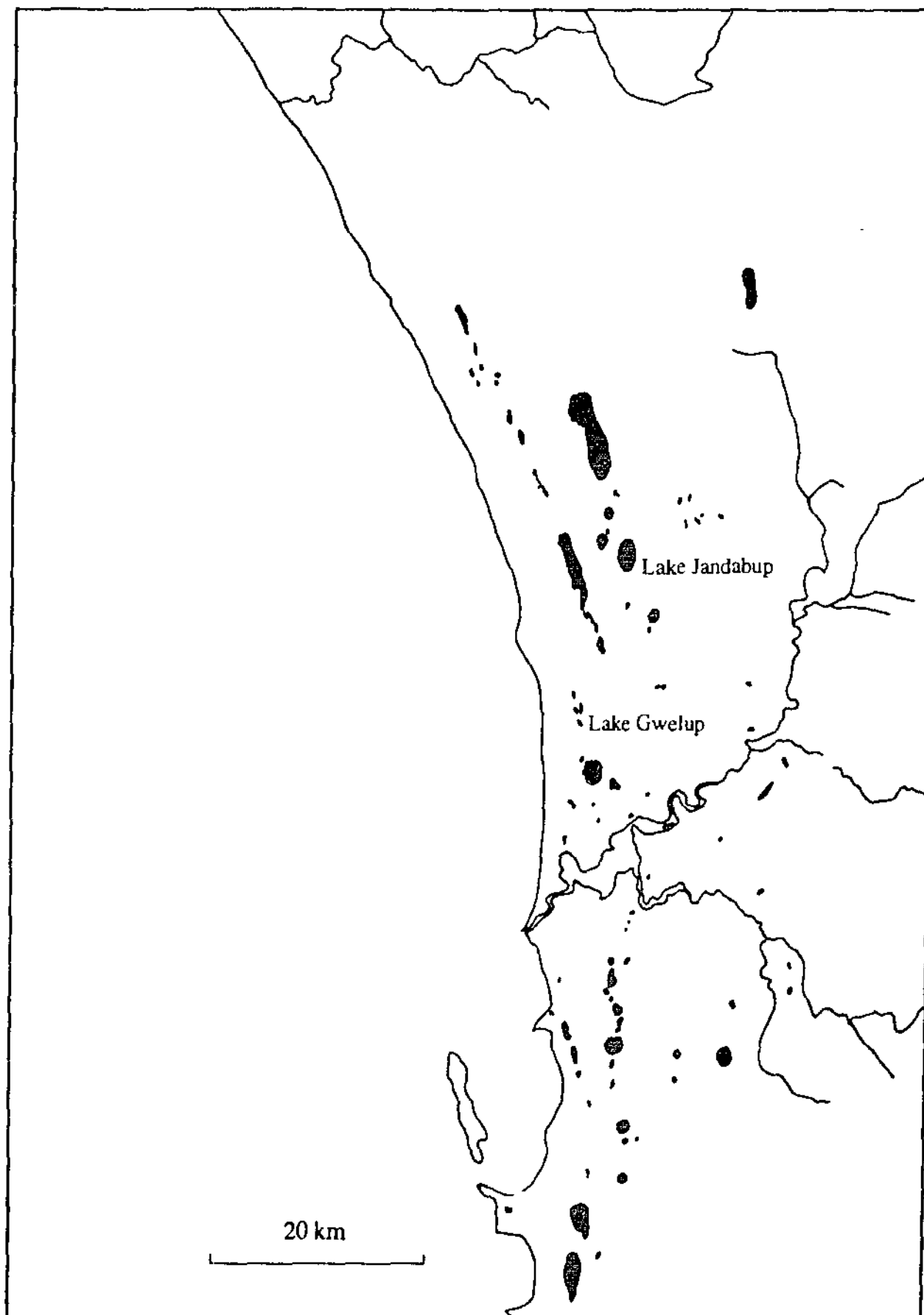


Figure 3.1: The location of Lake Jandabup and Lake Gwelup on the Swan Coastal Plain.
(Adapted from Davis *et al.*, 1993:20)

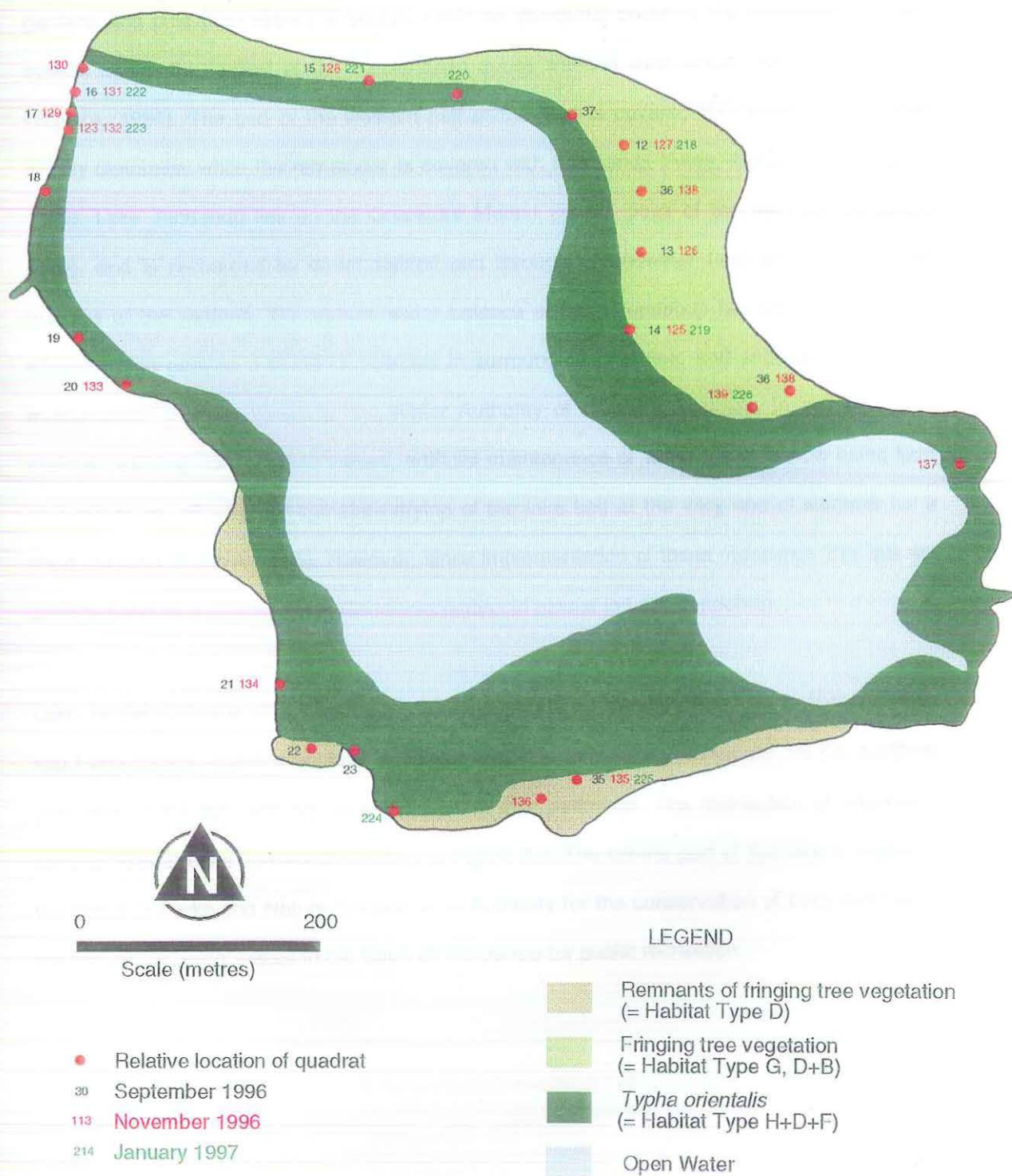


Figure 3.2 : Major Vegetation Communities at Lake Gwelup Western Australia. Corresponding habitat types which were identified by UPGMA classification are given. Relative location of sampling quadrats are also shown. (adapted from City of Stirling 1992. Drafted by G. Oakley Feb. 1997)

Lake Jandabup, situated 22 km north of Perth, is a relatively large (approx. 330 ha), coloured, seasonal, and shallow (<1.5m) wetland, surrounded by rural properties (agistment, market gardens and pine plantations). It occurs within an interdunal swale of the Bassendean dunes system and is the largest of the Bassendean dunes wetland suite which occurs in this area (WAWA, 1995). The bed of the western half of the lake is covered with organic sediments, mainly diatomite, while the remainder is covered with fine sands (Allen, 1979; cited in Ryder, 1993). Lake Jandabup lies on the Gnangara Mound (lowest point of the lake bed is 43.8m AHD), and is recharged by direct rainfall and through groundwater flow along the eastern margins of the wetland. The natural water balance of Lake Jandabup has been dramatically altered in the past as a result of changes in surrounding land use, and subsequent artificial maintenance of water levels by the Water Authority of Western Australia. In an attempt to maintain existing conservation values, artificial maintenance of water levels is now being kept at a minimum, allowing for complete drying of the lake bed at the very end of summer for a short duration (WAWA, 1995). However, since implementation of these measures, this has not occurred and as a consequence *Gambusia holbrooki* persist in Lake Jandabup.

Lake Jandabup has a wide littoral zone which supports a diversity of sedges (mainly *Baumea* spp.) and rushes. Isolated pockets of *Typha orientalis* exist along a channel on the southern perimeter of the lake and on the north-western lake perimeter. The distribution of vegetation communities at Lake Jandabup is shown in Figure 3.3. The central part of the lake is vested in the National Parks and Nature Conservation Authority for the conservation of flora and fauna, the remainder being vested in the Shire of Wanneroo for public recreation.

LEGEND

- Mixed Restionaceae / Cyperaceae
(= Habitat Type A,B,F)
- Baumea articulata* (Sparse)
(= Habitat Type C + F)
- Baumea articulata* (Dense)
(= Habitat Type F+D)
- Baumea* sp. A. (Sparse max. height < 1m)
(= Habitat Type C)
- Baumea* sp. B. (Sparse max. height > 1m)
(= Habitat Type E)
- Typha orientalis*
(= Habitat Type H)
- Open Water
- Alienated



0 500

Scale (metres)

- Relative location of quadrats
- 30 September 1996
- 113 November 1996
- 214 January 1997
- c Calibration quadrat

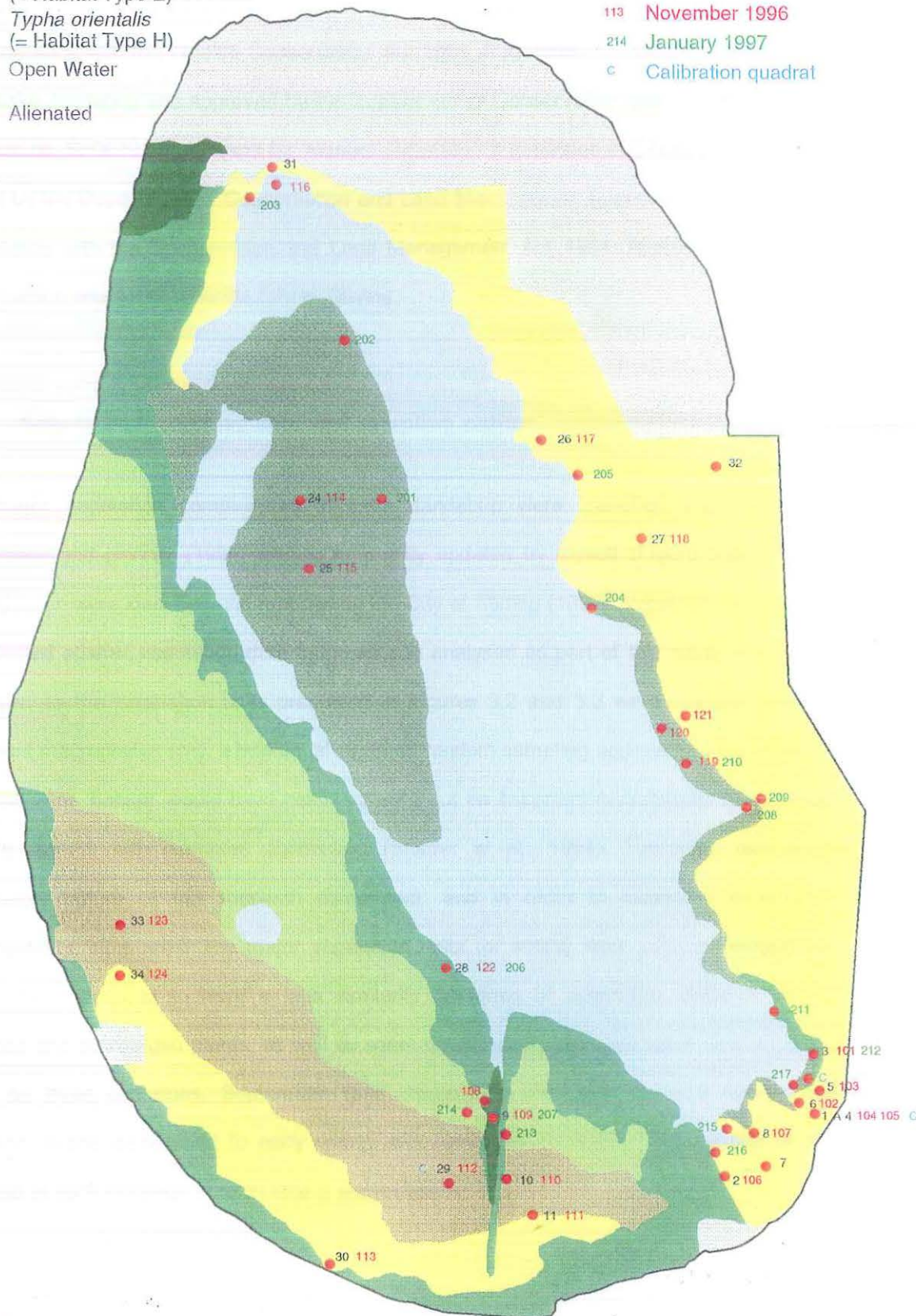


Figure 3.3 : Major Vegetation Communities at Lake Jandabup, Western Australia. Corresponding habitat types which were identified by UPGMA classification are given. Relative location of sampling quadrats are also shown.
(adapted from Richardson and Horwitz 1996. Drafted by G. Oakley Feb. 1997)

3.3 Materials and Methods

3.3.1 Licences and Permits

In accordance with the Wildlife Conservation Act 1950 -Regulation 17, the collection of fauna from Lake Jandabup was approved by the Department of Conservation and Land Management (Licence no. SF001936). A permit for 'research/educational excursion in CALM estate' was also issued by the Department of Conservation and Land Management (Licence no. NE001511) in accordance with the Conservation and Land Management Act 1984. Approval to sample at Lake Gwelup was granted by the City of Stirling.

3.3.2 Selection of sampling sites and sampling regime

The major vegetation communities at Lake Jandabup were identified and mapped by Richardson and Horwitz (1996) and subsequently updated by myself (Figure 3.3). Those at Lake Gwelup were identified and mapped by the City of Stirling (1992). Vegetation associations were tested against vegetation data gathered and analysed as part of this study (see below). However, as the vegetation units presented in Figures 3.2 and 3.3 were mapped based on emergent macrophytes only, a traditional stratified random sampling approach using vegetation association as 'habitat' would have risked missing out on important microhabitat types, and/or tadpole species with restricted distribution (Shaffer *et al.*, 1994). Therefore, due to the exploratory nature of this research component, and in order to maximize microhabitat heterogeneity, sites within the major vegetation units (or strata) were selected subjectively. Sites which appeared to have a high similarity (in terms of vegetation structure of both emerged and submerged plants, as well as water depth) were replicated twice. Sampling took place on three occasions, September 1996, November 1996 and January 1997. These sampling events correspond to early spring, late spring and summer. The number of sites sampled at each occasion at each lake is shown below:

<u>Sampling occasion</u>	<u>Lake Jandabup</u>	<u>Lake Gwelup</u>	<u>Total no. of sites per season</u>
September 1996	23	15	38
November 1996	24	15	39
January 1997	17	9	26
Total no. of sites per lake	64	39	(103)

The relative locations of quadrats are shown in Figures 3.2 and 3.3. Fewer sites were sampled at Lake Gwelup than at Lake Jandabup because the former lake is much smaller than the latter, and Lake Jandabup supports greater habitat heterogeneity than Lake Gwelup (cf. Shaffer *et al.*, 1994). Fewer sites were sampled in January (summer) than on the other two occasions due to loss of habitat as a result of drying of the lake beds.

The littoral zone only, up to a maximum depth of 105 cm, was sampled as this is the region where tadpoles and *Gambusia* mainly occur (Arthington and Lloyd, 1989; Casterlin and Reynolds, 1977; Heyer *et al.*, 1994) and in which the methods used were most practicable.

3.3.3 Sampling method

The sampling method involved staking out 4 x 4 metre quadrats. Large quadrats ('broad sampling') is recommended by Jaeger and Inger (1994) for sampling multi-species populations. The standard size quadrat used previously for amphibian studies has been 1 x 1m for small quadrats and 8 x 8m for large quadrats (Jaeger and Inger, 1994). This, however, is in relation to land sampling, or sampling for large aquatic amphibians such as salamanders. For aquatic microhabitat and multi-species sampling 8 x 8 m is considered too large, as it is very likely that the variability (eg. depth differences) in a quadrat of this size will be too great. In order to guarantee independence of sample quadrats, these were always placed at least 20 metres apart (Jaeger and Inger, 1994).

Sampling involved systematically dipnetting with a square (23 x 23cm) steel framed net. Pore size of the net meshing was 2 mm. This is considered large enough to allow easy passage of water while avoiding trapping too much detritus, and small enough to capture the smallest vertebrate hatchlings. Sampling effort was standardised by applying an equal number of sweeps in each quadrat, regardless of the amount of time this took, performed by the same investigator. Although it was not possible to standardise sweep lengths due to differences in vegetation structure between different quadrats, preliminary trials determined that 20 sweeps were sufficient to cover the surface area of a 4 x 4 metre quadrat. Tadpoles and *G. holbrooki* often occupy different vertical positions in the water column (that is, *G. holbrooki* generally swim close to the water surface, while tadpoles tend to seek refuge in the substrate or in vegetation). If *G. holbrooki* was observed in a quadrat, therefore, five additional (5 second-) sweeps, aimed specifically at the fish, were made.

Wind, fluctuating temperatures, rainfall, time of day, as well as the disposition of the investigator can influence the catchability of individuals (Donnelly and Guyer, 1994; Shaffer *et al.*, 1994). Although every effort was made to keep these effects to a minimum, standardising all of these variables was unrealistic. It was, for example, not possible to limit sampling to fine, or rainless days, as the time available for sampling was fixed. Similarly, due to the large number of samples taken, it was not possible to limit sampling to one or two hours per day. However, these forms of variability are not considered to be a serious problem for the following reasons. Firstly, microhabitat was characterised not only in terms of vegetation structure but also in terms of the following environmental variables: distance from shore, water depth, top and bottom water temperature, top and bottom Dissolved Oxygen concentration and top and bottom pH. Any differences in the number of individuals caught between sites could thus be related to these environmental data. Secondly, at every site a record was made of time of day, weather details, and how long it took to sample. In the case of any 'dubious' results this information could be consulted.

Net contents were bagged and taken back to the Honours laboratory at Joondalup to be identified. Tadpoles which could be identified in the field, as well as aggressive predators, such

as large water beetles, beetle and dragonfly larvae and leeches were recorded but then released straight away (outside of the quadrat area). Physico-chemical variables were measured at one corner of the quadrat prior to dipnetting, while the water column was still undisturbed. Dissolved oxygen concentration, pH and water temperature were measured using *Wissenschaftliche Technische Werkstätten* (WTW) portable field meters. After dipnetting, water depth, distance to shore, percent vegetation cover and height emerged or submerged of each plant species (vegetation structure) were measured and recorded. Samples of each plant species were taken back to the laboratory for identification.

3.3.3.1 Aquatic funnel traps

In addition, where water depth exceeded 40 cm, funnel traps made from translucent plastic 2-liter softdrink bottles (c.f. Richter, 1995) were positioned after dipnetting (Plate 3.1). At Lake Jandabup, two vegetation communities (dense *Baumea articulata* and *Typha orientalis*) were either too deep or too dense to sample with the dipnet, and therefore funnel traps only were used. Aquatic funnel trapping is one of the methods recommended for passively estimating species richness and relative abundance of amphibian larvae (Shaffer, *et al.*, 1994). These traps are designed so that animals enter through the funnel extending inward at one end (Figure 3.4). Animals enter through the funnel but are discouraged from leaving by the small diameter and central location of the exit hole at the bottom of the funnels (Shaffer *et al.*, 1994). Preliminary trials at Lake Jandabup revealed that traps baited with a few fish food pellets were more effective than unbaited traps at catching tadpoles, as well as macroinvertebrates. Traps were therefore baited. One trap was placed within each quadrat and left for 24 hours. The main aim of using these traps was to test whether any tadpole species were being missed by the net. Richter (1995) found that at some wetlands aquatic funnel traps captured amphibians that were not previously detected by visual searches or dipnetting. A further aim of using these traps was to test their efficacy at catching local tadpoles, as this has not been previously trialed. It was not intended to trap *G. holbrooki* as these devices fail to provide the stimulus of prey movement to which they are attracted, and as mentioned in Section 1.3., these fish tend to

positioned (although Pen and Potter (1991) do mention that the fish were found to feed throughout the water column).



Plate 3.1: Funnel trap used for capturing tadpoles

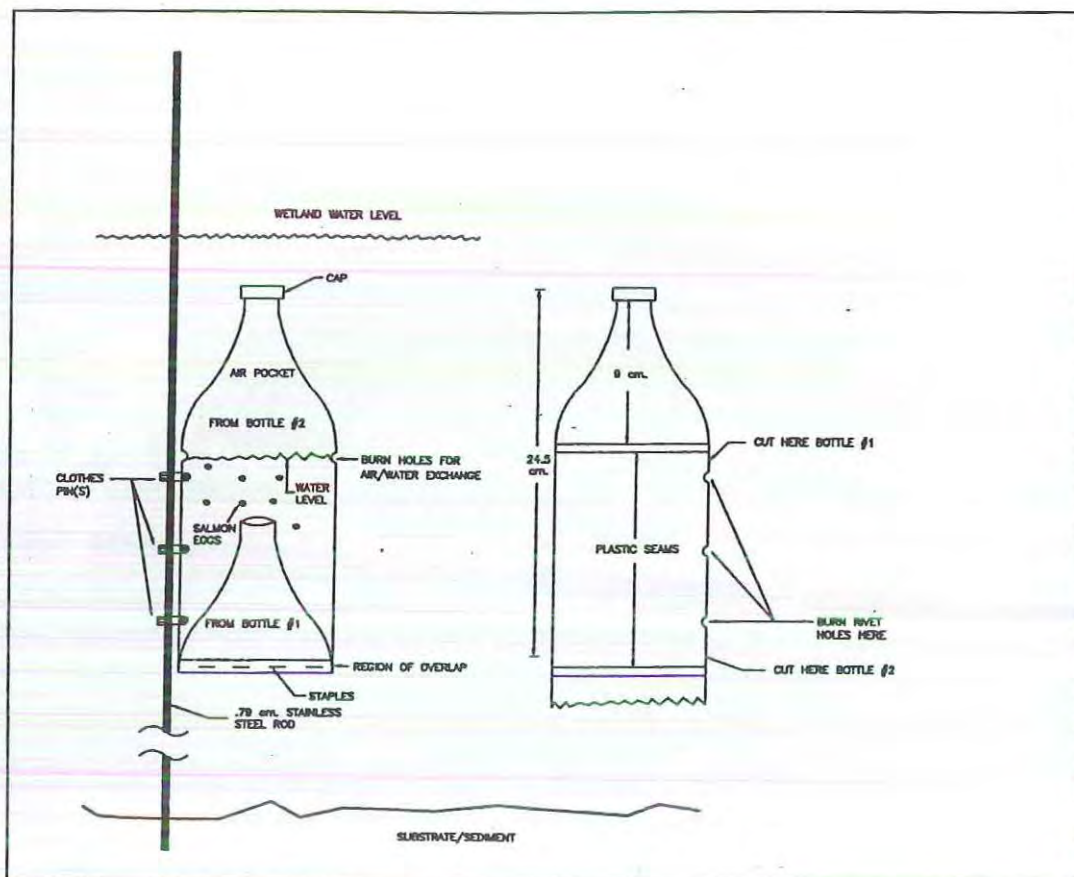


Figure 3.4: Diagram showing funnel trap assembly as designed by Richter 1995. (Source: Richter, 1995)

3.3.3.2 Calibration trials

In order to determine what proportion of the individual species present in a quadrat was captured with the dipnet, three calibration trials using netted enclosures for absolute sampling were carried out at Lake Jandabup. The three sites used for these trials were selected on the basis of water depth and fish density. Different vegetation densities could not be used as it was impractical to erect netted enclosures around the more densely vegetated sites. One site was shallow (10 cm) and had high fish densities, one was deep (75 cm) and had low fish densities, and the third was intermediate (45 cm deep). A 4x4m netted enclosure was erected (see Plate 3.2) and the number of fish and tadpoles captured with each sweep was recorded. This was continued until no more animals were being consistently caught, and it could be assumed that

most of the fish and tadpoles in the quadrat had been removed. The trials were conducted in November, as fish were either absent or found only in very shallow sites in September.

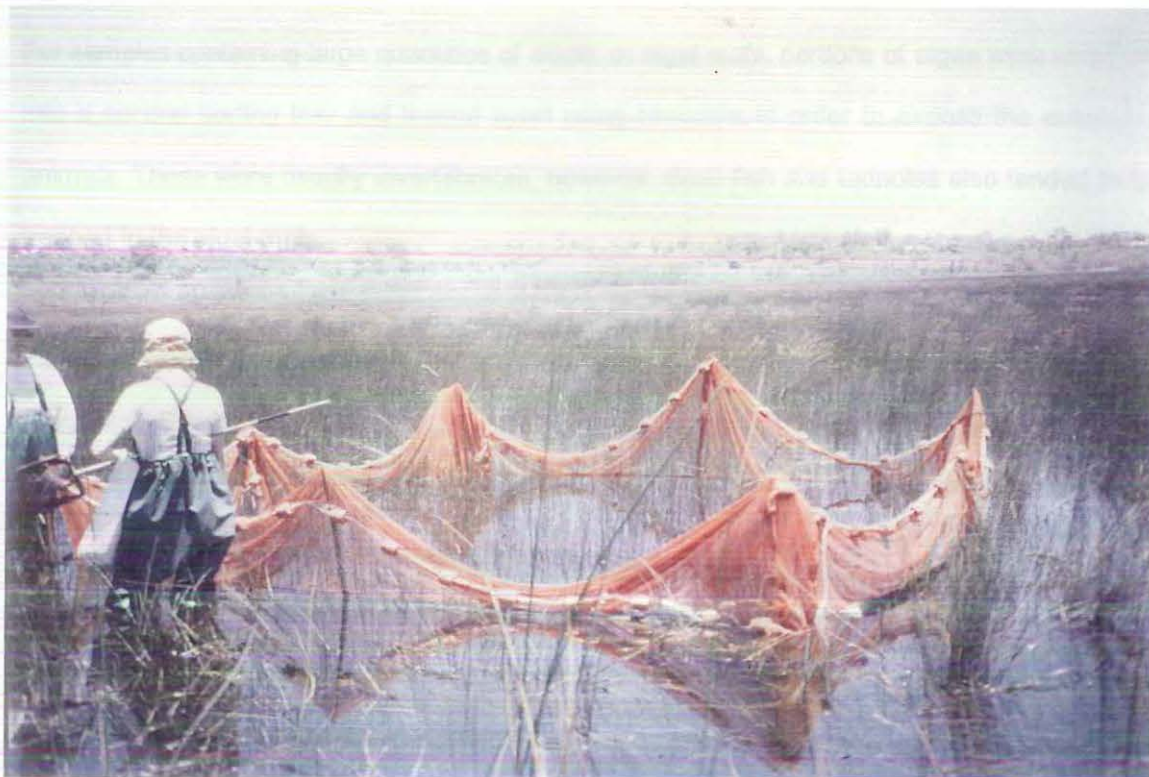


Plate 3.2: Netted enclosure used for calibration trials. Lake Jandabup, November 1996.

3.3.4 Sorting and identification of plant and animal specimens

Aquatic fauna

The fauna samples were emptied into white sorting trays. Tadpoles were picked out using a small aquarium net, sorted into species and counted. Tadpoles were usually released back as close as possible to the point of collection the next day. Fish (*G. holbrooki*, *Pseudogobius olorum* and *Carassius auratus*) were also picked out of the sorting trays using a small aquarium net. Due to the large number of (live and moving) fish sometimes present in the trays, it was found practicable to pick out only a few at a time (around ten), so that they could be counted properly. *G. holbrooki* were transferred to the aquarium in the lab and used for the feeding trials. *Pseudogobius olorum* were returned to Lake Gwelup the following day. The goldfish (*Carassius auratus*) were given to various people with home aquaria. Macroinvertebrates were

picked out of the trays using long tweezers, and preserved in small plastic vials containing 70% ethanol.

For samples containing large quantities of algae, or algal mats, portions of algae were removed into a second sorting tray and teased apart using tweezers in order to expose the entangled animals. These were usually invertebrates, however, dead fish and tadpoles also tended to be trapped in the algal mats.

Tadpoles were identified using the keys and descriptions given in Main (1965), the Alcoa Frogwatch Sheets (W.A. Museum, 1995), Tyler *et al.* (1984), Tyler (1989), and Tyler *et al.* (1993). Expert opinion was also sought, when necessary, from Dr. K. Aplin and Mr. M. Cowan from the W.A. Museum. However, apart from the two *Crinia* species which are virtually indistinguishable, each of the local tadpole species is rather distinctive (see Appendix 1), and after a while it becomes relatively easy to distinguish between them. Having samples of each species in the lab also facilitated identification.

Invertebrates, in most cases, were only identified to Order level (except for Odonates, where the distinction between Zygoptera and Anisoptera was made) using Williams (1980). Most of the beetles sampled belonged to the family Dytiscidae. Most members of this family are highly predaceous (Williams, 1980). Selection of predaceous macroinvertebrate orders was based on reports in the literature that these prey on amphibian eggs and tadpoles. Table 3.1 lists some of the published data on predation by macroinvertebrates on amphibian eggs and tadpoles. This list is by no means comprehensive.

Macroinvertebrate groups selected for sampling were therefore: Odonata (Zygoptera and Anisoptera), Coleoptera (adults and larvae, all larvae were Dytiscids), Hirudinae, Hemiptera, Trichoptera and the gilgie (*Cherax quinquecarinatus*). Hemiptera and Trichoptera were later excluded from analysis as it was doubtful that local representatives of these orders preyed on frog eggs or tadpoles.

Table 3.1: Published reports on macroinvertebrate predation on amphibian tadpoles

REFERENCE	MACROINVERTEBRATE
Anholt and Werner, 1995	Odonata (Anisoptera)
Barrett, 1995	Odonata: Anisoptera (<i>Aeshna brevistyla</i>)
Beebee, 1996	Trichoptera, Coleoptera (Dytiscidae), Hemiptera (<i>Notonecta</i> spp.), Odonata (Zygoptera and Anisoptera)
Brockelman, 1969	Hirudineae
Brodie and Formanowicz, 1983 and 1987	Coleoptera: Dytiscidae (<i>Dytiscus</i> sp.), Odonata: Anisoptera (<i>Anax junius</i>), Hemiptera (<i>Lethocerus americanus</i> and <i>Belostoma</i> sp.),
Formanowicz and Brodie, 1982	Coleoptera: Dytiscidae (<i>Dytiscus</i> sp.)
Gascon and Travis, 1992	Odonata: Anisoptera (<i>Tramea</i> sp.)
Hayes, 1983	Crustacea: Decapoda
Lardner and Sidenmark, 1996	Crustacea: Decapoda
Pearman, 1995	Coleoptera: Dytiscidae (<i>Dytiscus</i> sp.)
Resetarits and Wilbur, 1991	Odonata: Anisoptera (<i>Tramea</i> sp.)
Semlitsch, 1993	Odonata: Anisoptera
Werner and Anholt, 1996	Odonata: Anisoptera (<i>Anax</i> sp.)

Aquatic Vegetation

Vegetation community structure was classified in terms of percentage cover, and height emerged or submerged, of each species. Emergent macrophyte samples were individually bundled, tagged, and hung upside down to dry. Submerged and herbaceous plants were pressed. Identification was made using Sainty & Jacobs (1981) and Chambers *et al.* (1995). Expert opinion was also sought from Dr. K. Meeney (Kings Park Board), Dr. G. Keighery (Dept. of Conservation and Land Management), Dr. R. Froend (Edith Cowan University) and Dr. S. Connell (Edith Cowan University). However, it was not possible to identify every species. It appears that many aquatic plants, particularly emergent macrophytes, have yet to be described (G. Keighery, pers. comm.).

3.4 Data analysis

For the analysis of spatial and temporal associations in microhabitat use by five local tadpole species, *G. holbrooki* and macroinvertebrate predators, the data were classified and ordinated using multivariate techniques from the Pattern Analysis (PATN) software package (Belbin, 1991). Classification and ordination methods can reveal new details about the processes generating the data, and are useful tools for generating hypotheses about how processes are determining data variation (Belbin and McDonald, 1993; Faith and Norris, 1989). Another benefit of pattern analysis methods is that community composition may be predicted from environmental data. This is particularly useful when assessment of habitat is to be made in cases where extensive sampling is not possible (Faith and Norris, 1989). Analysis of this research component consisted of four main steps:

1. Classification of sites based on vegetation community structure;
2. Assignment of sites to specific habitat types (based on above classification) for the purpose of comparing faunal abundances and densities between different habitat types (seasonally and between the two lakes investigated);
3. Classification and ordination of sites based on faunal composition;
4. Projection of the environmental data onto the fauna ordination in order to see how well the environmental data fit (or correlate) into the ordination space (Belbin, 1991).

3.4.1 Classification of sites based on vegetation community structure

In order to normalise the data, percentage vegetation cover was arcsine transformed (Fowler and Cohen, 1990). It has been found that data which are as close to 'normal' as possible provide the best results for associations (M. Lund, pers. comm.). The transformed data were then standardised by range to values between 0-1 for the equal weighting of attributes (that is, common species were down-weighted). Analysis of the association between sites involves a dissimilarity measure which will equal zero when two sites are identical, and one when two sites have no common species. The Bray and Curtis association measure was used, as this has

consistently performed well in a variety of tests and simulations on different types of data (Belbin, 1994). Sites were classified using Flexible Unweighted Pair Group Arithmetic averaging strategy (UPGMA), an hierarchical polythetic agglomerative method of cluster analysis, and a dendrogram was produced. Groups, or 'Habitat Types' were initially selected from the dendrogram, by taking the square root of the number of sites (Belbin, 1991). This resulted in ten groups. After investigating the nature of these groups, the number was reduced to eight. Belbin (1991) suggests that algorithmic techniques which exist to scan the hierarchy and propose a cut-level, are not necessarily superior to using 'common sense'.

3.4.2 Faunal abundances

Faunal abundances (expressed as average number of animals per site) between three sampling occasions and the two lakes were compared. The SPSS software package was used to carry out Spearman Rank correlations in order to determine if there were any significant correlations between any of the faunal abundances.

Each site was then assigned to a Habitat Type based on the vegetation classification, and average abundances in each habitat type, broken down into season and lake, were compared.

3.4.2.1 Aquatic funnel traps

Descriptive statistics were used to compare capture frequency and presence/absence data for the two methods (trap and net) used. Only sites in which traps were set were compared.

3.4.2.2 Calibration trials

For each calibration site the cumulative number of tadpoles and *G. holbrooki* caught with each sweep was plotted on a graph in order to show what proportion of the total number of animals in a quadrat was caught with twenty-five (twenty plus five aimed at fish) sweeps. The graphs were also intended to show at what point (sweep number) the sampling curve starts to level off.

Descriptive statistics were used to compare the number of animals captured between the calibration sites and similar open sites. The proportion of tadpoles and *G. holbrooki* caught with twenty-five sweeps in an open quadrat was expressed as a percentage of the total number of animals caught in a closed (calibration) quadrat. Tadpole:*G. holbrooki* ratios were computed.

3.4.3 Classification and ordination of sites based on faunal assemblages

For purposes of data exploration, four classifications of the faunistic data were carried out: one using all species, one with *P. olorum* masked out, one with *P. olorum* and macroinvertebrates masked out (that is, tadpoles and *G. holbrooki* only), and one with tadpoles only. Each of these classifications was carried out in the same manner as described for the vegetation data. However, as the data consist of counts, these were log-transformed (Fowler and Cohen, 1992) prior to standardisation by range. The faunistic dataset was then inversed (ie., species were treated as objects, and sites as attributes) and further classifications by species were carried out. This was done in order to define species groups which, together with the site groups defined in the original classifications, were used for the construction of two-way tables. These tables were used to interpret the dendrograms and ordinations.

The faunistic data were ordinated using semi-strong hybrid (SSH in PATN) multidimensional scaling to produce a map of a dissimilarity matrix in a given number of dimensions specified by the analyst. An ordination space is derived such that the resulting distances between sites in space match (have a low *stress* value with) the corresponding dissimilarities among sites (Faith and Norris, 1989). The goodness of fit of a particular map is given by a stress formula that measures the degree to which the spatial configuration of points (sites) on the map has to be altered to fit the dissimilarity values among the sites. The lower the stress, the better the fit. Starting at two, the number of dimensions (axes) were increased until an acceptable stress level was attained.

3.4.4 Environmental data

As environmental attributes in this study were of mixed type, that is nominal (for example 'habitat type'), interval (for example water depth) and ratio (for example percent D.O. concentration), the DATN module in PATN was used to re-code these attributes to a set of ratio attributes (Belbin, 1994). For the analysis of association between sites based on environmental attributes, the Gower Metric association measure (which is suitable for continuous data with a linear response) was used (Balla and Davis, 1993).

Principal axis correlation (PCC) was used to display and evaluate the faunistic data. This is essentially a multiple-linear regression operation which can be used to see how well the environmental data fits into the ordination space (Belbin, 1991). In PATN, a correlation coefficient is given for each environmental attribute and this can be used as an indicator of significance (Belbin, 1991), or in other words, the degree to which each variable explains variation in the faunistic data.

3.5 Results

3.5.1 Classification of vegetation community structure

Four rare species which occurred only once each, and were not dominant, had to be excluded from the classification of vegetation community structure, as these were having a significant effect on the classification results (see Belbin and McDonald, 1993). After exclusion of these species, a total of 16 species and 103 sites were classified. Figure 3.5 shows the UPGMA clustering of sites from both Lake Jandabup and Lake Gwelup covering three sampling periods (September 1996, November 1996 and January 1997) based on Bray and Curtis dissimilarities. The cut-levels indicating the major groupings of the sites are marked with a solid circle. Groups are labelled with a letter representing a particular habitat type. Table 3.2 presents these habitat types (A-H) with a description of the corresponding vegetation community, and shows in which lakes each habitat type occurs.

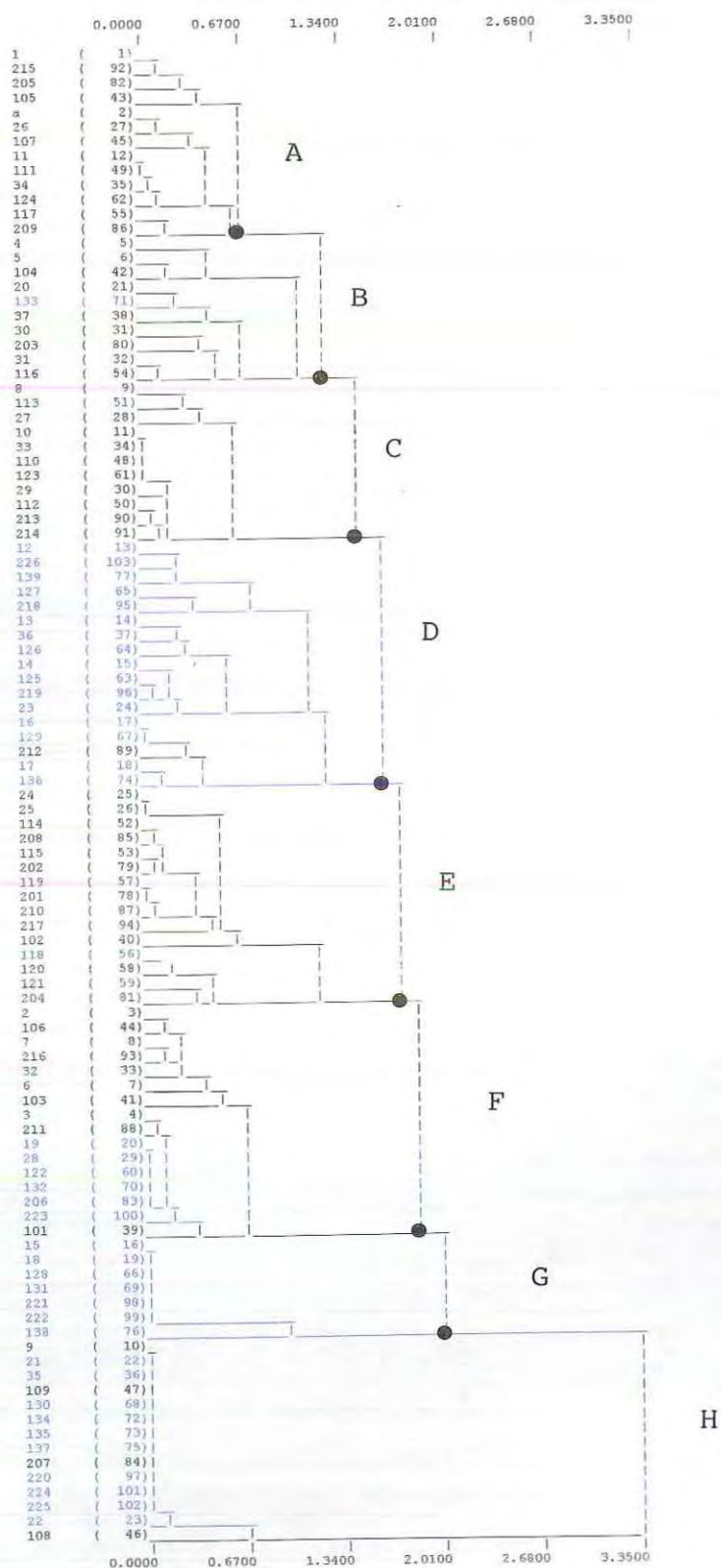


Figure 3.5: Dendrogram based on Bray and Curtis dissimilarities of sites characterised by vegetation community structure at Lake Jandabup (black) and Lake Gwelup (blue). Solid circles mark the eight major groupings (equating to 'habitat types') of sites. Samples were taken on three occasions: September 1996 (2-digit nos.), November 1996 (3-digit nos. commencing with '1') and January 1997 (3-digit nos. commencing with '2').

Table 3.2: Habitat types at Lake Jandabup and Lake Gwelup based on vegetation community structure

Code	Vegetation Community (given either as a general description of the community, or the dominant species)	Lake at which represented
A	Mixed Restionaceae/Cyperaceae	Lake Jandabup
B	Mixed sparse emergent vegetation with relatively dense submerged species (<i>Villarsia albiflora</i> , <i>Myriophyllum</i> sp.)	Lake Jandabup and Lake Gwelup
C	<i>Baumea arthropphylla</i> community	Lake Jandabup
D	Mixed near-shore communities with relatively dense submerged species (<i>Polygonum salicifolium</i> , <i>Elatinaceae</i> spp. and/or introduced grasses)	Lake Gwelup and Lake Jandabup
E	Mixed <i>Baumea juncea</i> and an unidentified <i>Baumea</i> sp. (max. height > 1m)	Lake Jandabup
F	<i>Baumea articulata</i>	Lake Jandabup and Lake Gwelup
G	<i>Melaleuca raphiophylla</i>	Lake Gwelup
H	<i>Typha orientalis</i>	Lake Gwelup and Lake Jandabup

A species list of the plants sampled at Lake Jandabup and Lake Gwelup is given in Appendix 1.

Examples of Habitat Types A to H are shown in Plates 3.3 - 3.11.



Plate 3.3: Mixed Restionaceae/Cyperaceae community at Lake Jandabup (Habitat Type A)



Plate 3.4: Mixed sparse emergent vegetation with relatively dense submerged species (*Villarsia albiflora*, *Myriophyllum* spp.) (Habitat Type B). This photograph was taken at Lake Jandabup in November, 1996.



Plate 3.5: *Baumea arthrophylla* community at Lake Jandabup (Habitat Type C), November, 1996



Plate 3.6: Mixed near-shore communities with relatively dense submerged species (*Polygonum salicifolium*, Elatinaceae and/or introduced grasses (Habitat Type D). Lake Gwelup, November, 1996.



Plate 3.7: Inundated area of introduced grass (Habitat Type D). Lake Gwelup, September, 1996.



Plate 3.8: Mixed *Baumea juncea* and/or an unidentified *Baumea* spp. (max. height > 1m) (Habitat Type E). Lake Jandabup, January, 1997.



Plate 3.9: *Baumea articulata* community (Habitat Type F). Lake Jandabup, November, 1996.



Plate 3.10: *Melaleuca raphiophylla* community (Habitat Type G). Lake Gwelup, November, 1996.



Plate 3.11: *Typha orientalis* community (Habitat Type H). Lake Gwelup, November, 1996.

3.5.2 Faunal abundances

A total of 103 sites were sampled at Lake Jandabup and Lake Gwelup on three sampling occasions. Five sites at Lake Jandabup were sampled using funnel traps only (as these were too dense/deep to sample with the dipnet, see Section 3.3.3.1), and these were excluded from the abundance analysis, bringing the total number of sites down to 98. The absolute abundances (raw data) and average abundances per site of five anuran species, *Gambusia holbrooki*, six macroinvertebrate predator groups and two other potential fish predators (from Lake Gwelup only) in each lake on each sampling occasion are shown in Table 3.3. Because the number of sites sampled at each lake on each sampling occasion differs, average abundances per site were mainly used for comparisons (equating to number of animals per 16 m²). Volumetric faunal densities, expressed as number of animals per m³ were not used, as these did not show seasonal trends as clearly due to distortions which resulted from decreasing water volume from September to January. Seasonal comparisons of species abundances sampled at Lake Jandabup and Lake Gwelup are presented graphically in Figure 3.6.

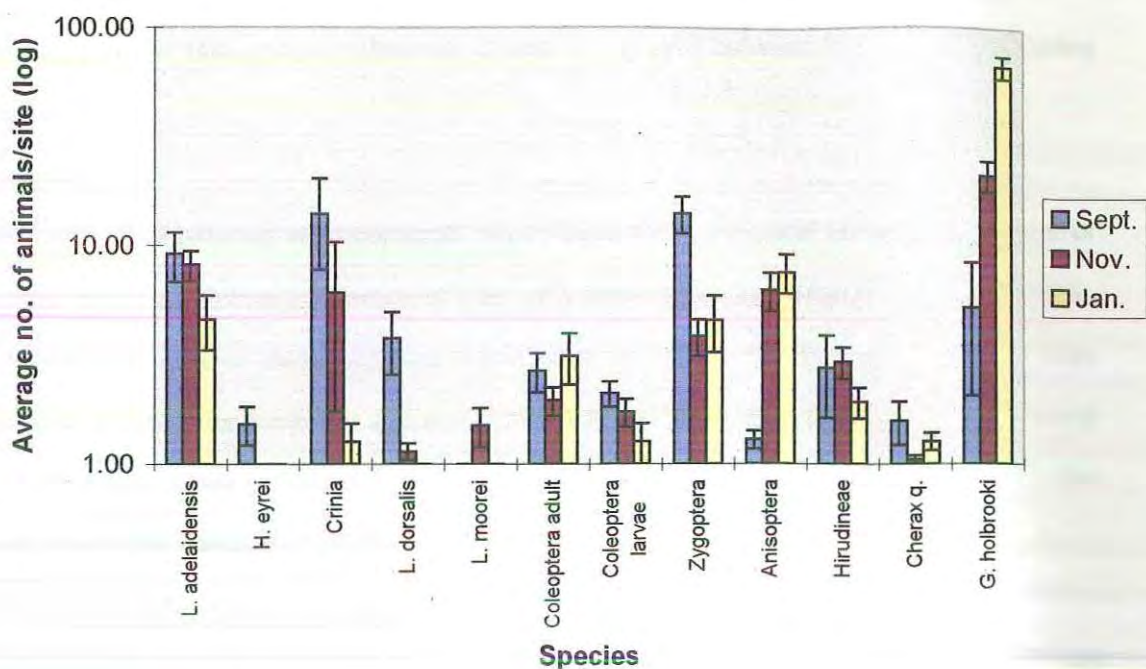
Overall, abundances of all tadpole species were higher at Lake Jandabup than at Lake Gwelup. Table 3.3 shows that there was a marked seasonal variation in the abundances of *Crinia* tadpoles in both lakes. Both absolute and average numbers of these tadpoles per site peaked in September. In November, the average abundance per site dropped to less than half at Lake Jandabup (from roughly 13 tadpoles per site to 5) and at Lake Gwelup to less than a sixth (from roughly 7 tadpoles per site to 1). In January, only four *Crinia* tadpoles were caught at Lake Jandabup and none at Lake Gwelup. The very high standard errors given for the average *Crinia* spp. abundances indicates that there was also a significant spatial variation in their distribution.

The seasonal variation in the average abundances for *L. adelaidensis* tadpoles was more marked at Lake Jandabup than at Lake Gwelup. However, at both lakes this was not as pronounced as with the *Crinia* tadpoles. While at both lakes there was only a small difference in the average number of *L. adelaidensis* tadpoles per site in September and in November, this

Table 3.3: Absolute abundances (raw data) and average abundances per site of five anuran species, *Gambusia holbrooki*, six invertebrate predator groups and two other potential fish predators sampled at Lake Jandabup and Lake Gwelup on three sampling occasions. Standard errors for the average abundances per site are given in brackets. Tadpoles and *G. holbrooki* data are shown in red.

	Absolute Numbers						Average Numbers per site (SE)					
SPECIES	LAKE JANDABUP			LAKE GWELUP			LAKE JANDABUP			LAKE GWELUP		
	Sept.	Nov.	Jan.	Sept.	Nov.	Jan.	Sept.	Nov.	Jan.	Sept.	Nov.	Jan.
	(n = 21)	(n = 22)	(n = 15)	(n = 15)	(n = 16)	(n = 9)	(n = 21)	(n = 22)	(n = 15)	(n = 15)	(n = 16)	(n = 9)
<i>L. adalaidensis</i>	171	157	54	52	56	23	8.14 (±2.32)	7.14 (±1.28)	3.60 (±1.29)	3.47 (±1.71)	3.73 (±1.11)	3.29 (±1.02)
<i>H. eyrei</i>	11	0	0	5	0	0	0.52 (±0.30)	0.00	0.00	0.33 (±0.27)	0.00	0.00
<i>Crinia spp.</i>	274	112	4	104	16	0	13.05 (±6.28)	5.09 (±4.34)	0.27 (±0.26)	6.93 (±3.39)	1.07 (±0.96)	0.00
<i>L. dorsalis</i>	58	3	0	0	1	0	2.76 (±1.20)	0.14 (±0.09)	0.00	0.00	0.07 (±0.06)	0.00
<i>L. moorei</i>	0	11	0	0	0	1	0.00	0.50 (±0.30)	0.00	0.00	0.00	0.11 (±0.11)
Coleoptera adult	35	21	32	41	22	1	1.67 (±0.54)	0.95 (±0.29)	2.13 (±0.82)	2.73 (±1.39)	1.47 (±1.35)	0.11 (±0.11)
Coleoptera larvae	23	16	4	5	7	1	1.10 (±0.27)	0.73 (±0.24)	0.27 (±0.26)	0.33 (±0.27)	0.47 (±0.26)	0.11 (±0.11)
Zygoptera	272	62	53	97	103	119	12.95 (±2.62)	2.82 (±0.72)	3.53 (±1.30)	6.47 (±2.48)	6.87 (±1.73)	13.22 (±3.67)
Anisoptera	6	116	99	7	48	38	0.29 (±0.12)	5.27 (±1.25)	6.6 (±1.54)	0.47 (±0.27)	3.20 (±0.77)	4.22 (±2.24)
Hirudineae	37	43	14	1	23	0	1.76 (±1.13)	1.95 (±0.48)	0.93 (±0.31)	0.07 (±0.06)	1.53 (±0.66)	0.00
<i>Cherax q.</i>	12	1	4	7	0	0	0.57 (±0.35)	0.05 (±0.04)	0.27 (±0.11)	0.47 (±0.29)	0.00	0.00
<i>G. holbrooki</i>	88	437	981	41	629	627	4.19 (±3.14)	19.86 (±3.48)	65.40 (±7.98)	2.73 (±1.73)	41.93 (±19.12)	69.67 (±15.20)
<i>P. olorum</i>	0	0	0	218	238	287	0.00	0.00	0.00	14.53 (±4.33)	15.87 (±3.44)	31.89 (±5.48)
<i>C. auratus</i>	0	0	0	4	20	1	0.00	0.00	0.00	0.27 (±0.26)	1.33 (±0.47)	0.11 (±0.11)

a)



b)

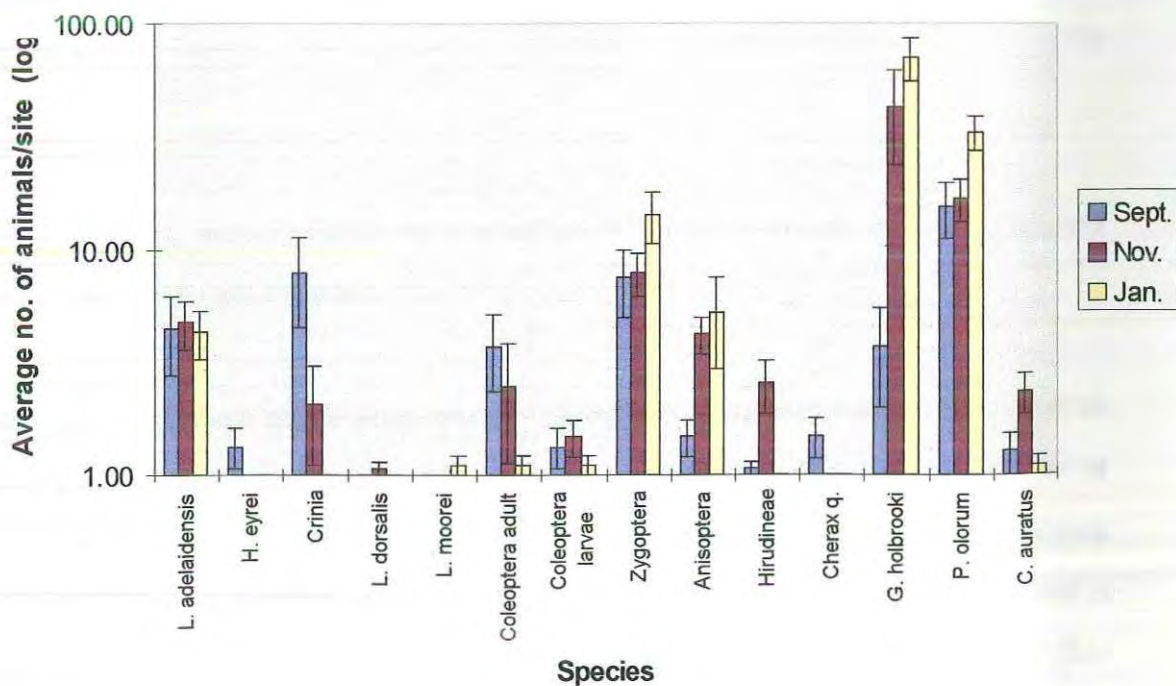


Figure 3.6: Seasonal comparison of species abundances (average number of animals per site) at Lake Jandabup (a), and Lake Gwelup (b). Standard error bars are indicated. (One was added to each average before log-transformation in order to eliminate zeros.)

figure dropped to roughly half (from 7.14 tadpoles in November to 3.6 in January) at Lake Jandabup by January. At Lake Gwelup the average number of *L. adalaidensis* sampled per site remained more or less constant (between 3 and 4 tadpoles) between the different sampling seasons.

Heleioporus eyrei tadpoles were captured only in September, and most of these were large or late stage tadpoles. This is a reflection of their early breeding season (March-May, Main, 1965). By November, most of these tadpoles would have emerged from the water. The average number of tadpoles captured per site was similarly low at both lakes (0.52 at Lake Jandabup and 0.33 at Lake Gwelup). Standard errors were high, again indicating spatial variability in the distribution of this species.

Limnodynastes dorsalis tadpoles were collected mainly in September, and mainly at Lake Jandabup. In September, the average abundance of *L. dorsalis* tadpoles per site at Lake Jandabup was 2.76, while at Lake Gwelup none at all were sampled (although adult males were heard calling at both lakes). In November three tadpoles were caught at Lake Jandabup and only one at Lake Gwelup, while in January no tadpoles of this species were caught at any of the lakes.

Overall, only 11 *L. moorei* tadpoles were caught (all in November) at Lake Jandabup, and only one (in January) at Lake Gwelup.

Both absolute numbers and average abundances per site of *Gambusia holbrooki* showed an almost exponential increase from September to January. In November, the average number of *G. holbrooki* caught per site was roughly twice as high at Lake Gwelup than at Lake Jandabup (41.93 vs. 19.86 fish per site). However, average abundances per site in September and in January were very similar at both lakes, despite the fact that one lake is seasonal and the other permanent. For both lakes, the calculated standard errors for January were much lower (in relation to average abundances per site) than for September and November. This indicates that

variability in the spatial distribution of this species is less marked in January than in the other two sampling occasions.

The seasonal trend in average abundances of macroinvertebrate predators differs between the two lakes. For adult Coleopterans, the trend is towards lower average number of animals per site from September to January at Lake Gwelup, while no such trend is evident for Lake Jandabup. Coleopteran larvae were overall more abundant at Lake Jandabup than at Lake Gwelup. At Lake Jandabup the trend is towards lower number of animals per site from September to January, similar to most of the tadpole species sampled. At Lake Gwelup the average Coleopteran larval abundance per site was slightly higher in November (0.47) than in September (0.33), but was also lowest in January (0.11). Zygopterans were most abundant at Lake Jandabup in September, while at Lake Gwelup they were most abundant in January. Apart from Zygopterans in September (Lake Jandabup), macroinvertebrate predator abundances were low compared to *G. holbrooki* abundances.

3.5.2.1 Aquatic funnel traps

Traps were erected in a total of 41 quadrats. Two-way tables showing comparisons of the number of each species trapped and netted in each site (total abundance and presence/absence data) were constructed but are too lengthy to present here. Table 3.4 shows both absolute numbers and presence/absence data of the fauna captured in the funnel traps and by dipnetting. This is graphically displayed in Figures 3.7 and 3.8. Table 3.4 and Figure 3.7 show that for the majority of the fauna (ie., *L. adalaidensis*, *H. eyrei*, *Crinia* spp., Coleopteran larvae, Zygopterans, Anisopterans, Hirudineae, *G. holbrooki*, *P. olorum*, and *C. auratus*) more animals were captured with the dipnet than with the funnel trap. However, for *L. moorei*, Coleopteran adults, and *Cherax quinquecarinatus* ('gilgie') the funnel traps captured more animals than the dipnet. An equal number of *L. dorsalis* tadpoles were captured with the funnel traps and with the dipnet (4 tadpoles each). A single *G. holbrooki* was captured with the traps. This trap had dislodged itself and was lying horizontally on the water surface. *H. eyrei* was the only species never caught with a funnel trap. However, in preliminary trials carried out in

SPECIES	CAPTURE FREQUENCIES		NO. OF SITES PRESENT	
	Trap	Net	Trap	Net
<i>L. adelaidensis</i>	63	303	19	36
<i>H. eyrei</i>	0	1	0	1
<i>Crinia</i>	10	31	4	12
<i>L. dorsalis</i>	4	4	3	3
<i>L. moorei</i>	12	10	3	3
Coleoptera adult	83	52	16	12
Coleoptera larvae	4	24	3	12
Zygoptera	9	380	5	37
Anisoptera	4	128	4	28
Hirudineae	1	47	1	16
<i>Cherax q.</i>	23	2	5	2
<i>G. holbrooki</i>	1	879	1	30
<i>P. olorum</i>	116	575	21	23
<i>C. auratus</i>	2	18	2	9

Table 3.4: Number of tadpoles, macroinvertebrate predators and fish captured in traps and with a dipnet at 41 sites at Lake Jandabup and Lake Gwelup, and number of sites at which each species was captured.

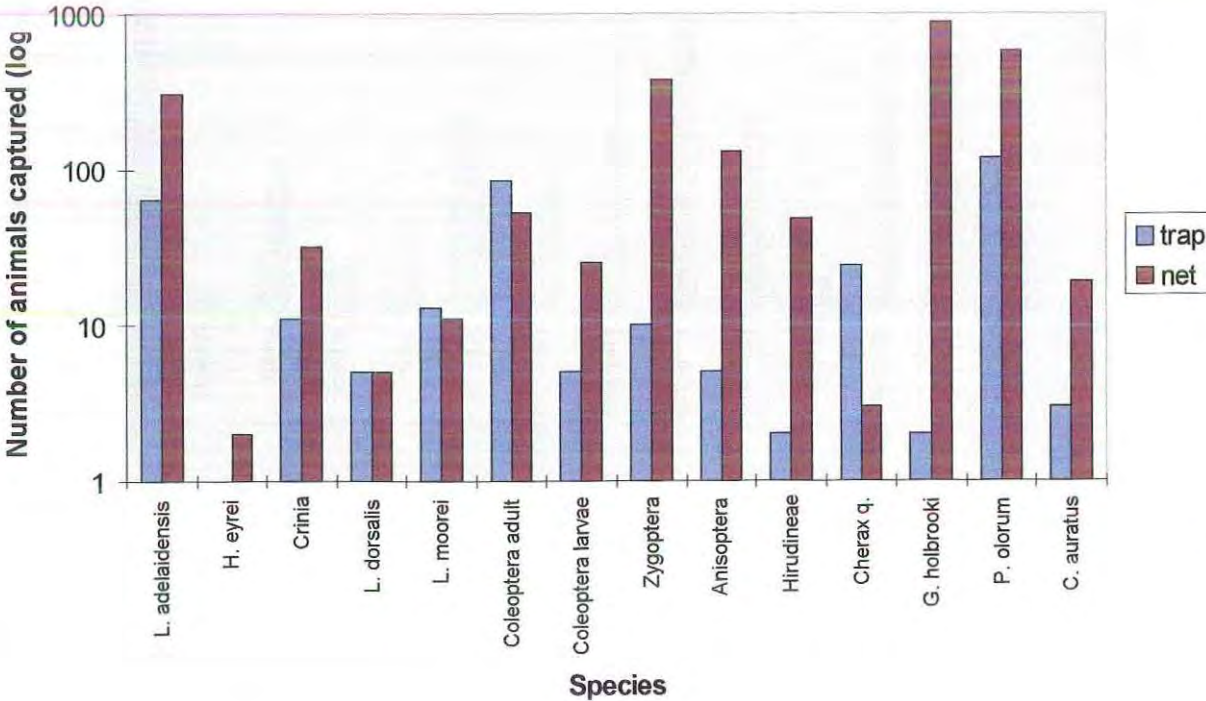


Figure 3.7: Number of tadpoles, macroinvertebrate predators and fish captured in traps and with a dipnet in 41 quadrats at Lake Jandabup and Lake Gwelup. (One was added to each total before log-transformation in order to eliminate zeros.)

August, six large *H. eyrei* were captured in a single trap at Lake Jandabup, and two in two different traps were captured at Lake Gwelup.

Figure 3.8 shows the number of sites at which each species was captured by dipnetting and by trapping. Similarly to total abundances, trap and net presence/absence data, as listed in Table 3.4 and graphically presented in Figure 3.8, show that most species were sampled at many more sites with the dipnet than with the funnel traps. Only Coleopteran adults and *Cherax quinquecarinatus* were trapped at more sites than they were netted. *L. moorei* and *L. dorsalis* tadpoles were both trapped at three sites each, and netted at three sites each. *P. olorum* were trapped at almost as many sites as they were netted (21 / 23 fish respectively).

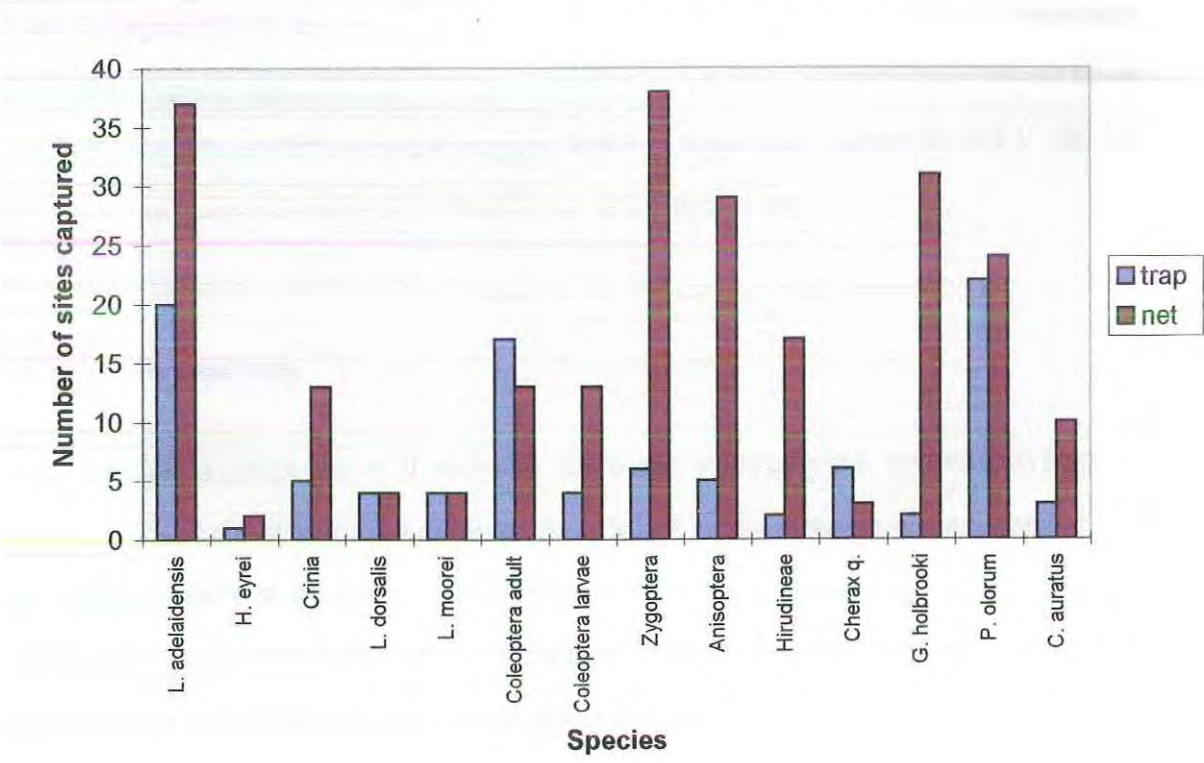


Figure 3.8: Number of sites at which tadpoles, macroinvertebrate predators and fish were captured with traps and with a dipnet from a total of 41 sites at Lake Jandabup and Lake Gwelup

With regards to presence/absence data of local tadpoles, what is more of interest is at how many sites a certain species was captured with one sampling method, but not with the other.

Table 3.5 lists the number of times a tadpole species was captured by trapping but not by netting, and vice versa.

Table 3.5: Number of sites (of a possible 41 sites) at which tadpoles were captured by trapping, but not by netting, and by netting, but not by trapping.

Tadpole Species	Trap Yes / Net No	Trap No / Net Yes
<i>L. adelaidensis</i>	6	23
<i>H. eyrei</i>	0	1
<i>Crinia spp.</i>	2	10
<i>L. dorsalis</i>	2	2
<i>L. moorei</i>	1	1
Total	11	37

Table 3.5 again shows that netting was more successful at detecting a species' presence in a given area. Nevertheless, the funnel traps succeeded in capturing species where the net failed at eleven sites. These trials may also suggest that the dipnet might have detected *L. dorsalis* and *L. moorei* tadpoles at only 50% of the sites in which they occur.

3.5.2.2 Calibration trials

Table 3.6 gives a comparison of *G. holbrooki*, *Crinia spp.* tadpoles and *L. adelaidensis* tadpoles caught in closed and similar open quadrats. Sampling of closed quadrats was assumed to give an 'absolute' count of *G. holbrooki* and tadpoles. Trial number one was carried out within habitat type B, trial number two within habitat type C, and trial number 3 within habitat type E (see Section 3.5.1 for description of habitat types). In general, the higher absolute fish densities were, the lower the proportion of fish that were caught with 25 sweeps in open quadrats. While in open quadrat No. 1 only 15.7% of the absolute number of fish present in the closed quadrat were caught, in open quadrat No. 3, 76.5% (of the absolute number of fish in the closed quadrat, ie. 17) were caught. For the *Crinia spp.* tadpoles, a similar proportion of tadpoles were caught at 25 sweeps in closed and open quadrats (18.7% / 19.5% respectively), while the ratios of *G. holbrooki* to *Crinia spp.* tadpoles in closed and open quadrats, as well as the absolute ratio, were also similar. In the densest site, the absolute ratio of *Crinia spp.* tadpoles to *G.*

holbrooki (2.96:1) lies inbetween the ratio of these tadpoles to *G. holbrooki* from 25 sweeps in the closed quadrat (2.19:1) and the open quadrat (3.69:1).

Table 3.6: Number of *G. holbrooki*, *L. adelaidensis* and *Crinia* spp. tadpoles captured in closed and open quadrats at three faunal densities and water depths (1: dense/shallow; 2: medium density/medium depth; 3: sparse/deep)

Quadrat	Closed 1	Open 1	Closed 2	Open 2	Closed 3	Open 3
Total no. of <i>G. holbrooki</i> caught in closed quadrat	166		97		17	
No. (%) of <i>G. holbrooki</i> caught with 20 (+ 5) sweeps	42 (25.3%)	26 (15.7%)	17 (17.5%)	32 (33%)	7 (41.2%)	13 (76.5%)
Total no. of <i>L. adelaidensis</i> caught in closed quadrat	-		70		48	
No. (%) of <i>L. adelaidensis</i> caught with 20 (+ 5) sweeps	-	-	9 (12.9%)	5 (7.1%)	21 (43.7%)	8 (16.7%)
Total no. of <i>Crinia</i> spp. caught in closed quadrat	491		-			
No. (%) of <i>Crinia</i> spp. caught with 20 (+ 5) sweeps	92 (18.7%)	96 (19.5%)	-	-		
Absolute ratio of tadpoles: <i>G. holbrooki</i>	2.96:1		0.72:1		2.82:1	
Ratio of tadpoles: <i>G. holbrooki</i> at 20 (+ 5) sweeps	2.19:1	3.69:1	0.53:1	0.16:1	3.0:1	0.62:1
No. of sweeps required to clear closed quadrat	150		120		75	

As with the fish, the proportion of *L. adelaidensis* tadpoles (to absolute number of tadpoles present in the closed quadrat) captured in the denser (and shallower) open quadrat is lower than in the less dense (and deeper) quadrat (7.1% / 16.7% respectively). Overall, the ratios of *G. holbrooki* to tadpoles in the closed quadrats were similar to the absolute ratios of *G. holbrooki* to tadpoles, but those in the open quadrats differed.

Figure 3.9 graphically displays the number of tadpoles and fish caught with each sweep (cumulative) in each of the calibration trials carried out. These graphs show that a very large number of sweeps are required until tadpole and fish numbers even out.

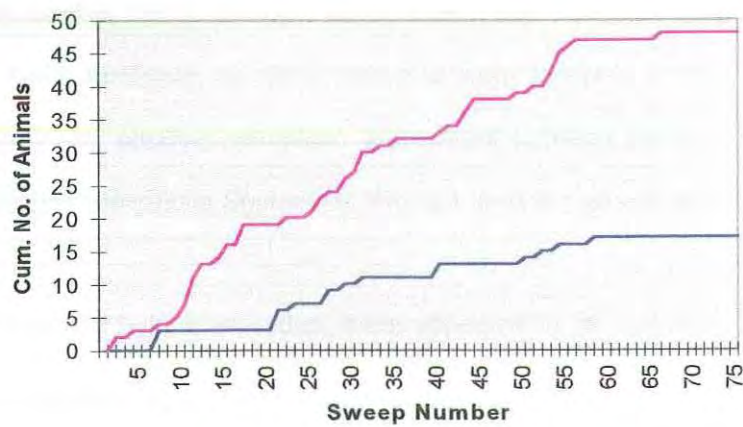
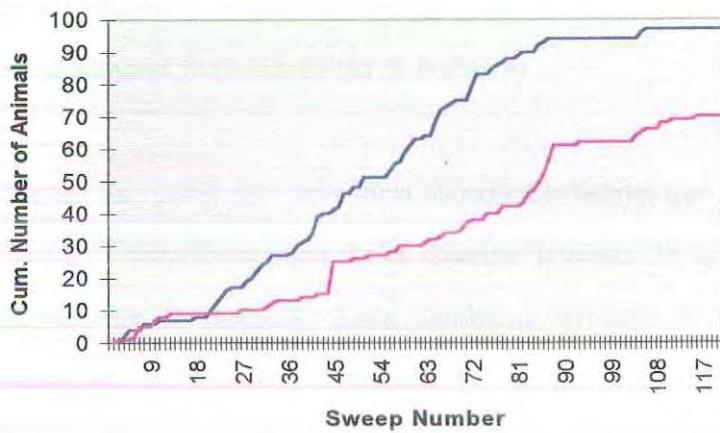
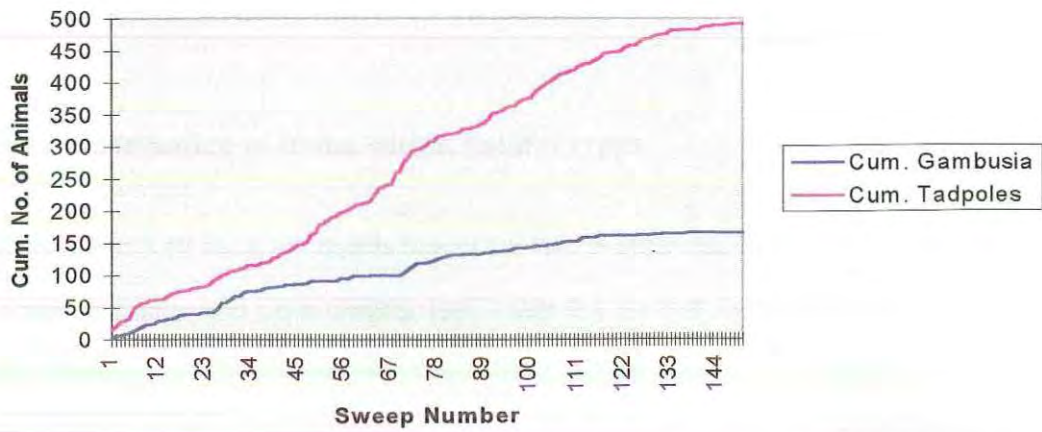


Figure 3.9: Number of tadpoles and *G. holbrooki* captured with each sweep (cumulative) in three calibration trials. (a) high fish density/shallow water (*Crinia* spp. tadpoles), (b) medium fish density/medium water depth (*L. adelaidensis* tadpoles); and (c) low fish density/deep water (*L. adelaidensis* tadpoles).

3.5.3 Distribution of fauna within habitat types

Tables 3.7 to 3.10 show the distribution of the fauna within the eight habitat types represented at Lake Jandabup and Lake Gwelup (see Table 3.1 for descriptions of each habitat type). At Lake Jandabup, no *G. holbrooki* were captured in habitat types A, C, E and F in September. By November, *G. holbrooki* were found in all habitat types but not in all quadrats. At Lake Gwelup, no *G. holbrooki* were captured in habitat types F and G in September. In November habitat type F (although one quadrat only) still did not reveal any *G. holbrooki*. In January, every quadrat sampled (both lakes) had *G. holbrooki*.

In September, *Crinia* spp. were most abundant in habitat type B in both lakes (Lake Jandabup: average 51 tadpoles/quadrat; Lake Gwelup: average 28 tadpoles/quadrat), where they co-occurred with *G. holbrooki* (Lake Jandabup: average 22 fish/quadrat; Lake Gwelup: 1.5 fish/quadrat). In November, most of the *Crinia* tadpoles were found in habitat type A at Lake Jandabup (average 24 tadpoles/quadrat), while at Lake Gwelup they were still most abundant in habitat type B (average 15 tadpoles/quadrat), although this consisted of only one quadrat. In this quadrat 236 *G. holbrooki* were netted. Apart from four individuals sampled in habitat type C at Lake Jandabup, no *Crinia* tadpoles were sampled in January. There was a modest, but significant, positive correlation (Spearman) between the numbers of *G. holbrooki* and *Crinia* tadpoles sampled in September ($r=0.521$, $p<0.01$), as well as in November ($r=0.424$, $p<0.01$).

In terms of habitat utilisation, there appeared to be a strong segregation between *Crinia* spp. and *L. adalaidensis* tadpoles. There was, in fact, a modest but significant inverse correlation (Spearman) between the numbers of *Crinia* spp. and *L. adalaidensis* tadpoles sampled in September ($r=-0.462$, $p<0.01$). *L. adalaidensis* tadpoles were most abundant in habitat types C and E at Lake Jandabup in both September (average of 18 and 21 tadpoles respectively) and November (average of 8 and 9 tadpoles respectively). In January they were found mainly in habitat type E, as habitat type C had almost completely dried up. In November, *L. adalaidensis* co-occurred with moderate numbers of *G. holbrooki* (approx. 18 per quadrat in both habitat

HABITAT TYPE	A			B			C			D		
	Sept	Nov	Jan	Sept	Nov	Jan	Sept	Nov	Jan	Sept	Nov	Jan
SPECIES	(n = 5)	(n = 5)	(n = 3)	(n = 4)	(n = 2)	(n = 1)	(n = 5)	(n = 4)	(n = 2)	(n = 0)	(n = 0)	(n = 1)
<i>L. adelaidensis</i>	8.00 (± 4.76)	5.00 (± 1.96)	4.67 (± 3.28)	0	7.50 (± 1.50)	0.00	17.6 (± 4.95)	8.00 (± 2.34)	0.00	-	-	2.00
<i>H. eyrei</i>	1.60 (± 1.16)	0.00	0.00	0.50 (± 0.5)	0.00	0.00	0.00	0.00	0.00	-	-	0.00
<i>Crinia spp.</i>	3.00 (± 2.75)	24.25 (± 21.39)	0.00	50.75 (± 26.8)	1.00 (± 1.0)	0.00	2.60 (± 1.88)	0.25 (± 0.25)	2.00 (± 2.00)	-	-	0.00
<i>L. dorsalis</i>	0.20 (± 0.20)	0.00	0.00	6.75 (± 4.70)	0.50 (± 0.50)	0.00	3.60 (± 2.90)	0.00	0.00	-	-	0.00
<i>L. moorei</i>	0.00	0.00	0.00	0	2.50 (± 0.50)	0.00	0.00	0.00	0.00	-	-	0.00
Coleoptera adult	2.00 (± 0.94)	1.75 (± 1.05)	2.33 (± 1.85)	1.75 (± 0.75)	0.5 (± 0.50)	7.00	2.80 (± 1.95)	0.50 (± 0.50)	2.00 (± 2.00)	-	-	10.00
Coleoptera larvae	1.40 (± 0.67)	0.75 (± 0.22)	0.00	0.50 (± 0.5)	1.00 (± 0.00)	0.00	1.60 (± 0.60)	0.50 (± 0.28)	0.00	-	-	4.00
Zygoptera	11.20 (± 3.05)	5.00 (± 3.03)	2.00 (± 0.57)	3.00 (± 3.0)	3.50 (± 2.50)	1.00	24.2 (± 5.43)	1.25 (± 1.25)	0.00	-	-	18.00
Anisoptera	0.20 (± 0.20)	6.75 (± 4.55)	4.67 (± 0.88)	0.25 (± 0.25)	5.00 (± 2.00)	12.00	0.20 (± 0.20)	2.50 (± 0.95)	4.00 (± 3.0)	-	-	24.00
Hirudineae	0.60 (± 0.06)	2.25 (± 0.42)	1.00 (± 1.0)	7.00 (± 5.70)	2.00 (± 0.00)	1.00	0.20 (± 0.20)	2.25 (± 1.03)	0.00	-	-	1.00
<i>Cherax q.</i>	0.00	0.25 (± 0.22)	0.33 (± 0.33)	0.75 (± 0.75)	0.00	0.00	0.40 (± 0.24)	0.00	0.00	-	-	1.00
<i>G. holbrooki</i>	0.00	13.25 (± 4.24)	48.67 (± 14.65)	22.0 (± 14.67)	61.0 (± 8.0)	80.00	0.00	17.75 (± 5.89)	32.0 (± 6.00)	-	-	133.00

Table 3.7: Distribution of tadpoles, *G. holbrooki* and macroinvertebrate predators within Habitat Types A - D at Lake Jandabup. Figures are average number of animals sampled per Habitat Type (\pm SE) and are shown separately for each sampling occasion (September 1996, November, 1996 and January 1997).

HABITAT TYPE	E			F			H		
	Sept (n = 2)	Nov (n = 7)	Jan (n = 6)	Sept (n = 5)	Nov (n = 3)	Jan (n = 2)	Sept (n = 0)	Nov (n = 1)	Jan (n = 0)
SPECIES									
<i>L. adelaidensis</i>	20.5 (± 2.50)	9.00 (± 3.13)	5.00 (± 2.70)	0.40 (± 0.40)	1.00 (± 0.00)	4.00 (± 2.00)	-	15.0000	-
<i>H. eyrei</i>	0.00	0.00	0.00	0.20 (± 0.20)	0	0	-	0.0000	-
<i>Crinia spp.</i>	0.00	1.43 (± 1.26)	0.00	8.60 (± 5.22)	0.67 (± 0.33)	0	-	0.0000	-
<i>L. dorsalis</i>	0.00	0.29 (± 0.28)	0.00	2.40 (± 1.69)	0	0	-	0.0000	-
<i>L. moorei</i>	0.00	0.00	0.00	0	2.00 (± 2.00)	0	-	0.0000	-
Coleoptera adult	0.00	0.86 (± 0.40)	0.17 (± 0.16)	0.80 (± 0.58)	1.67 (± 0.88)	1.50 (± 1.50)	-	0.0000	-
Coleoptera larvae	0.50 (± 0.50)	0.29 (± 0.28)	0.00	1.00 (± 0.63)	1.67 (± 1.66)	0	-	0.0000	-
Zygoptera	26.0 (± 2.00)	2.29 (± 0.80)	4.17 (± 1.77)	6.20 (± 4.39)	2.67 (± 1.20)	1.50 (± 1.50)	-	1.0000	-
Anisoptera	0.00	4.57 (± 1.57)	5.17 (± 1.72)	0.60 (± 0.40)	11.0 (± 4.72)	5.00 (± 3.00)	-	1.0000	-
Hirudineae	0.00	2.71 (± 1.34)	1.00 (± 0.51)	1.00 (± 0.44)	0.33 (± 0.33)	1.50 (± 1.50)	-	0.0000	-
<i>Cherax q.</i>	0.00	0.00	0.17 (± 0.16)	1.40 (± 1.40)	0	0.50 (± 0.50)	-	0.0000	-
<i>G. holbrooki</i>	0.00	18.0 (± 3.29)	73.17 (± 10.2)	0	13.67 (± 8.83)	59.5 (± 17.50)	-	8.0000	-

Table 3.8: Distribution of tadpoles, *G. holbrooki* and macroinvertebrate predators within Habitat Types E, F and H at Lake Jandabup. Figures are average number of animals sampled per Habitat Type (\pm SE) and are shown separately for each sampling occasion (September 1996, November, 1996 and January 1997).

HABITAT TYPE	B			D			F		
	Sept	Nov	Jan	Sept	Nov	Jan	Sept	Nov	Jan
SPECIES	(n = 2)	(n = 1)	(n = 0)	(n = 7)	(n = 6)	(n = 3)	(n = 1)	(n = 1)	(n = 1)
<i>L. adelaidensis</i>	0.00	0.00	-	5.29 (± 3.56)	4.67 (± 2.52)	1.67 (± 1.66)	4.00	5.0000	0.00
<i>H. eyrei</i>	2.00 (± 2.00)	0.00	-	0.00	0.00	0.00	0.00	0.0000	0.00
<i>Crinia spp.</i>	27.5 (± 24.50)	15.00	-	5.57 (± 2.03)	0.17 (± 0.16)	0.00	0.00	0.0000	0.00
<i>L. dorsalis</i>	0.00	0.00	-	0.00	0.17 (± 0.16)	0.00	0.00	0.0000	0.00
<i>L. moorei</i>	0.00	0.00	-	0.00	0.00	0.00	0.00	0.0000	0.00
Coleoptera adult	0.00	21.00	-	1.00 (± 0.72)	0.17 (± 0.16)	0.33 (± 0.33)	2.00	0.0000	0.00
Coleoptera larvae	2.00 (± 2.00)	1.00	-	0.00	1.00 (± 0.63)	0.33 (± 0.33)	0.00	0.0000	0.00
Zygoptera	3.50 (± 3.50)	1.00	-	5.14 (± 3.37)	5.50 (± 2.17)	18.0 (± 10.11)	11.00	1.0000	4.00
Anisoptera	0.00	7.00	-	0.00	2.83 (± 1.24)	11.00 (± 5.00)	1.00	0.0000	1.00
Hirudineae	0.00	0.00	-	0.00	0.67 (± 0.33)	0.00	0.00	0.0000	0.00
<i>Cherax q.</i>	2.00 (± 2.00)	0.00	-	0.29 (± 0.28)	0.00	0.00	0.00	0.0000	0.00
<i>G. holbrooki</i>	1.50 (± 1.50)	236.00	-	5.00 (± 3.61)	56.67 (± 32.8)	105.6 (± 24.6)	0.00	0.0000	35.00
Pseudogobius olorum	4.00 (± 2.00)	0.00	-	17.71 (± 7.36)	21.33 (± 6.89)	30.33 (± 14.5)	30.00	2.0000	30.00
Carassius auratus	0.00	7.00	-	0.57 (± 0.57)	1.00 (± 0.63)	0.33 (± 0.33)	0.00	1.0000	0.00

Table 3.9: Distribution of tadpoles, *G. holbrooki* and macroinvertebrate predators within Habitat Types B, D and F at Lake Gwelup. Figures are average number of animals sampled per Habitat Type (\pm SE) and are shown separately for each sampling occasion (September 1996, November, 1996 and January 1997).

HABITAT TYPE	G			H		
	Sept	Nov	Jan	Sept	Nov	Jan
SPECIES	(n =2)	(n = 3)	(n =2)	(n =3)	(n = 4)	(n = 3)
<i>L. adelaidensis</i>	1.00 (± 1.00)	5.00 (± 2.51)	0.50 (± 0.50)	3.00 (± 2.00)	8.00 (± 0.91)	5.67 (± 1.45)
<i>H. eyrei</i>	0.00	0.00	0	0.33 (± 0.33)	0.00	0.00
<i>Crinia spp.</i>	1.50 (± 1.5)	0.00	0	2.33 (± 1.20)	0.00	0.00
<i>L. dorsalis</i>	0.00	0.00	0	0.00	0.00	0.00
<i>L. moorei</i>	0.00	0.00	0	0.00	0.00	0.33 (± 0.33)
Coleoptera adult	1.50 (± 1.5)	0.00	0	9.67 (± 5.78)	0.00	0.00
Coleoptera larvae	0.50 (± 0.50)	0.00	0	0.00	0.00	0.00
Zygoptera	16.0 (± 16.0)	6.67 (± 3.71)	6.50 (± 6.50)	3.67 (± 2.02)	48.0 (± 4.69)	16.0 (± 1.15)
Anisoptera	0.50 (± 0.50)	6.67 (± 0.88)	0	1.67 (± 1.20)	4.00 (0.40)	1.33 (0.88)
Hirudineae	0.00	0.67 (± 0.66)	0	0.33 (0.33)	17.0 (± 2.09)	0.00
<i>Cherax q.</i>	0.00	0.00	0.00	0.33 (± 0.33)	0.00	0.00
<i>G. holbrooki</i>	0.00	5.67 (± 4.70)	13.0 (± 6.0)	1.00 (± 1.00)	36.0 (± 6.39)	83.0 (± 12.28)
<i>Pseudogobius olorum</i>	23.0 (± 17.0)	9.33 (± 4.97)	21.0 (± 2.00)	3.33 (± 2.02)	80.0 (± 4.74)	41.3 (± 8.00)
<i>Carassius auratus</i>	0.00	1.33 (± 0.66)	0	0.00	2.00 (± 0.28)	0.00

Table 3.10: Distribution of tadpoles, *G. holbrooki* and macroinvertebrate predators within Habitat Types G and H (Lake Gwelup). Figures are average number of animals sampled per Habitat Type (\pm SE) and are shown separately for each sampling occasion (September 1996, November, 1996 and January 1997).

types), and in January with very large numbers (approx. 73/quadrat). At Lake Gwelup, *L. adalaidensis* tadpoles were most abundant in habitat types D, F and H. The highest abundances were in November in habitat type H (average of 8 tadpoles/quadrat).

L. moorei were captured in habitat types B and F (Lake Jandabup) in November, where they co-occurred with large numbers of *G. holbrooki* (average of 61 and 14 fish/quadrat respectively).

H. eyrei tadpoles were sampled in low numbers in habitat types A, B and F at Lake Jandabup, and in habitat types B and H at Lake Gwelup.

L. dorsalis were found to be less habitat-specific than the other tadpole species. They were usually found in conjunction with at least two other tadpole species, and were netted in habitat types A, B, C, E and F at Lake Jandabup.

Pseudogobius olorum were often more abundant than *G. holbrooki* in September and November at Lake Gwelup, especially in deeper water. In habitat type G, more *P. olorum* were sampled than *G. holbrooki*, even in January. *Carassius auratus* were sampled only rarely.

3.5.5 Pattern analysis

3.5.5.1 UPGMA classification of sites based on faunal assemblages

Figure 3.10 shows the UPGMA classification of sites based on faunal assemblages. The dendrogram shows that the September samples (2-digit numbers) tend to cluster together, indicating that they are more similar to each other than to samples taken from similar locations in November or January. It is further evident from the dendrogram that samples taken in November (3-digit numbers commencing with '1') and January (3-digit numbers commencing with '2') are intermingled. A hierarchical classification of species was performed in order to provide an ordering of the species for the construction of a two-way table (Belbin, 1991), and is shown in Figure 3.11.

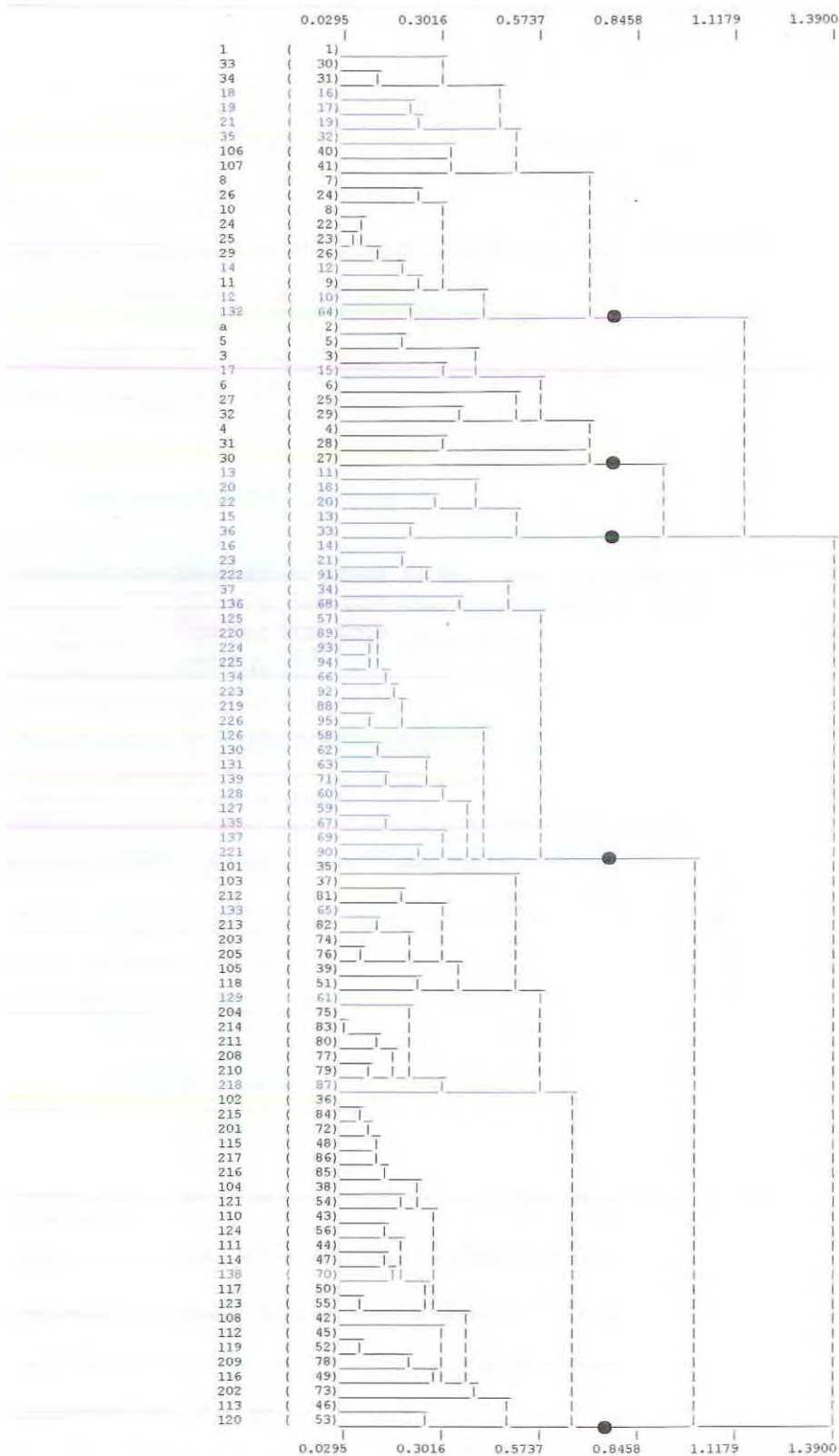


Figure 3.10: Dendrogram based on Bray and Curtis dissimilarities of sites characterised by faunal assemblages (tadpoles, fish and macroinvertebrates) at Lake Jandabup (black) and Lake Gwelup (blue). Samples were taken on three occasions: September 1996 (2-digit nos.), November 1996 (3-digit nos. commencing with '1') and January 1997 (3-digit nos. commencing with '2'). Solid circles mark the cut levels for 5 groups.

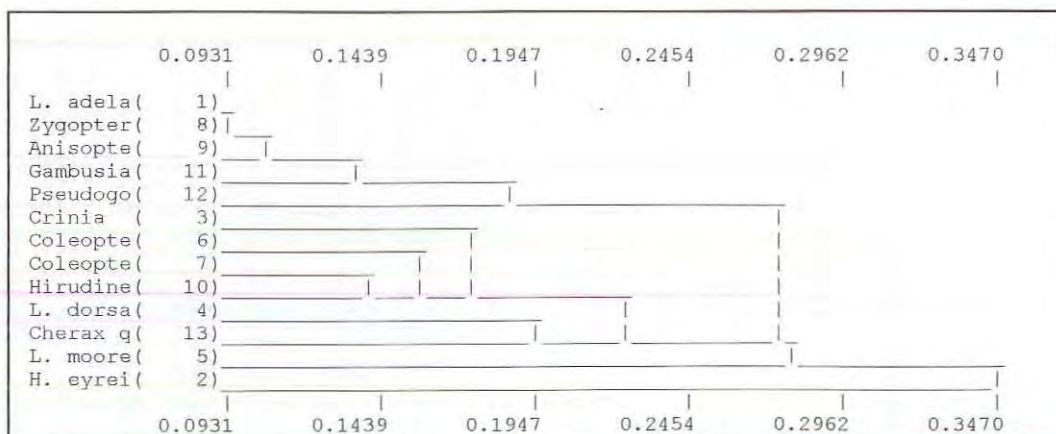


Figure 3.11: Dendrogram based on Bray and Curtis dissimilarities of species occurrences (tadpoles, fish and macroinvertebrates) at Lake Jandabup and Lake Gwelup. Samples were taken on three occasions: September 1996, November 1996 and January 1997.

Based on four cut points, the dendrogram in Figure 3.11 shows that the following groups of species tend to occur together:

- Group 1: *L. adalaidensis*, Zygopterans, Anisopterans, *G. holbrooki* and *P. olorum*
- Group 2: *Crinia* spp., Coleopteran larvae, Coleopteran adults, Hirudineae, *L. dorsalis* and *C. quinquecarinatus*
- Group 3: *L. moorei*
- Group 4: *H. eyrei*

Based on five site groupings (selected from the dendrogram shown in Figure 3.10) and four species groupings, a two-way table designed to aid in the interpretation of the ordinations presented in Section 3.5.5.2 was constructed. This table, however, is too lengthy to present here, and therefore only the average number of animals and standard errors for each group are shown in Table 3.11.

Table 3.11: Two-way data matrix showing site and fauna groupings based on UPGMA classifications of sites and fauna, using all species. Average number of animals (including SE) sampled per group are given.

Group Number	No. of sites		<i>L. adalaidensis</i>	Zygoptera	Anisoptera	<i>G. holbrooki</i>	<i>P. olorum</i>	<i>Crinia</i> spp.	Col. adult	Col. larvae	Hirudineae	<i>L. dorsalis</i>	<i>Cherax</i> q	<i>L. moorei</i>	<i>H. eyrei</i>
1	19	MEAN	11.63	15.58	0.58	0.95	6.00	0.47	2.58	0.89	0.21	0.21	0.11	0.00	0.00
		SE	2.36	2.78	0.23	0.49	2.95	0.23	1.12	0.31	0.12	0.16	0.07	0.00	0.00
2	10	MEAN	0.40	6.90	0.40	8.80	0.00	27.80	2.50	1.00	3.40	5.10	1.10	0.00	0.00
		SE	0.27	2.65	0.22	6.45	0.00	11.83	0.69	0.42	2.32	2.34	0.72	0.00	0.00
3	5	MEAN	0.20	0.60	0.00	0.00	13.60	14.60	0.40	0.00	0.00	0.00	1.00	0.00	0.00
		SE	0.45	0.89	0.00	0.00	19.45	21.52	0.89	0.00	0.00	0.00	1.73	0.00	0.00
4	22	MEAN	3.23	9.68	3.14	35.18	25.32	0.95	0.05	0.50	0.86	0.05	0.09	0.05	0.00
		SE	0.83	1.93	1.02	9.11	3.20	0.56	0.05	0.25	0.49	0.05	0.09	0.05	0.00
5	39	MEAN	5.51	2.90	5.77	49.49	0.10	3.36	1.72	0.38	1.51	0.08	0.10	0.28	0.00
		SE	0.94	0.64	0.94	8.22	0.10	2.48	0.62	0.13	0.31	0.06	0.05	0.18	0.00

The first site group appears to be characterised by *L. adalaidensis*, Zygopterans and no, or very few, *G. holbrooki*, and contains mainly September samples taken from both lakes. The second and third groups consist of September samples only. The second group appears to be characterised mainly by *Crinia* spp., *G. holbrooki* (although present at only 2 out of 10 sites in this group), *L. dorsalis* and comparatively low abundances of a variety of macroinvertebrates, sampled predominantly from Lake Jandabup, while the third group is characterised by *Crinia* spp. and *P. olorum* sampled from Lake Gwelup. The fourth site group consists of samples taken from Lake Gwelup exclusively, and is characterised mainly by species listed in group one of the species groups, with high *G. holbrooki* and *P. olorum* abundances. These are predominantly November and January sites. The last group consists mainly of Lake Jandabup sites, and is characterised by the same species assemblages as in group 4, however, predominantly without *P. olorum*, and very high *G. holbrooki* abundances. The sites in the last group are also a combination of November and January sites.

The classifications and dendrograms of sites which were carried out without *P. olorum*, without *P. olorum* and macroinvertebrates, and with tadpoles only are not presented here, however, Tables 3.12 - 3.14 show the average number of animals and standard errors which were calculated for each group from the two-way tables constructed from the raw data. These were

also used for the interpretation of the ordinations presented in Section. 3.5.5.2. Prior to the classification of sites based on tadpoles only, twelve sites were masked out as these did not contain any species.

Table 3.12: Two-way data matrix showing site and fauna groupings based on UPGMA classifications of sites and fauna, excluding *P. olorum*. Average number of animals (including SE) sampled per group are given.

Group Number	No. of sites		<i>L. adalaidensis</i>	Zygoptera	Anisoptera	<i>G. holbrooki</i>	Hirudineae	<i>Crinia spp.</i>	Col. adult	Col. larvae	<i>H. eyrei</i>	<i>L. dorsalis</i>	<i>Cherax q.</i>	<i>L. moorei</i>
1	16	MEAN	13.13	17.00	0.25	0.44	0.06	0.31	1.31	0.69	0.13	0.25	0.06	0.00
		SE	2.63	3.14	0.11	0.44	0.06	0.15	0.63	0.25	0.13	0.19	0.06	0.00
2	14	MEAN	0.71	3.43	0.21	8.79	3.86	25.79	1.79	0.57	1.00	4.55	1.29	0.00
		SE	0.32	1.52	0.15	4.78	1.83	8.76	0.58	0.31	0.49	1.73	0.56	0.00
3	5	MEAN	0.00	13.60	0.20	10.60	2.40	1.00	0.00	1.80	0.00	0.00	0.00	0.00
		SE	0.00	3.97	0.20	7.94	1.91	0.55	0.00	0.80	0.00	0.00	0.00	0.00
4	2	MEAN	0.00	0.50	0.00	0.00	0.00	2.00	1.00	0.00	0.00	0.00	0.00	0.00
		SE	0.00	0.50	0.00	0.00	0.00	1.00	1.00	0.00	0.00	0.00	0.00	0.00
5	58	MEAN	5.03	5.26	5.19	45.29	1.21	2.33	1.66	0.43	0.00	0.07	0.09	0.21
		SE	0.70	0.90	0.73	6.50	0.23	1.67	0.54	0.13	0.00	0.04	0.04	0.12

Table 3.13: Two-way data matrix showing site and fauna groupings based on UPGMA classifications of sites and fauna, using tadpoles and *G. holbrooki* only. Average number of animals (including SE) sampled per group are given.

Group Number	No. of sites		<i>L. adalaidensis</i>	<i>G. holbrooki</i>	<i>H. eyrei</i>	<i>Crinia spp.</i>	<i>L. dorsalis</i>	<i>L. moorei</i>
1	16	MEAN	13.13	0.44	0.13	0.31	0.25	0.00
		SE	2.63	0.44	0.13	0.15	0.19	0.00
2	21	MEAN	0.52	8.52	0.67	22.62	2.43	0.29
		SE	0.22	3.39	0.34	7.21	1.23	0.29
3	1	MEAN	0.00	0.00	0.00	0.00	0.00	0.00
		SE	0.00	0.00	0.00	0.00	0.00	0.00
4	57	MEAN	5.11	46.04	0.00	0.53	0.07	0.11
		SE	0.71	6.59	0.00	0.28	0.04	0.06

Table 3.14: Two-way data matrix showing site and fauna groupings based on UPGMA classifications of sites and fauna, using tadpoles only. Average number of animals (including SE) sampled per group are given.

Group Number	No. of sites		<i>L. adelaidensis</i>	<i>L. moorei</i>	<i>H. eyrei</i>	<i>Crinia</i> spp.	<i>L. dorsalis</i>
1	18	MEAN	3.5	0.667	0.111	0.222	0.167
		SE	0.601	0.37	0.111	0.129	0.121
2	41	MEAN	10.68	0	0	0.268	0.122
		SE	1.228	0	0	0.116	0.08
3	15	MEAN	0.533	0	0.8	22.13	0
		SE	0.291	0	0.46	8.078	0
4	5	MEAN	0.4	0	0.4	28.4	10.2
		SE	0.4	0	0.4	19.38	3.426
5	4	MEAN	0.25	0	0	5.25	0
		SE	0.25	0	0	3.326	0

3.5.5.2 SSH multidimensional ordination of faunal assemblages and principal axis correlation (PCC) of environmental variables

An initial ordination of 95 sites based on all fauna (abundances) required three dimensions to adequately describe the data (stress = 0.124), and is presented in Figure 3.12 (a). This ordination gave very good separation of the two lakes. Separation of seasons was also good for the September samples, while the November and January samples tended to be intermixed. Correlations of the environmental variables with the ordination of the fauna are displayed in Figure 3.12 (b). Correlation coefficients were: pH top 0.77, pH bottom 0.78, depth 0.71, temperature top 0.65, temperature bottom 0.65, distance from shore 0.59, habitat type 0.50, D.O. top 0.33, and D.O. bottom 0.35. The correlations for pH, depth and temperature are relatively strong, indicating that these environmental variables correspond well with the site groupings. Distance from shore and habitat type correspond moderately with the site groupings, while the correlation for D.O. is poor.

Because separation of the two lakes in the ordination was thought to be largely an artefact of the single species not common to both (*Pseudogobius olorum*, which is restricted to Lake Gwelup), a further ordination was carried out without this species. This ordination, along with the correlations with environmental variables, is presented in Figure 3.13 (a) and (b). Three dimensions were again required to reduce stress to an acceptable level (0.145). Separation of lakes in this ordination was now poor, although some September Jandabup sites still formed a separate group. Seasonal separation was very similar to the ordination which included *P. olorum*, with the September sites forming a separate entity, while the November and January sites tended to be intermingled. Exclusion of *P. olorum* resulted in the correlation coefficients of all environmental variables dropping. pH, which previously had a strong correlation with the ordination space, dropped to a very low 0.20 (top) and 0.24 (bottom), as did the correlation for habitat type (0.24), indicating that these environmental variables now do not correspond with the way sites are grouped. The correlation coefficients for depth (0.65) and temperature (top 0.60, bottom 0.63), although also lower than previously, still corresponded relatively well with the site groupings. Distance from shore (0.40) and D.O. (top 0.25, bottom 0.23) correlated poorly with the ordination space.

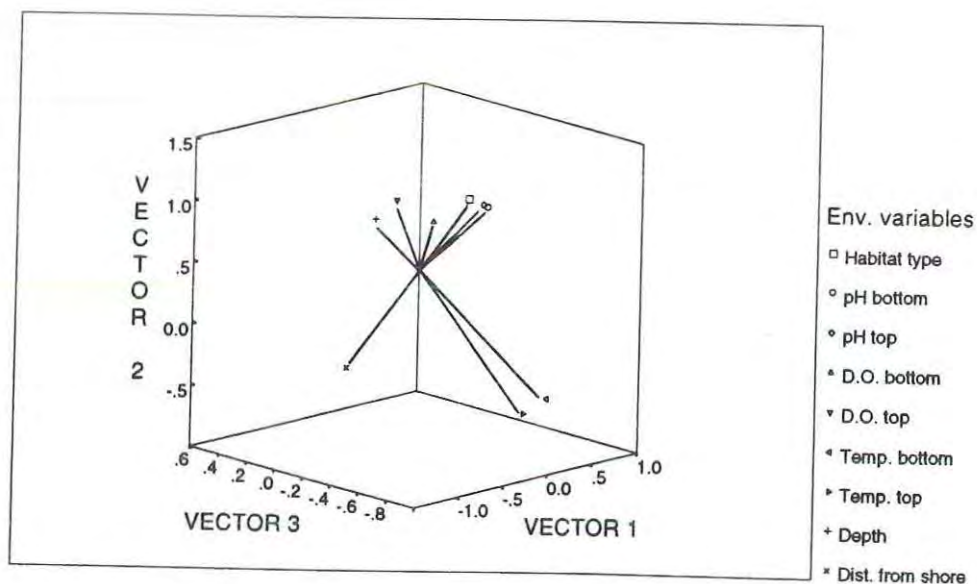
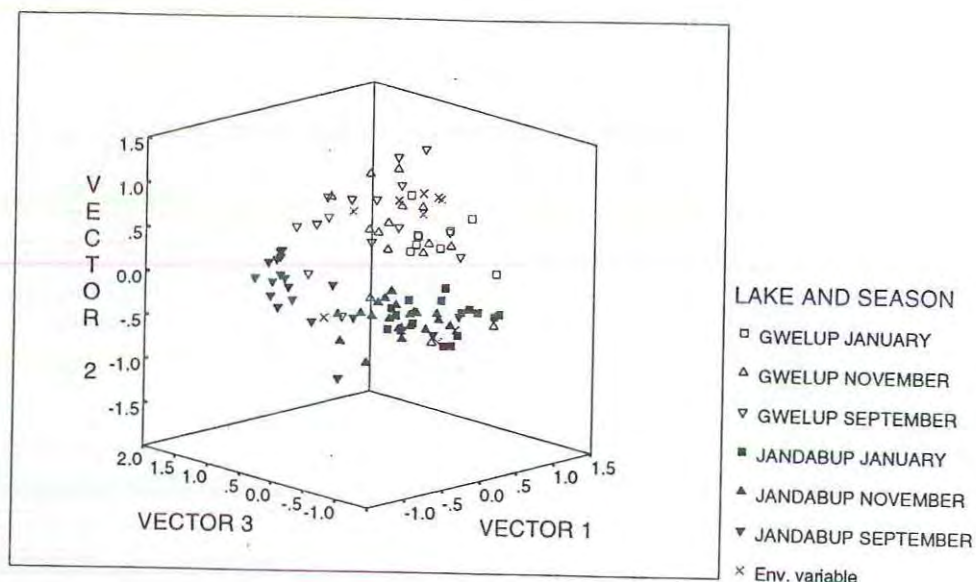


Figure 3.12: SSH Ordination of sites sampled in September 1996, November 1996 and January 1997 at Lake Jandabup and Lake Gwelup, using all fauna. (a) Separation by season and lake. (b) Directions of maximum linear correlations with environmental variables.

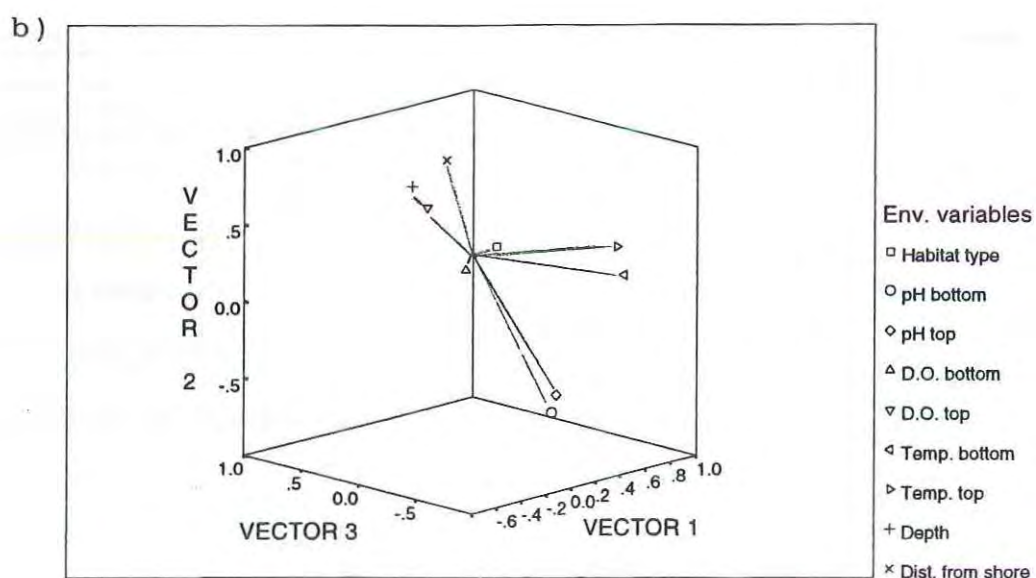
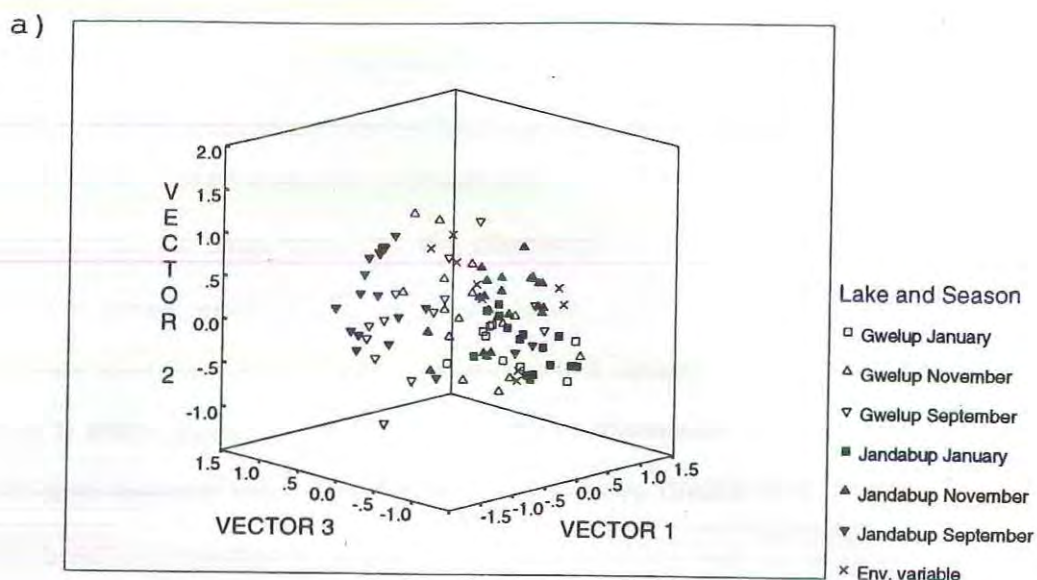


Figure 3.13: SSH Ordination of sites sampled in September 1996, November 1996 and January 1997 at Lake Jandabup and Lake Gwelup, with *P. olorum* excluded. (a) Separation by season and lake. (b) Directions of maximum linear correlations with environmental variables.

A further ordination was carried out with tadpoles and *G. holbrooki* only in order to be able to assess what influence macroinvertebrates are having on the clustering of sites. This ordination required only two dimensions in order to achieve an acceptable stress level (stress = 0.138), and is displayed in Figure 3.14. Correlations of the environmental variables with the ordination of sites based on tadpoles and *G. holbrooki* are projected directly onto this ordination. As with the previous ordination which included macroinvertebrates, seasonal patterns are more evident than separation of the two lakes. Generally, the site groupings are similar to those shown in Figure 3.13. Four groups, which roughly correspond to the UPGMA classification groups (see Table 3.13), were identified. The majority of November and January sites group into a dense cluster (group 1) which appears to be characterised by *L. adalaidensis* and high *G. holbrooki* numbers. A rough seasonal trend from November to January (Vector 2) is evident in this cluster. This trend is characterised (again roughly) by relatively high *L. adalaidensis* and moderate *G. holbrooki* numbers towards (upwards on Vector 2) progressively lower *L. adalaidensis* numbers but higher *G. holbrooki* numbers. The September sites display one relatively dense cluster (lower end of both vectors, group 2) involving mainly Lake Jandabup sites characterised predominantly by *L. adalaidensis* tadpoles and the absence of *G. holbrooki*. Another looser group of September sites (group 3) is characterised by *Crinia spp.*, *H. eyrei*, very few *L. adalaidensis* and either no *G. holbrooki*, or very high numbers of *G. holbrooki*. The center of this group is composed of sites with very high numbers of both *Crinia spp.* tadpoles and *G. holbrooki*. The upper and lower ends of this group are sites with no *G. holbrooki*, the upper end being composed of *Crinia spp.* and *L. dorsalis*, the lower by *Crinia spp.* and *H. eyrei*. A last, loose group of sites (group 4) is again mainly characterised by no, or very few, *L. adalaidensis*, but all with relatively high numbers of *G. holbrooki* and *Crinia spp.*

Correlations of the environmental variables with the ordination of tadpole and *G. holbrooki* abundances again all dropped further (depth 0.54, temp. top 0.47, temp. bottom 0.52, distance from shore 0.39, D.O. top 0.27, D.O. bottom 0.24, pH top 0.17, pH bottom 0.21, and habitat type 0.16), indicating that patterns in spatial and temporal distribution of macroinvertebrates between the two lakes differ.

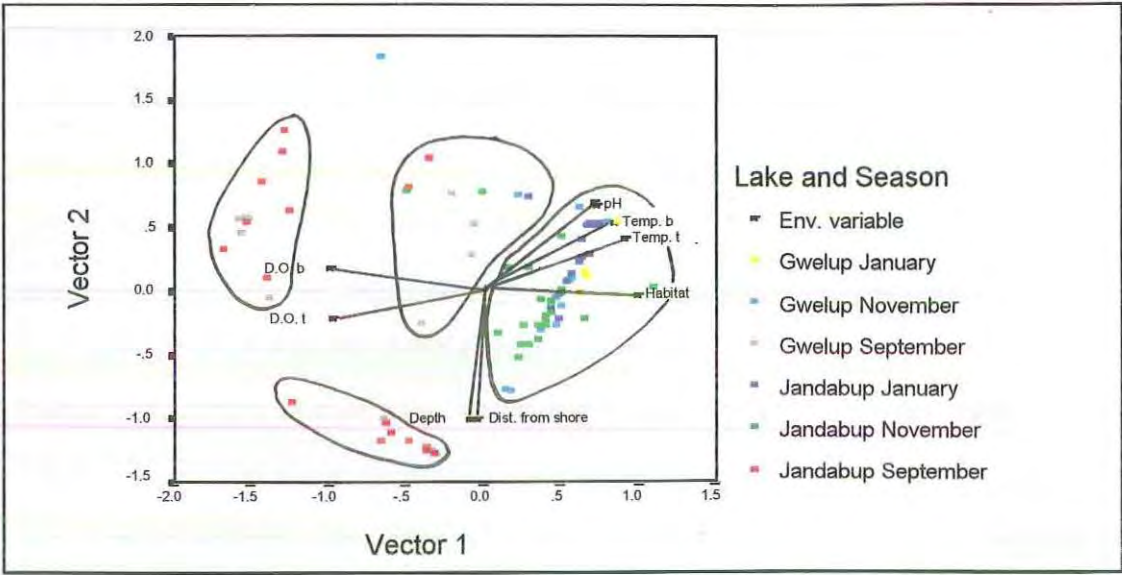


Figure 3.14: SSH Ordination of sites sampled in September 1996, November 1996 and January 1997 at Lake Jandabup and Lake Gwelup, based on tadpole and *G. holbrooki* abundances only. Directions of maximum linear correlations with environmental variables are also shown.

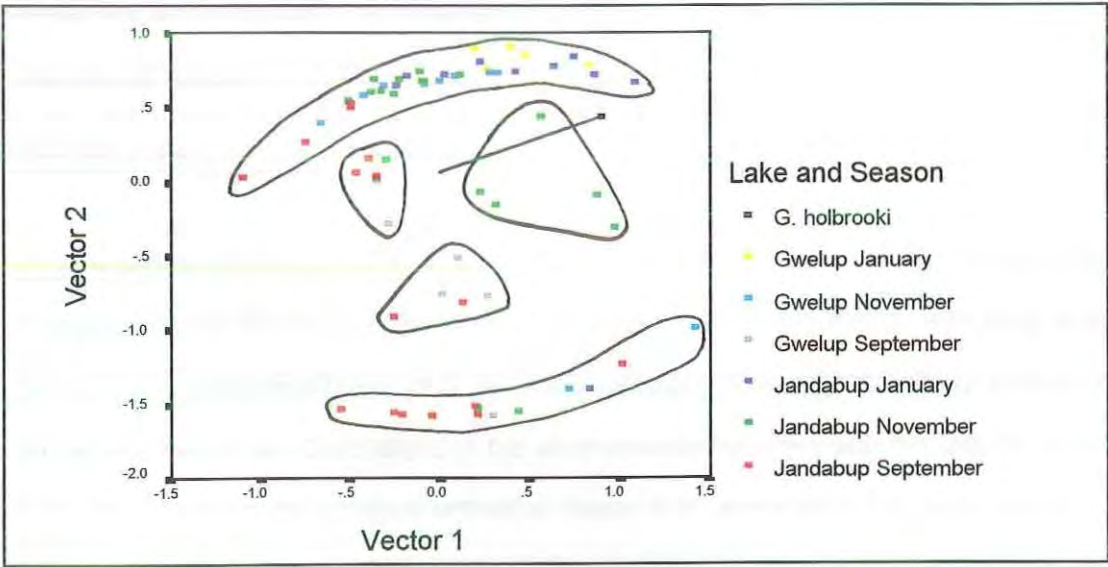


Figure 3.15: SSH Ordination of sites sampled in September 1996, November 1996 and January 1997 at Lake Jandabup and Lake Gwelup, based on tadpole abundances only. Direction of maximum linear correlation with the ordination based on *G. holbrooki* abundances is also shown.

The ordination of sites based on tadpole abundances only is shown in Figure 3.15. As with the previous ordination, only two dimensions were required, the stress level dropping to 0.112. Onto this ordination is projected the correlation with the ordination of sites based on *G. holbrooki* abundances. Twelve sites in which no tadpoles were present were not included in this ordination. This ordination clearly displays the segregation between *L. adelaidensis* and *Crinia* spp. tadpoles which was also evident when sites were assigned to specific habitat types (see Section 3.5.2). Five clusters were identified from the ordination, and are superimposed in Figure 3.15. The first is a group of sites in which *Crinia* spp. only were sampled. Group two are sites in which relatively high numbers of *Crinia* spp. co-occurred with very low numbers of *L. adelaidensis*. Most of these sites also supported either *L. dorsalis* or *H. eyrei*. A third group of sites is characterised by high *L. adelaidensis* and low *Crinia* spp. numbers. Adjacent to this group, is a looser cluster (group 4) also consisting of high *L. adelaidensis* and low *Crinia* spp. numbers, but with *L. moorei* also present. The largest group of sites, which also shows a seasonal trend, consists of *L. adelaidensis* and no *Crinia* spp. Towards the low end of Vector 1 are sites consisting of *L. adelaidensis* in association with either *L. dorsalis* or *H. eyrei*. In the center are sites with high *L. adelaidensis* abundances (and no other species), and towards the high end of Vector 1 are sites consisting of low numbers of *L. adelaidensis* (and no other species).

The correlation of the ordination of sites characterised by *G. holbrooki* abundances with the ordination based on tadpole abundances was relatively strong (0.62), indicating that the temporal and spatial distribution of *G. holbrooki* corresponds well with the site groupings based on tadpole distribution. Correlations of the environmental variables with the tadpole ordination were very similar to the previous ordination (depth 0.55, temp. top 0.29, temp. bottom 0.33, distance from shore 0.39, D.O. top 0.31, D.O. bottom 0.27, pH top 0.17, pH bottom 0.20, and habitat type 0.28).

3.6 Discussion

3.6.1 Faunal abundances

Overall, tadpole abundances were higher at Lake Jandabup than at Lake Gwelup. It is possible that this is related to overall habitat complexity, which is greater at Lake Jandabup. However, it is more likely that the areas surrounding Lake Jandabup provide better habitat for adult frogs, than the built up area surrounding Lake Gwelup, and therefore, the higher abundances of tadpoles per site observed at Lake Jandabup is probably related to the larger number of adult frogs present (and corresponding better recruitment). The distribution of *Crinia* spp. tadpoles, although the most abundant of all of the tadpoles sampled, was extremely patchy in both lakes. They appear to be strong microhabitat specialists, preferring to utilise temporarily inundated sites which become available at both permanent and seasonal lakes in winter and spring. These sites are typically shallow, warm and moderately vegetated with herbaceous plants. In the literature, it is reported that *Crinia glauerti* breed throughout the year after rain, except in the middle of summer (Main, 1965, W.A. Museum, 1995). If it is true that larval life is longer than 100 days (Main, 1965; *Crinia glauerti* tadpoles reared from eggs in the lab required 2½ months to completely metamorphose), and it did rain on a number of occasions in November and December, then it is somewhat surprising that practically no tadpoles were sampled in middle January. As *Crinia glauerti* tadpoles and *G. holbrooki* have very similar habitat preferences, it is difficult to dismiss the suspicion that predation by *G. holbrooki* may be playing a role in this absence.

L. adalaidensis tadpoles, almost as abundant as the *Crinia* tadpoles, displayed a more even spatial distribution, as reflected by lower standard errors (see Figure 3.6). Although possibly related to the particular weather conditions in spring/early summer 1996, this species appears to have a more extended breeding period than reported in the literature. This potentially puts *L. adalaidensis* tadpoles at higher risk of co-occurring with *G. holbrooki*. The reason why the seasonal variation in abundances of *L. adalaidensis* tadpoles was more marked at Lake

Jandabup, than at Lake Gwelup, is because large areas of *L. adelaidensis* habitat at Lake Jandabup had dried up by January. Despite this, overall abundances of this species were higher at Lake Jandabup than at Lake Gwelup in January.

In this survey, tadpoles of the larger frogs, that is, *H. eyrei*, *L. dorsalis* and *L. moorei*, were sampled a lot less frequently than tadpoles of the smaller frogs. Large tadpoles swim faster, and are therefore more likely to be able to evade a net, than smaller tadpoles. Hatchlings of these species, however, are very small, yet even these were sampled infrequently. For *H. eyrei*, this is not surprising, due to the early breeding season of this species, and the method of egg deposition (in burrow). *L. dorsalis* breed mainly from early winter to early spring (Main, 1965), however, this may extend into early summer (W.A. Museum, 1995). As development is slow, tadpoles should have theoretically been present in the lakes in higher numbers in September and November. It is possible that this species prefers to dwell in deeper water, than that sampled in this survey. This would also explain why more *L. dorsalis* were captured at Lake Jandabup than at Lake Gwelup. At Lake Gwelup the littoral zone is narrow, making access to deeper water easier for both the frogs and the tadpoles (but more difficult for the aquatic researcher). Nevertheless, *L. dorsalis* tadpoles were netted in a number of sites at Lake Jandabup in September in very shallow water (in association with *Crinia* tadpoles and *G. holbrooki*). However, these were very large tadpoles, and in this respect, it is unlikely that they would be adversely affected by the presence of *G. holbrooki*.

In terms of timing and location of egg deposition, the hatchlings of *L. moorei* tadpoles are potentially very susceptible to predation by *G. holbrooki*. The fact that so few of these tadpoles were sampled in this survey is reason for concern. However, it must be noted that *L. moorei* are long-lived frogs, and do not necessarily breed every year (K. Aplin, pers. comm.).

The exponential increase in *G. holbrooki* numbers observed from September to January in both lakes accords with reports in the literature about the life history of this species (for example, Krumholz, 1948, Lloyd *et al.*, 1986, Pen and Potter, 1991, Trendall, 1982). The fact that relative abundances were very similar in both lakes, despite the differences between the two lakes (that

is, the extent of drying at Lake Jandabup is of an order of magnitude greater than at Lake Gwelup), is interesting. As this fish is extremely fecund (Arthington and Mitchell, 1986), it appears that the number of surviving offspring is related to the availability of resources, rather than to the size of the founder population. Another interesting observation made in this survey was that the progressively higher relative abundances of *G. holbrooki* observed from September to January was accompanied by a wider, and more even, spread of this fish within the wetlands. This is most likely to be related to water temperature. It indicates that the warmer water temperature is, the less important habitat type becomes in the distribution of this species. This is reflected in the low correlations for 'habitat type' and high correlations for water temperature in the ordinations presented in Section 3.5.5.2.

The fact that an introduced predator is more abundant than groups of naturally occurring macroinvertebrate predators, is in itself reason for concern. However, even if *G. holbrooki* do prey on tadpoles, it cannot be concluded that the fish are therefore more important predators of tadpoles than macroinvertebrates, as this would depend on many other factors (eg. the availability of alternative prey, prey preferences, microhabitat utilisation, etc.). Because abundances, as well as seasonal trends, of most macroinvertebrate groups differed not only between the two lakes, but also among the different groups, it is very difficult to speculate about what possible secondary effects might be occurring by having an introduced predator in the system. Anisopteran naiads, which are important predators of tadpoles (eg. Barrett, 1995), were the only macroinvertebrate group which appeared to follow a similar seasonal trend in abundances as *G. holbrooki* in both lakes. These animals are 'sit-and-wait' predators, usually remaining motionless and well concealed within benthic debris, before ambushing their prey. *G. holbrooki*, on the other hand actively pursue and attack prey, mainly close to the water's surface, but also within the entire water column (Pen and Potter, 1991). It could be speculated that, in habitat types where both Anisopteran naiads and *G. holbrooki* occur, these differential predatory tactics leave tadpoles with no opportunity to alter microhabitat utilisation in order to avoid predation, as all microhabitats are occupied with predators.

3.6.1.1 Aquatic funnel traps

All local tadpole species were captured with the funnel traps. However, as overall more species, and higher numbers of each species, were captured with the dipnet at individual sites, trapping is not considered to be an efficient method for estimating tadpole species richness or diversity, if it is used on its own. However, Calef (1973), has shown that the tadpole population size of a single species in an entire lake can be estimated by calibrating capture success of traps against known number of tadpoles in enclosures.

It is interesting to note that *L. dorsalis* and *L. moorei*, which were captured least frequently with the dipnet, had similar capture success rates for both methods. This suggests that relative abundances of these tadpole species based on net captures should be treated with caution. As traps proved useful in detecting the presence of tadpole species which the net missed on 11 (or in just over a quarter of all sites in which traps were erected) occasions, it is certainly recommended to use traps, whenever possible, in conjunction with other sampling methods. The traps were also considered useful for sampling areas which were too densely vegetated, or too deep, to sample using a conventional dipnet.

3.6.2.2 Calibration trials

The findings of the calibration trials carried out in this study correspond only in part with Shaffer *et al.*'s. (1994) conclusion, that dipnets capture a rather constant fraction of tadpoles present, and that the proportion captured is species-specific.

In the present study it was found that, firstly, the proportion of *G. holbrooki* captured with a set number of sweeps in open and closed (calibration) quadrats differed depending on water depth/density of the animals present. At sites in which fish density was high, fish abundances tended to be underestimated in open quadrats, while in lower density sites they tended to be overestimated. Secondly, the proportion of *Crinia* tadpoles captured in open and closed quadrats was very similar. This suggests that in sites where *Crinia* tadpoles and *G. holbrooki* co-occurred, the ratio of tadpoles to *G. holbrooki* was likely to be overestimated. Thirdly, for *L.*

adelaidensis, the proportion of tadpoles captured in open and closed quadrats was also more or less similar in the higher density site, but was much lower in the low density open site. In both cases, it appears that the ratio of tadpoles to fish would be likely to be underestimated in open quadrats.

In comparing closed and open quadrats, it should be borne in mind that only 'similar', and not 'identical' sites were compared, and therefore differences were bound to occur. Unfortunately, because it is time consuming and laborious to conduct such trials, no replicate trials were carried out, and not all tadpole species could be covered. The results of these trials, therefore, only give an indication of the fraction of tadpoles and fish captured by the dipnet. It is recommended to repeat such trials as, apart from being very useful for calibrating dipnet catches, they also provide valuable insight into absolute densities of local tadpoles, about which very little is known. For example, it has not previously been documented that *Crinia* tadpoles can occur at such high densities as they were encountered in the calibration trial carried out at Lake Jandabup.

The number of sweeps employed in each quadrat is considered to have been adequate because (as mentioned in Section 3.3.3) it was sufficient to cover the surface area and water column of the whole quadrat. Twenty (plus five for fish) sweeps is a high number of sweeps and it would not have been practical to increase it, particularly as in the less dense sites often nothing was caught after the first ten or so sweeps. Furthermore, in relation to the calibration trials, increasing the number of sweeps would not have achieved much, as these, too, would have had to be calibrated.

3.6.2 Distribution of fauna within habitat types

L. adelaidensis and *Crinia* tadpoles were found to be strongly habitat specific, while the same cannot be concluded for the other tadpole species due to the lower numbers sampled. What is most apparent in the distribution of tadpoles within habitat types is that all tadpole species were found to co-occur with *G. holbrooki* in one or more of the sampling occasions. *L. moorei* always

co-occurred with this fish (although, as mentioned in the previous section, very few tadpoles of this species were sampled). For most tadpole species, relative abundances of tadpoles tended to decrease, as relative *G. holbrooki* abundances increased from September to January. There may be two reasons for this. Given that the main breeding activity of most of the frog species is in winter/spring, it may be a reflection of the natural seasonal fluctuations in tadpole numbers, that is, as the seasons progress, more of the tadpoles would have emerged. Alternatively, the presence of *G. holbrooki* may be amplifying the seasonal fluctuations in tadpole numbers. Long-term field surveys will be necessary to determine which is the case.

There were habitat types in September in both lakes (see Tables 3.4 - 3.7) in which all tadpole species (apart from *L. moorei*) had the opportunity to develop without the presence of *G. holbrooki*. However, these were not necessarily the preferred habitat types of some species. *Crinia* tadpoles (which tended to occur at very high densities), for example, almost always co-occurred with large numbers of *G. holbrooki*. Although it is possible that tadpoles and fish would be utilising different sections of the water column, water depth in these sites was usually very shallow (> 15 cm). It is therefore difficult to imagine that interactions would not occur.

3.6.3 Temporal and spatial patterns

Although *G. holbrooki* and *Crinia* tadpole numbers were positively correlated, the groups identified from the classification of species (see Section 3.5.5.1) clearly showed that in fact *L. adelaidensis* tadpoles were more often found in association with *G. holbrooki*, than *Crinia* tadpoles. This is presumably because *L. adelaidensis* was the most commonly sampled species in January when *G. holbrooki* was most abundant, and present at every site.

Once *P. olorum* (the only species not common to both lakes) was excluded, the ordinations showed stronger separation of seasons than separation of the two lakes. From this it is concluded that faunal assemblages based on tadpole, *G. holbrooki* and macroinvertebrate predator abundances are similar in both lakes. This is despite the presence of other fish species at Lake Gwelup, and the fact that one lake is permanent and the other more seasonal.

Therefore, the impact *G. holbrooki* on local tadpoles, if any, does not differ significantly between Lake Gwelup and Lake Jandabup. However, this conclusion cannot be generalised for all permanent and seasonal wetlands, as the lakes were not replicated in this study. It is possible, for example, that the availability of shallower habitat at Lake Jandabup compensates for smaller population crashes which probably occur at the end of the season at Lake Gwelup.

Although separation of lakes in general was not strong, the seasonal separation of sites was stronger for Lake Jandabup than for Lake Gwelup (see in particular Figure 3.14). This is a reflection of the seasonal drying which was much more extensive at Lake Jandabup.

pH strongly correlated with the first ordination which included all species because the separation of lakes evident in this ordination strongly reflected the differences in pH between the two lakes. Lake Jandabup has low, while Lake Gwelup has high pH. The low correlation with pH in the following ordinations indicates that fluctuations within the range of 4.93 (lowest measured at Lake Jandabup) and 9.40 (highest measured at Lake Gwelup) do not greatly influence the distribution of local tadpoles or *G. holbrooki*.

Likewise, the differences in habitat type between the two lakes was not reflected by the way sites were grouped, once *P. olorum* was excluded from the ordination. The (manual) assignment of sites to specific habitats (see Section 3.5.3) showed that certain faunal assemblages were associated with specific habitat types, and therefore the relatively low correlations of habitat type with the ordinations which excluded *P. olorum* were somewhat surprising at first. However, it appears that the low correlations with habitat type are a reflection of the patchy distribution of the fauna within the different habitat types (as shown by the high standard errors, see Tables 3.7 - 3.10). Depth and temperature were correlated well with all of the ordinations, indicating that these environmental variables were important in determining the spatial and temporal distribution of tadpoles and *G. holbrooki*. Depth and temperature also corresponded better with the distribution patterns of the fauna than habitat type, because habitat type remained more or less the same, while depth and temperature changed with season, along with the faunal abundances. The good correlation of the distribution of *G.*

holbrooki with the distribution of tadpoles is again an indication of significant microhabitat overlap between this introduced fish and local tadpoles.

4. Synthesis

4.1 General

The feeding trials carried out in this study have shown that tadpoles (and for *L. adelaidensis* also eggs) of local frog species were consumed or injured by *G. holbrooki*. There were differences in survival and consumption rate between tadpole species and between larval developmental stages, but as significantly more of the early stage (that is, small) than later stage tadpoles were taken, and all fish survived their ingestion, these differences were attributed to the gape limitation of the predator, rather than to differences in palatability of the prey. Because the experiments were carried out in a highly over-simplified environment, extrapolation of conclusions to potential interactions in the field cannot be made without careful consideration of other influencing factors. It was, for example, not possible to observe the full range of anti-predation behaviours of the tadpoles, a factor which would certainly influence the outcome of potential predation in the field. However, experiments which isolate a single predator-prey relationship can never be truly representative of the natural situation, no matter how elaborate the experimental design.

The relatively extensive field survey carried out in this study revealed that microhabitat utilisation of *G. holbrooki* and some local tadpole species is overlapping, and thus there is a potential for interactions to occur between the fish and these tadpoles. Without the information provided by the feeding trials, it would not have been possible to sensibly evaluate observations made in the field, and likewise the relative significance of the experimental results could not have been assessed without knowing whether the species concerned co-occur in nature. In order to be able to construct scenarios of potential interactions between these species in the field, the combined results of both of these research components must be assessed in the light of other influencing factors such as the phenology (seasonal timing of breeding and occurrence of peak densities) of the tadpoles and *G. holbrooki*, the availability of alternative prey and, as mentioned above, predator defense behaviours displayed by the tadpoles.

One difficulty in the interpretation of the field survey results is that, although increased fish abundance generally coincided with decreased tadpole abundances, it is very problematic to pinpoint exactly at which point this constitutes natural, seasonal fluctuations in tadpole abundances, and at which point potential predator-induced fluctuations are involved. Another obvious limitation of the field survey is that the availability of alternative prey was not investigated. As discussed in Section 3.1, the extent of predation by *Gambusia* on a given prey species depends on the availability of alternative prey. This is something that will have to be incorporated into future research if the true impact of *G. holbrooki* on local tadpole species is to be determined. In a survey of wetlands of the Swan Coastal Plain, Balla and Davis (1993) found that aquatic invertebrate species richness was generally highest in spring, and abundance and biomass were lowest in autumn. Invertebrate abundance was considered to be comparatively low at Lake Jandabup (although species richness was high). In this case, progressively higher *G. holbrooki* abundance would coincide with progressively lower invertebrate abundance, thus increasing the likelihood of this fish preying on tadpoles (if present). It should also be considered that the impact of *G. holbrooki* on tadpoles could be indirect. The depletion of other prey (Cladocerans, etc.) sources by *G. holbrooki* might in fact be diverting macroinvertebrate predators to increase predation on tadpoles. Alternatively, by hiding or altering microhabitat use in order to avoid predation, tadpoles may die from starvation. Other indirect effects of predation are discussed in Section 1.7.

Bearing the above factors in mind, the relative significance of this research for the individual frog species concerned is discussed below.

4.2 Significance for *Crinia* spp.

It is not considered likely that *Crinia insignifera* or *C. glauerti* eggs would be susceptible to predation by *G. holbrooki*. Although *C. glauerti* tadpoles, and therefore probably also eggs were found to co-occur with relatively large numbers of *G. holbrooki*, the position of the eggs (laid singly or in small clumps which sink to the bottom, Main, 1965) probably make it very difficult

for a surface feeding fish to detect. It was observed in the laboratory that fish pellets which had sunk to the bottom of the aquarium, and which had a similar diameter (approx. 1.3 mm) to *Crinia* eggs were totally ignored by the fish. Even when the fish were not fed for 2 or 3 days, the pellets were left lying on the bottom. This feeding behavioural aspect of *G. holbrooki*, as well as the fact that *Crinia* eggs are well camouflaged within the substrate, suggests that predation by *G. holbrooki* on these eggs is not probable, even if they were palatable.

However, *Crinia* tadpoles were consumed by *G. holbrooki* in the laboratory trials, and even relatively large tadpoles were fatally injured. As discussed in Section 3.6.1 and 3.6.2, in preferred habitat types these tadpoles occurred together with high *G. holbrooki* abundances in September and November at which time peaks in *G. holbrooki* abundance in the wetlands had not yet been reached. The effect of potential predation by *G. holbrooki*, however, need not necessarily be negative. As *Crinia* tadpole numbers were positively correlated with *G. holbrooki* numbers, it is possible that predation by *G. holbrooki* may in fact be increasing survival of the tadpoles by reducing density pressures. It is well documented in the literature that predation can reduce the intensity of competitive interactions among tadpoles. Reducing competition among tadpoles permits the survivors to grow rapidly enough to escape a drying pond (Wilbur, 1980). Gascon and Travis (1992) found that at low tadpole densities the addition of predators (dragonfly naiads) decreased tadpole survival rates significantly, but at high tadpole densities they increased them significantly. Morin (1986), on the other hand, discovered that predatory salamanders failed to reduce competition substantially among larval *H. crucifer*, because tadpoles altered their microhabitat use to avoid predators. Again, research involving *G. holbrooki* and tadpoles of *C. insignifera* and *C. glauerti* will be necessary in order to describe the outcome of competition among, and the effect of predation by *G. holbrooki* on these tadpoles.

The absence of *Crinia* tadpoles in January may have four possible explanations. The most likely is that all of the tadpoles have successfully emerged from the water by January. The second possibility is that predation by *G. holbrooki* eliminated all tadpoles by January. The third possibility is that predation pressure by *G. holbrooki* may have prompted a shift in breeding

activity in the frogs to avoid high fish densities in summer, and the fourth might be that the tadpoles developed more quickly in the presence of high predator densities. These are all ideas which might be formulated into tangible hypotheses in order to be tested in the future.

4.3 Significance for *Litoria adelaidensis*

In the feeding trials carried out in this study *L. adelaidensis* eggs and tadpoles were consumed by *G. holbrooki*. *L. adelaidensis* commence breeding in late winter (Main, 1965) and, at Lake Jandabup in 1996, this extended into early summer. Although eggs were still encountered in early December at Lake Jandabup, and early stage tadpoles were still observed at Lake Gwelup in January, the main breeding event appeared to be in September, when relatively large quantities of eggs were encountered (particularly at Lake Jandabup). At this time no *G. holbrooki* were observed in the main breeding areas at Lake Jandabup, however, low densities were present at Lake Gwelup. *L. adelaidensis* eggs are laid in small clusters and are attached to stems of aquatic vegetation below the surface of the water (Main, 1965). At Lakes Jandabup and Gwelup eggs were found between 5 and 15 cm below the surface of the water. As the eggs appear somewhat elongated, and are loosely attached to vegetation, it is possible that water currents would cause these to move, which may in turn attract *G. holbrooki*. It is unlikely that eggs deposited early in the breeding season would be seriously impacted by *G. holbrooki* due to their absence (or low densities) from habitat types preferred by *L. adelaidensis*. Likewise, *L. adelaidensis* hatchlings (which were shown to have high mortality in the presence of *G. holbrooki* under experimental conditions) occurring early in the season would have an advantage over later occurring ones, as *G. holbrooki* numbers not only increase as water temperature warms towards summer, but the fish were also shown to be present in every habitat type occupied by these tadpoles.

As discussed for the *Crinia* tadpoles, research will also have to be carried out involving *L. adelaidensis* in order to describe the outcome of competition among, and the effect of predation by *G. holbrooki*, as these tadpoles usually co-occurred with *G. holbrooki* at much

lower densities than did the *Crinia* tadpoles, and would therefore, by corollary to Morin's (1986) work, be more likely to be adversely affected by predation by this fish.

4.4 Significance for *Litoria moorei*

In this study, *Litoria moorei* was always found in association with high *G. holbrooki* densities. *Litoria moorei* may commence breeding in early Spring and extend well into the summer months (W.A. Museum, 1995). However, although males may call over an extended period of time, the main breeding event may occur 'explosively' over a relatively short period of time (M. Cowan, pers. comm.). A large number of eggs are deposited within a highly cohesive jelly envelope and attached to floating or submerged vegetation (Main, 1965). Eggs found at Lake Jandabup in November were deposited onto dense (submerged) introduced grass in warm and shallow water. Unfortunately, it is not known, whether *Litoria moorei* eggs are palatable to *G. holbrooki*. If they were, the timing and position of ovipositing would make these very susceptible to predation by *G. holbrooki*. However, as mentioned above, the highly cohesive jelly surrounding the eggs would make it very difficult for the fish to dislodge them, and the many eggs at the center of the clutch would be protected. It would probably be less energy-consuming and more rewarding for the fish to pick the tadpoles as they hatch free from the nest. Reynolds (1995) established the palatability of *L. moorei* hatchlings.

Because *L. moorei* is closely related to *L. aurea*, a species whose declining populations in eastern Australia have been attributed, at least in part, to predation by *G. holbrooki* (Daly, 1995; Harris, 1995; Morgan and Buttemer, 1996), and so few tadpoles were collected in this survey, it is recommended that adult and larval populations of *L. moorei* be monitored closely in the future. As with *L. aurea* in eastern Australia, the phenology of *L. moorei* is such that it co-occurs with peak *G. holbrooki* abundance during the critical larval stages. In addition to this, both *L. moorei* and *G. holbrooki* tend to be associated with disturbed sites (K. Aplin, pers. comm).

4.5 Significance for *Limnodynastes dorsalis*

Limnodynastes dorsalis breed in late autumn, winter and spring (Main, 1965), when *G. holbrooki* densities are still low. A large number of eggs (>500, M. Cowan, pers. comm.) are deposited on the surface of the water as a foam nest. This is usually hidden beneath overhanging vegetation (W.A. Museum, 1995). The feeding trials carried out in this study provide no conclusive evidence that *L. dorsalis* eggs are palatable to *G. holbrooki* (only 15% mortality). But even if they were, it is unlikely that predation by *G. holbrooki* would be important due to the inaccessibility of the majority of *L. dorsalis* eggs within the floating foam nest, and the seasonality of ovipositing. Although all larval developmental stages of *L. dorsalis* had very high mortality (hatchlings had 100% mortality) in the presence of *G. holbrooki* in the laboratory, it is suspected that the bulk of tadpoles would be protected from predation by this fish, mainly due to early breeding, but also due to the preference of this species for deeper water (see also Section 3.6.1).

4.6 Significance for *Heleioporus eyrei*

Heleioporus eyrei eggs are deposited in burrows where they are not accessible to *G. holbrooki*. Although tadpoles were found in association with low *G. holbrooki* numbers in September, these were very large tadpoles and therefore the potential impact of predation by *G. holbrooki* would probably be minimal.

5. Conclusions and implications for management

This study has provided valuable insight into the microhabitat distribution, as well as relative abundances, of a suite of local tadpoles, about which previously not much was known. Although the more subtle details of microhabitat utilisation, such as timing of diel activity and utilisation of the water column, could not be investigated (as this was beyond the scope of this study), the spatial and temporal distribution of local tadpoles and the introduced predator, *G. holbrooki*, nevertheless indicate that there is considerable potential for interactions to occur for some species. These are *Crinia glauerti*, *C. insignifera*, *Litoria moorei* and *L. adelaidensis*. Feeding trials carried out in this study, and previously by Reynolds (1995), showed that tadpoles (and for *L. adelaidensis* also eggs) of these species were either consumed, or if too large, injured by *G. holbrooki*. It is therefore possible that potential interactions in the field would include predation. There is also a strong potential for *G. holbrooki* to impact local frog populations indirectly by interfering with the natural competitive forces among tadpoles, as well as by altering predation levels of macroinvertebrate predators.

These findings are in contrast with conclusions made by Reynolds (1995). Reynolds hypothesised that, although *G. holbrooki* consumed tadpoles in the laboratory, the effects of predation by *G. holbrooki* on tadpoles in the field would be minimal, because the breeding periods of the majority of local frog species do not coincide with peaks of fish abundance (unlike in eastern Australia, where they do). What the present study has determined, is that although frog breeding periods may not coincide with peaks of fish abundance, suitable microhabitat types may nevertheless be fully saturated with *G. holbrooki*, well before peak fish numbers are reached in the wetland as a whole. It was observed that the concentration of fish in such areas in early September was often greater than fish concentrations later in the season when they started to disperse into deeper water.

It was further established in this study that some frog species (eg., *L. adelaidensis*) can have more extended breeding periods than that reported in the literature. This potentially increases

the risk of small tadpoles co-occurring with higher numbers (and larger individuals) of *G. holbrooki*. It is also suspected that *G. holbrooki* may have a more extended breeding period in Perth lakes than that reported in the literature for some South-west rivers (Pen and Potter, 1991; Trendall, 1981). Aggregations of *G. holbrooki* in shallow water were first observed at Lake Jandabup towards end of July, while at Big Carine Swamp schools of small fish were observed in the middle of June!

This study involved exploratory research and as such has provided a baseline from which future research and long-term field surveys can be conducted in order to determine whether tadpoles found to have overlapping microhabitat distributions with *G. holbrooki* can co-exist with this introduced fish in the long term. Unfortunately, in the meantime the potentially threatening process of predation by *G. holbrooki* on local tadpoles, and its impact on the recruitment of local frogs already under threat by other factors, will continue.

As *G. holbrooki* have been shown to have a negative impact on other components of aquatic ecosystems, research is urgently required into developing realistic eradication methods. Using piscicides (eg. Rotenone[®]) is not a realistic control method as native fish, if present, would also be affected, as would tadpoles (Lannoo, 1996). So far, complete drying of the lake bed appears to be the only way to eradicate *G. holbrooki*. Water level and land management practices of land surrounding seasonal wetlands should therefore allow for the complete drying of these wetlands at least every few years. Lake Jandabup has not completely dried for a number of years. In 1989 and again in 1991, when the lake would have dried completely, the water level was artificially maintained (WAWA, 1994). Balla and Davis (1993) maintain that drying of the lake would not have impacted macroinvertebrate assemblages, as the non-mobile fauna are all able to tolerate drying, while the mobile fauna are not unique to the lake and would have recolonised the following season. Vegetation communities at Lake Jandabup are also adapted to a seasonal water regime. Given the high conservation value of Lake Jandabup, and the fact that there are no surface drains into the lake which might cause re-infestation with fish, it may be a feasible proposition to artificially drain the lake at the end of summer/autumn when water levels are lowest, in order to eradicate *G. holbrooki*. The temporary water breeding frog species

are adapted to this sort of drying, while the loss of the few remaining tadpoles of the permanent water breeding species (*L. moorei* and *L. dorsalis*) would be greatly outweighed by the lack of predation by *G. holbrooki* in the future. In the case of Lake Gwelup, as with other permanent lakes, such drastic measures may be unrealistic.

The negative impacts of *G. holbrooki*, and the doubtful role they play in mosquito control, are now widely acknowledged by wetland managers, and it is therefore assumed that these fish are no longer being intentionally released. However, there still appears to be a general lack of awareness of the public regarding the dangers of releasing introduced fish into local waterways (see eg. Breheny, 1996, Pollard, 1989), an issue which will have to be addressed.

And finally, whether perceived frog declines on the Swan Coastal Plain are real or not, it is always wise to take a precautionary approach. Maintaining healthy, unpolluted and pest-free wetlands will not only benefit frogs, but also all other components of aquatic ecosystems.

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APPENDIX 1

Tadpoles of some frog species occurring on the Swan Coastal Plain



Plate A1.1: *Heleioporus eyrei* tadpole, SL: 50 mm. (Photo by M. Cowan)



Plate A1.2: *Limnodynastes dorsalis* tadpole, SL 85 mm (Photo by M. Cowan)

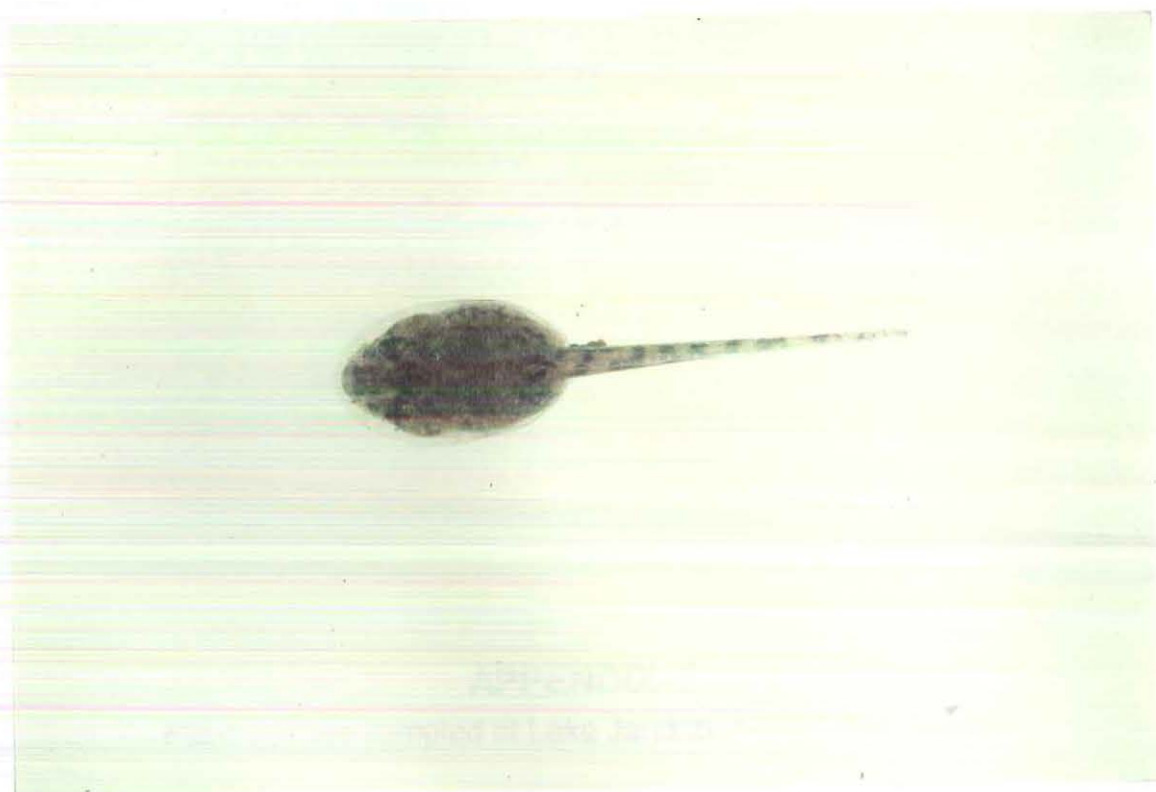


Plate A1.3 *Crinia insignifera* tadpole, SL 13 mm (Photo by M. Cowan)

APPENDIX 2

Plant species sampled at Lake Jandabup and Lake Gwelup

List of plant species that occurred in quadrats sampled at Lake Jandabup and Lake Gwelup. [The list is by no means complete; these are simply the species that occurred within the quadrats]

SPECIES	LAKE JANDABUP	LAKE GWELUP
<i>Astartea</i> sp.	X	
<i>Aster</i> sp.	X	X
<i>Baumea arthropphylla</i>	X	
<i>Baumea articulata</i>	X	X
<i>Baumea juncea</i>	X	
<i>Baumea preisii</i>	X	
<i>Baumea</i> sp.	X	
<i>Chara</i> sp.	X	X
<i>Cortadeira selloana</i>	X	
<i>Cyperus</i> sp.	X	X
Elatinaceae sp.		X
<i>Eucalyptus rudis</i>		X
<i>Hypolaena exsulca</i>	X	
Introduced grass	X	X
<i>Juncus pallidus</i>	X	X
<i>Leptocarpus scariosus</i>	X	
<i>Lepyrodia muirii</i>	X	
<i>Melaleuca raphiophylla</i>		X
<i>Myriophyllum</i> sp.	X	X
<i>Potamogeton</i> sp.	X	X
<i>Polygonum salicifolium</i>		X
<i>Regelia</i> sp.	X	
<i>Schoenus subfascicularis</i>	X	
<i>Typha orientalis</i>	X	X
<i>Villarsia albiflora</i>	X	X