Environmental Stability: Its role in structuring fish communities and life history strategies in the Fortescue River, Western Australia

Leah Beesley
B.Sc. (Hons.) *W. Aust.*

This thesis is presented for the degree of
Doctor of Philosophy at The University of Western Australia

School of Animal Biology
The University of Western Australia
2006

Dedication

This thesis is dedicated to the fish of the Fortescue River, particularly those that lost their lives in its making.

Thinking of Ned and my family.

Nobody's watching but I'm coming up
under the earth there are no stars
the motorbike slips on a patch in the freeway
waking up I know they never knew me
face of mine
where have you gone
through the secret cupboard
push the buttons
and I change
feelings within moments
never last
but even when I'm lost I keep on walking
and when I hear his voice I know I'm talking
and the tree-trunk bed-bunk secret land
is where he went
and I've got to find him
and I try to look
in clever places
but I hid him and I left no traces
and when he left I don't know what he took
a catchy rat-trap
shag rug bath mat
clever teacher
taught me
he read in his mind
the pages of books he didn't know he'd read
I said thanks
and tried to write him down
that blue-eyed boy
he didn't frown
he went away
and all I ever say
the words I hope he'd want me to
a conscience
a cloud in my favourite sky
a new boy on a different day
I'm looking…
nsb

Abstract

This study investigated the organisational role of environmental stability on the fish communities that inhabit the Fortescue River, an intermittent and variable system in north-Western Australia. It did so by examining the relationships between pool stability (measured by persistence of water through time, and variation in maximum pool depth through time) and the number and type of species within pools, temporal fluctuations in total fish abundance and intra-specific abundance, population size frequency distributions, and growth rate. It also examined the association between life history traits and the stability of the environments occupied within the river, and the stability of the river at large.

The results indicated that environmental stability was the major factor structuring the fish communities. Among-pool comparisons revealed that unstable pools contained fewer species, a greater fraction of juvenile size classes, and underwent greater fluctuations in total and intra-specific numerical abundance through time, than stable pools. Species inhabiting the river had life histories predicted by the stability of the river at large. However, there was little association between life history traits and the environmental sub-set that a species occupied within the river. Pool stability was not related to fish growth rate.

The organizational role of stability was largely independent of other within-pool physical factors (i.e. pool depth and surface area, water conductivity and turbidity) and landscape factors (stream order and distance to a permanent water source). This result differs from most other rivers where stability parallels the longitudinal progression from the headwaters to the lowlands. In the Fortescue River pool stability is dictated primarily by the locality of water storages, that is, connections to the aquifer and bank storage. The novel aspects of this river do not mean that environmental stability will be unimportant in other systems.

Stability affected community structure by determining (or describing) the probability that a pool would undergo periods of extreme shrinkage, that is, the likelihood that fish will be exposed to extreme physico-chemical fluctuations and complete eradication.

While the physical environment (acting through stability) primarily structured the fish communities of the Fortescue River there was indirect evidence that even within this variable river system, biological interactions played a role, albeit minor. Future investigations into the role of environmental stability will benefit from the use of accepted and quantitative methods by all stream ecologists.

Acknowledgements

I owe a great debt of gratitude to my principle supervisor Dr. Jane Prince (The University of Western Australia), who took over the reins from Prof. Peter Davies when he moved from Perth to Albany, and spared no expense in critically appraising the draft chapters of this thesis. Her knowledge and ability to see the 'big picture' have greatly enhanced this work.

I am also grateful to my then fellow Ph.D. student Dr. James Gilmour, for extensive assistance and guidance in the preliminary stages of this study. He helped to design the net with which I sampled the fish communities, and was my field partner for five trips. You underwent extreme physical discomfort to help me and I sincerely thankyou.

I thank my other supervisors, Prof. Peter Davies (The University of Western Australia), Dr. Peter Kendrick (Department of Conservation and Land Management), and Dr. Mark Meekan (Australian Institute of Marine Science). Peter Davies first inspired my interest in river systems and helped me to obtain funding from Land and Water Australia. Peter Kendrick took the time to help me to identify my study sites, provided a limitless source of knowledge on all aspects of the Pilbara, perpetual inspiration on the best way to live, and showed me how to skin a roo and repair tyres. Mark Meekan was fabulous to work with, being endowed with a ton of scientific enthusiasm, a brilliant mind, and a great sense of humour. I would also like to thank Dr. Michael Mackie (Fisheries Department of Western Australia), who has been a surrogate supervisor to me. Mackie, thanks for sharing all of your expertise in fisheries biology, looking at countless histological sections, critiquing Chapter 7, and for being a great friend.

I thank my funding bodies, Land and Water Australia, and the University of Western Australia without whose interest none of this work would have been possible. I also thank The River Basin Management Society for their contribution to this project.

I would like to acknowledge the indigenous owners of the land on which I worked, and the permission of the pastoralists who kindly allowed me to work on their land. David Thompson and David Barton of Mardie Station (thanks also Allan Munroe), the Parsons of Coolawanyah Station (thanks Kim), and Richardsons of Mount Florence Station (thanks Tony and Robin).

I thank the staff of the Department of Zoology (now School of Animal Biology) for all their help, especially Assoc. Prof. Bob Black for helping me with advice regarding statistical analyses, Dr. Andrew Storey and Assoc. Prof. Tom Turner for advice on all things fishy, Prof. Mike Johnson for helping me out with problems regarding evolution and for critiquing a draft of chapter 7, Dr. Jamie O'Shea for helping me with my proposal, and Prof. Lyn Beazley and Dr. Phil Vercoe for their smiling faces and good humour. Thanks to Prof. Johnson and Dr. Brenton Knott for being on my review panel and taking the time to read this thesis.

Thanks to the technical staff of the University, especially Rick Roberts and Cam, Kerry, Tom, Leon and Ray from the Workshop who saved my neck on several occasions and helped with the design of the drop-net, Lidia Bednarek, Garry Cass and

Elizabeth Halldain. I thank the former Animal Science Department for lending me equipment that I couldn't get from Zoology (cheers JB).

Thanks Prof. Jim Puckridge (SA) for providing data which I used in Chapter 2, and general advice on catching fish, similarly I thank Stephen Balcombe (QLD). David Dianich from the USA donated the mesh that I used in the drop-net (Chapter 3), which was a very kind act and most appreciated. Cheers to the staff at Millstream National Park, especially 'Jamie the Ranger'.

It is critical to thank my family, who provided not only emotional and financial support, but who (aside from J. Gilmour) provided all of the field support for this project. I thank my wonderful, beloved, and most beautiful mother who participated in three field trips, spent countless hours reading and correcting this thesis, typing in references, and still managed to find optimism in my findings. My father who is the source of scientific inquiry within our family, random acts of mathematical genius (e.g. Pascal's triangle), and who took part in one field trip, weighed numerous otoliths, and critically analysed all of my scientific methodology and reasoning. My twin sister Shona for taking part in two field trips, critiquing several chapters of the thesis, and providing me with a lot of encouragement. My cousin Sharne (aka Bees), for taking part in two summer time field trips, working a 16 hour day in 45+ºC heat on her birthday and managing good humour at all times.

I thank my friends, particularly Patience my Ph.D. buddy, for her fabulous vocabulary, sensitive nature, and her up to date knowledge of the best places to dance and drink in Perth. Thanks to Dan for being a bigger geek than me, and for all the games of Trivial Pursuit. Thanks Sammy the Iron Man for the Limo. Thanks to my bro Guy for a steady supply of very dry gin-martinis towards the end of my candidature, which provided a reason to make it through the week, and to my best friend Key (aka Christianne White) for providing the exceedingly agreeable conversation to compliment the aforementioned drinks, and for numerous pep talks (re: the beast), and a lot of marathon love (bring on Sydney 2006 and New York 2007). I also thank Guy for giving me the best finishing present imaginable, tickets and a trip to the world cup in Germany, and the *Tour de France*.

Heartfelt thanks to the directors of Biota Environmental Sciences (Garth, Roy and Michi), who let me have time off from work to complete the last stages of the thesis.

I would like to acknowledge my examiners: Professors Isaac Schlosser, Kirk Winemiller and William Matthews. Your comments will be very helpful when I come to publish the findings of this thesis.

I apologise to, and thank anyone whom I may have forgotten.

Last but definitely not least, I would like to thank my beloved betrothed Alasdair Grigg (☺) for not only being an amazing human being, but for loving me so well, encouraging all of my idealistic notions, and providing me with a happy and safe environment in which to write up this thesis. I love you so much!

Oh yeah, and cheers to Bevan the beast, the best field assistant a girl could have – Brmm (only 4 flat tyres).

Table of Contents

This page has been left blank intentionally.

Chapter 1

General Introduction

Describing the differences between communities (or populations) is a simpler task than determining what creates these differences. While differences can arise because species have different life history strategies (i.e. longevity, size, age at maturity, number of offspring etc.) (Stearns 1976, Ebert 1981, Stearns 1992), ecologists typically focus on the interactions between individuals (or species), and interactions with the physical environment (Schlosser 1987a, Capone and Kushlan 1991). Interactions between individuals (or species) are referred to as 'biological', and encompass predation, and competition for resources such as space and food (Capone and Kushlan 1991). Interactions with the environment are referred to as 'physical', and encompass the effects that the physical environment has on a species' presence and its abundance (Capone and Kushlan 1991).

While ecologists agree that both physical and biological interactions occur within every community, they propose that their strength varies with the stability of the environment (Schlosser 1987a, Poff and Ward 1989, Capone and Kushlan 1991, Bayley and Li 1992). Stability refers to the constancy of an environment through time. Whilst constant environments are classified as stable, those that fluctuate are further separated into those that undergo predictable changes though time – seasonal (or periodic), versus those that undergo unpredictable or stochastic changes through time - unstable.

In a perfectly stable environment, resource availability does not fluctuate and biological interactions are thought to be the main determinants of community (or population) structure (Schlosser 1987a, Bayley and Li 1992). This is because a constant environment enables populations to grow in size until resources are limiting (the carrying capacity of their environment) (Pianka 1970). Survival, therefore, is related to the ability to obtain the resource (e.g. compete for food), and to avoid becoming a resource (i.e. being preyed upon). The considerable competition within stable environments shapes the structure of the community such that populations will be composed predominantly of relatively large individuals because competitive success (and vulnerability to predation) is commonly a function of size (Werner and Gilliam 1984, Schlosser 1987a, Hutchings 1997). They will also contain a relatively great number of species when compared to unstable environments, because competition is energetically expensive and natural selection will favour species that

specialise, thereby reducing these negative interactions (Grossman *et al.* 1998). Populations in stable environments will also be relatively constant through time, because competition for food resources (hence survival, growth rate, and reproductive output) is inversely related to population size and thus density dependent. For example, if a population decreases slightly in number, competition will decrease and survival, growth rate and reproductive output will increase, causing the population to grow in number (Jobling 1995). Conversely, if a population increases slightly in number, competition will increase and survival, growth and reproductive output will decrease, causing the population to decline in number (survival is density-dependent) (Jobling 1995).

At the other extreme, in unstable environments, physical interactions are thought to be the main determinants of community (or population) structure (Schlosser 1987a, Bayley and Li 1992). Survival is related more to physiological tolerances and climatic patterns than competitive ability (survival is density-independent) (Pianka 1970, Grossman *et al.* 1998). An individual's physiological tolerance may alter with size, for example, small fish may be more susceptible to flooding than large fish (John 1964), and large fish may be more susceptible to low levels of dissolved oxygen commonly found in shrinking pools (Trammer 1977). However, in general, communities in unstable environments should be dominated by small individuals (specifically, juveniles), because the typically older age of large fish increases their exposure to potentially fatal environmental conditions. Population size will fluctuate over time in response to favourable and unfavourable changes in the environment (Gorman and Karr 1978, Sale and Douglas 1984, Schlosser 1987a). Communities will also have relatively few species when compared with stable environments, because fluctuations in the physico-chemical environment preclude the existence of fragile species (Matthews and Styron 1981, Begon and Mortimer 1986, Matthews 1987, Delucchi 1988, Poff and Ward 1989). The remaining robust species will use a wide range of resources (i.e. be generalists) so that they can make the most of any condition that presents itself (Poff and Allan 1995).

In seasonal environments, the dominant regulatory processes change predictably through time. Physical interactions are likely to be more important during periods of habitat expansion (wet), whereas both physical and biological interactions will be

important during periods of habitat contraction (dry) (Zaret and Rand 1971, Schlosser 1987a). Note that while the strength of biological interactions change in intensity this does not mean that a seasonal environment can be compartmentalized into discrete phases of stability and instability.

While stability will affect the strength of physical and biological interactions it also affects the life history strategies of species on a generational and evolutionary scale (Pianka 1970, Southwood *et al.* 1974). This is because, within a particular environment, certain characteristics (or traits) will increase the reproductive success (of an individual) more than others (Stearns 1992). Species inhabiting stable environments will mature late and produce a relatively small number of large offspring - termed an 'equilibrium' strategy (Stearns 1992, Winemiller 1992). Delaying maturation and attaining a large size is advantageous in this setting because survivorship is related to competitive ability, which is typically a function of size (Winemiller 1992, Winemiller and Rose 1992). Breeding at a large size also increases the amount of energy available for reproduction, and when traded off with offspring number, will maximize offspring size (Winemiller 1992). The low fecundity of equilibrium species means that populations cannot increase rapidly, hence are relatively stable through time (Pianka 1970, Jobling 1995). Species inhabiting environments that fluctuate seasonally, that is, pass through temporal intensification and relaxation of competitive interactions, will delay their maturation to coincide with the season where competition is lowest, and produce a large number of small offspring – termed a 'periodic' strategy (Stearns 1992, Winemiller 1992). Delaying maturation and attaining a larger size not only increase fecundity but enhance survival when competition is strongest, and survivorship is likely to be related to size (Stearns 1976, Winemiller 1992). The high fecundity of periodic species means that populations can increase rapidly (Winemiller 1992). Species inhabiting unstable environments will mature early, ensuring that they have a chance to reproduce before the unstable environment wipes them out (Murphy 1968). While early maturation keeps body size small, constraining fecundity, breeding occurs at a high frequency, which enables a high net reproductive output (Winemiller 1989). In addition, this strategy is adaptive because any unfavourable environmental change will eliminate only a fraction of total reproductive output (Lewontin 1965, Stearns 1989). Individuals in unstable environments should also display considerable phenotypic

plasticity (Lewontin 1965, Stearns 1989, Hutchings 1997). This combination of traits is termed a 'colonising' strategy (Winemiller 1992). The high reproductive effort of colonizing species means that populations can undergo rapid increases in size when conditions are favourable (Pianka 1970, Stearns 1976).

The preceding discussion outlines why environmental stability is likely to be a major factor determining community structure. Ecologists studying freshwater fish have found considerable empirical evidence supporting a role for stability, but examples to the contrary, and gaps in knowledge also exist. The following section presents these findings and discusses factors that complicate the researcher's goal to determine the role of environmental stability. It also elaborates on areas that require additional study.

Studies conducted among river systems have found that stability shapes many community features including species richness (Horwitz 1978), species density (Pusey *et al.* 2000), the strength of relationships between physical factors and community structure (Rincon *et al.* 2000), the functional organisation of fish, that is whether species are resource specialists or generalists (Poff and Allan 1995), and the life history traits of species (Baltz 1984, Fox and Keast 1991, Fernandez-Delgado and Herrera 1995, Wanzenbock and Keresztessy 1995). However, at least one study, conducted within a seasonal environment, reports that a community is shaped by predation (Rodriguez and Lewis 1994).

Temporal studies among river systems have noted that communities (species composition and abundance) in unstable systems fluctuate more than those in stable systems (Ross *et al.* 1985, Matthews *et al.* 1988, Fausch and Bramblett 1991). Researchers propose that the disturbance events (e.g. floods and droughts) in unstable systems are responsible for the increased fluctuation of their communities (Starrett 1951, Taylor *et al.* 1996, Medeiros and Maltchik 2001). Some argue that disturbances erode the relationships that exist between community structure and the within-stream physical and biological environment leading to random (stochastic) regulation of communities (Grossman *et al.* 1982, Fausch and Bramblett 1991, Saint-Paul *et al.* 2000). Others have found that communities, following disturbance, return to their previous state (Moyle and Vondracek 1985, Matthews 1986, Meffe and Berra 1988).

These researchers argue that community structure is regulated by deterministic processes[1], that is, interactions with the physical and biological environment (Moyle and Vondracek 1985, Matthews 1986, Matthews *et al.* 1988, Hoeinghaus *et al.* 2003). Debate between stochastic versus deterministic regulation has been considerable in the past (Grossman *et al.* 1982, Rahel *et al.* 1984, Yant *et al.* 1984, Grossman *et al.* 1985, Ross *et al.* 1985, Matthews *et al.* 1988, Grossman *et al.* 1990), and appears to be related to the frequency of disturbances a community is exposed to, and the breeding biology of the resident species (Moyle and Vondracek 1985, Freeman *et al.* 1988). That said, most of these temporal studies have studied fish communities in relatively permanent segments of streams (for a review see Grossman *et al.* 1990 but see Taylor *et al.* 1996 as an exception) providing little information on differences in the ways that communities change through time between stable and unstable sections within a river.

Studies examining the relationship between environmental stability and life history strategies have found that fish living in the same environment can have different life history strategies (Kramer 1978, Beumer 1979, Puckridge and Drewien 1988, Spranza and Stanley 2000, Winemiller 1989). For example, Winemiller (1989) found that the general stability of Venezuelan water bodies described ~70% of resident species' life history strategies. While Winemiller (1989) suggested that size (related to phylogeny) and diet were responsible for the 30% of species that didn't conform to the theory, it is possible that fine-scale variation in environmental stability was responsible. There have been relatively few studies examining the relationship between environmental stability and life history strategies on a fine-scale, that is, along the length of a river (but see Spranza and Stanley 2000) as most researchers working at this scale have focussed on the role of predation (Reznick and Endler 1982, Gilliam *et al.* 1993, Rodd and Reznick 1997). The influence of extraneous factors on life history strategies suggests that additional research, ideally remote from the location where existing

[1] Deterministic regulation was initially used to describe the prevalence of biological interactions in the structuring of a community, whereas stochastic regulation referred to the prevalence of interactions between species and the physical environment (Grossman *et al.* 1982). More recently 'determinism' has been used to describe the relationships amongst species (biological interactions) and relationships between species and the physical environment, i.e. community structure is a predictable outcome of physical and biological interactions. Whereas, 'stochastic' refers to the breakdown of these patterns, due to the random and complex effects of disturbance, i.e. flood and drought (Rodriquez and Lewis 1994, Hoeinghaus *et al.* 2003). This study follows the latter definitions.

models have been formulated, needs to be done to determine the broad applicability of theories linking environmental stability and life history strategies in freshwater fish.

Little has been done to examine the relationship between the environmental stability that parallels the progression from the headwaters to the lowlands, and the number and types of species occurring within a river (but see Schlosser 1987a, Fausch and Bramblett 1991). Most researchers studying this longitudinal progression have focused on the role of physical or biological factors (Gorman and Karr 1978, Capone and Kushlan 1991, Gilliam *et al.* 1993, Rodd and Reznick 1997, Brown 2000, Ostrand and Wilde 2002, Hoeinghaus *et al.* 2003). The notable exception is Schlosser's (1987a) conceptual framework of fish communities in the small, warm-water streams of North America (U.S.A.). Unfortunately, the increasing stability that he notes as one travels from the headwaters to the lowlands is paralleled by changes in other physical factors (such as depth and habitat heterogeneity), making it difficult to assess the role of stability (Grossman *et al.* 1982). Landscape features may also complicate this type of research. Landscape features include: distance to the nearest refuge, location within the catchment (i.e. stream order), and barriers to dispersal; all of which can affect the types of fish species present (and their size class) (Gilliam *et al.* 1993, Pusey *et al.* 1998, Schlosser 1998). Their importance on community structure is being increasingly recognised (Dunning *et al.* 1992, Schlosser 1995b, Snodgrass *et al.* 1996, Poff 1997, Jackson *et al.* 2001).

This study contributes empirical findings to dialogue regarding the importance of environmental stability to the structure of fish communities. It does so by examining the fish communities inhabiting the Fortescue River, a seasonal but highly variable river system situated within the arid zone of northern Western Australia. Specifically it examines:

- The relationships between within-pool physical factors, pool stability, landscape factors and community structure (species presence, type and abundance) (Chapter 4);
- The relationship between pool stability and changes in community structure (total fish abundance, species abundances, size structure) through time (Chapter 4 and Chapter 5);

- The relationship between pool stability and the size structure of populations (Chapter 5);
- The relationship between pool stability and fish growth rate (Chapter 6);
- The relationship between the stability of the river at large and the life history traits of its species (Chapter 7); and
- The relationship between the stability of the pools that species occupy within the river and the life history traits of these species (Chapter 7).

This river provides a good opportunity to examine the role of stability because: (1) the river exists, for most of the time, as a series of isolated pools, allowing a discrete quantification of communities and environmental stability (pool stability); (2) it contains pools that vary markedly in their stability; and (3) the stability of pools in this river appears to be related more to the presence and quantity of underground water storages rather than a function of pool development (i.e. stability may not be correlated with other physical factors).

The thesis commences by describing the Fortescue River, the stability of the system, and its fish fauna (Chapter 2). As the correlative nature of this study relies upon an accurate description of the fish community, the sampling methods have been described in some detail (Chapter 3). The thesis concludes with a general discussion of the relevance of environmental stability to: the structure of fish communities within the river, and the life histories of the species that inhabit the river (Chapter 8).

Chapter 2

The Fortescue River: Stability, Study Sites and Fishes

The Environment

The Fortescue River is situated within the Pilbara region of Western Australia (Figure 2.1). This region covers over 510,000 km^2 (Napier and van Leeuwen 1996), comparable to the size of Spain, and extends from the Indian Ocean to the Northern Territory border (Figure 2.1). It forms part of the larger, ancient landmass of the Pilbara Craton, dated at approximately 2.8 billion years old, and containing rocks of 3.6 billion years of age (Copp 2005). While low relief typifies the weathered landscape, remnants of once great mountain ranges create some topographic variability. There has been relatively little clearing of native vegetation, but extensive pastoralism has brought with it exotic plant species. In many low-lying areas, especially along riverbanks, buffle grass (*Cenchrus ciliaris*) has replaced spinifex as the dominant understorey species. The overstorey in these areas is predominantly eucalyptus (*Eucalypus camaldulensis* and *E. victrix*) (Masini 1988). Melaleuca (*Melaleuca leucadendron* and *M. argentea*) trees occur adjacent to permanent water sources (Masini 1988, Napier and van Leeuwen 1996).

The Fortescue River is a major feature of this environment, traversing over 570 km and encompassing a catchment of 48,000 km^2[2,1]. Its headwaters are in the Opthalmia, eastern Hamersley, and southern Chichester Ranges (near Newman) in the interior, and its mouth is at Diver Inlet (south of Cape Preston) on the coast (Dames and Moore 1984). The river is unusual in that it contains two catchments. The interior and western catchments are separated by the Goodiadarrie Hills (Dames and Moore 1984, Masini 1988). Flow in the interior catchment causes flood-out in the area adjacent to the hills, and during periods of great rainfall, this floodplain region can extend back up the river for a 100 km (Masini 1988). Such an event results in the creation of a massive wetland, which is seasonally inhabited by vast numbers of migratory birds. Flow in the western catchment, by comparison, runs to the ocean unimpeded. The western catchment has numerous connections to underground water storages, the most prominent occurring at Millstream National Park, where the aquifer discharge creates a string of large, permanent pools that traverse 20 km of the main channel[2].

The climate of the Pilbara is arid. Records by the Public Works Department at Millstream National Park from 1897 to 1977 reveal that the annual average pan evaporation (3365 mm) is an order of magnitude greater than the average annual rainfall (352 mm) (Dames and Moore 1984). Temperature varies seasonally, with the lowest maximum daytime temperatures during June (26.6 ºC) and the highest during December (46.4 ºC) (Dames and Moore 1984). Rainfall is also seasonal, the majority

[1] http://www.wrc.wa.gov.au/under/statewqassess/Fortescue_home.htm
[2] http://www.deh.gov.au/biodiversity/publications/series/paper4

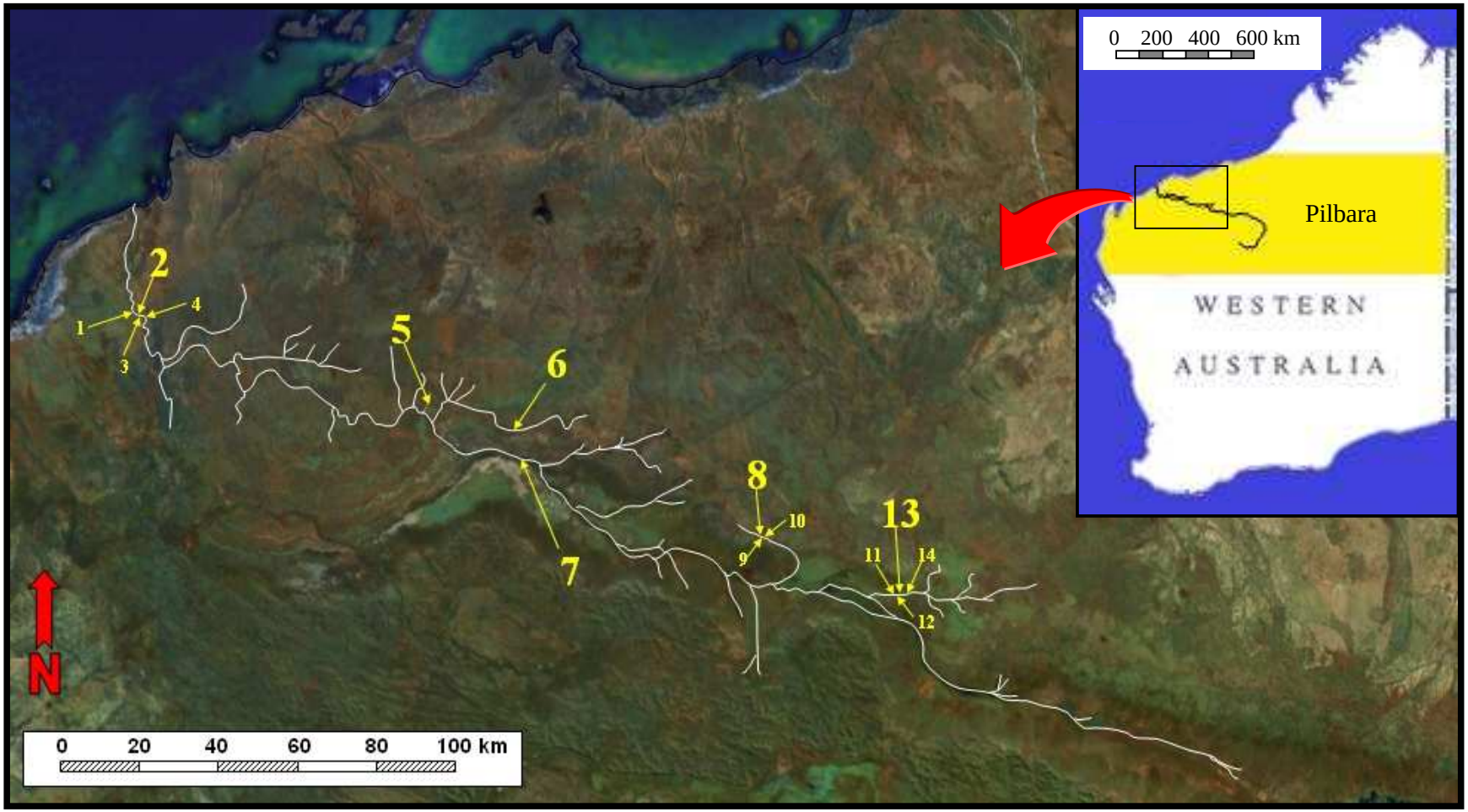


Figure 2.1. The western section of the Fortescue Basin showing the location of the 14 study pools. Primary pools are shown in a larger font and have names: pool 2 = Bilanoo, 5 = Railbridge, 6 = Portland, 7 = Palm, 8 = Mallina, 13 = Hooley. The location of the entire river within the Pilbara region of Western is also shown (see inset).

occurs between the summer months of December and April, ("the wet season"), and is associated with cyclones and tropical thunderstorms (Dames and Moore 1984, WRAP 1997). Very little rain falls during the rest of the year creating a pronounced "dry season" (Masini 1988). On occasion, rain does fall during the early half of the dry period (May to June); however, it is associated with southerly cold fronts and is typically restricted to the south-western section of the region (Masini 1988).

While precipitation is seasonal, the amount of rain that falls each year is hyper-variable (WRAP 1997, Figure 2.2). For example, between January 1998 and December 1999 a total of 1262 mm of rain fell on Mt Florence Station (near sites 11 to 14, Figure 2.1), yet in March of 2000 243 mm (or ~20% of the previous two years rainfall) was recorded in a 48 hour period[3]. Such variability is largely attributed to tropical cyclones (Masini 1988). The spatial distribution of rain across the catchment also varies considerably (Figure 2.3). The variability of flow in the Fortescue River is analysed and discussed in more detail later under 'Stability of the System' in this chapter.

Shaped by the aforementioned climatic conditions, the Fortescue River typically exists as a chain of pools. Most of these pools contract markedly during the dry season; however, pools with connections to underground water stores remain relatively constant. These semi-permanent/permanent pools act as refuges for aquatic life. Following significant rainfall events the pools become connected and may spill out onto the surrounding floodplain.

Stability

While the general introduction outlined the consequences of stable, seasonal, and unstable environments on community structure (see Chapter 1), how does one determine which of these endpoints, or where on the continuum that exists between them, a system lies? Currently, there is no single accepted method of quantifying the stability of an environment. Researchers use different methods depending on the scale of their study and their area of expertise. In this study stability is addressed at two levels: (1) at the river or catchment level, and (2) at the pool level.

[3] Data taken from the Bureau of Meteorology's website www.bom.gov.au

The Stability of the River

Many ecologists studying freshwater fish describe the stability of a river or stream using no defined criteria. They rely simply on their knowledge of the flow patterns and physico-chemical fluctuations within the system (Ross *et al.* 1985, Matthews *et al.* 1988). Classifications of this kind are generally relative, for example "Brier Creek is overall more physically harsh and fluctuating than Piney Creek" (Matthews *et al.* 1988). This method makes it difficult to compare the results of one study with another, and it is vulnerable to errors of misjudgement.

A more objective way of assessing the stability of a river is by quantifying the variability of its discharge (Poff and Allan 1995, Pusey *et al.* 2000, Rincon *et al.* 2000). This has involved using the coefficient of variation of annual flow (Mahon *et al.* 1979), but more recently, a suite of descriptors having biological relevance, that is, those that describe the timing, frequency, duration, rate of change, and magnitude of the flow, are being used (Poff and Ward 1989, Richter *et al.* 1996, Richter *et al.* 1997, Puckridge *et al.* 1998).

The variability of Australia's arid rivers is often quoted, but rarely quantified to any more than a cursory degree (e.g. presenting the coefficient of variation for annual flow) (McMahon 1979, Poff 1996). One notable exception is Puckridge *et al.* (1998) who compared the flow variability of two Australian rivers with rivers elsewhere in the world, using 23 different measures to quantify the timing, frequency, duration, rate of change and magnitude of hydrological variability. Puckridge *et al.* (1998) found that the Cooper Creek and the Diamantina River, two of arid Australia's largest rivers, were more variable than all of the other 50 large rivers included in their survey.

While the Fortescue is an arid zone river like the Cooper Creek and Diamantina River, differences exist between them. The Fortescue lies on the western side of the continent, draining to the western seaboard (Indian Ocean), whereas the Cooper and Diamantina lie with an endorheic basin and drain southwards to an inland lake (Lake Eyre). The different localities of these rivers mean that they are exposed to quite different climatic systems. The Fortescue River is also considerably smaller, and while discharge variability is often thought to increase as stream size decreases, in Australia flow variability decreases with decreasing catchment size (McMahon 1979).

Consequently, it was deemed necessary to quantify the variability of the Fortescue River.

The variability of the Fortescue River was determined by examining 20 years of discharge data (1969-1988) from a site on the western catchment of the Fortescue River, Gregory's Gorge (Figure 2.2, see Appendix I). Only one site was used as Puckridge *et al.* (1998) found that one site was sufficient to characterise a rivers' variability on a large (global) scale. The data were analysed in accordance with Puckridge *et al.*'s (1998) methodology, and were range standardised with the raw data used by Puckridge *et al.* (1998) to enable a meaningful comparison. The Fortescue had a summary median that was higher than that recorded for the Cooper Creek and the Diamantina, confirming that the river is amongst the most variable systems in the world.

The Stability of Pools within the River

The stability of an environment within a river (e.g. a pool) is often described using no defined criteria. Like many studies between rivers, researchers rely on their knowledge of the flow patterns and physico-chemical fluctuations within the system (Fausch and Bramblett 1991, Spranza and Stanley 2000). Such classifications are generally relative, for example "first order streams are ephemeral and have poorly developed pools… that fluctuate in size and discharge…in the lower basin…there are well-developed pools" (Spranza and Stanley 2000). This method makes it difficult to compare the results of one study with another, and it is vulnerable to errors of misjudgement.

A more objective way of assessing the stability of a section of the environment within a river (e.g. a pool) is by quantifying changes in the in-river environment through time. Researchers use a number of different techniques including: persistence of water, temporal variability in habitat volume, and temporal heterogeneity in within-pool (or stream) habitats (Schlosser 1987a, Capone and Kushlan 1991, Wanzenbock and Keresztessy 1995). The persistence of water is used in different ways by researchers and can range from whether a pool contains water throughout the study period (i.e. permanent) or dries during the study period (i.e. temporary) (see Wanzenbock and Keresztessy 1995), to the number of days or months that a pool

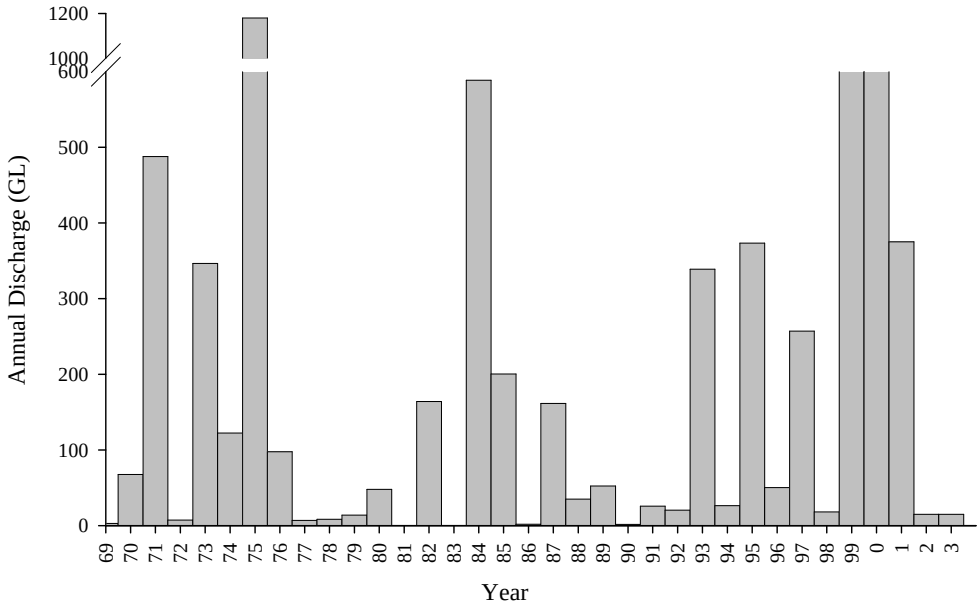


Figure 2.2. Total annual discharge for one site on the Fortescue River, Gregory's Gorge, from 1969 to 2003. Gregory's Gorge is located 18.5 km downstream of Millstream National Park (site 7).

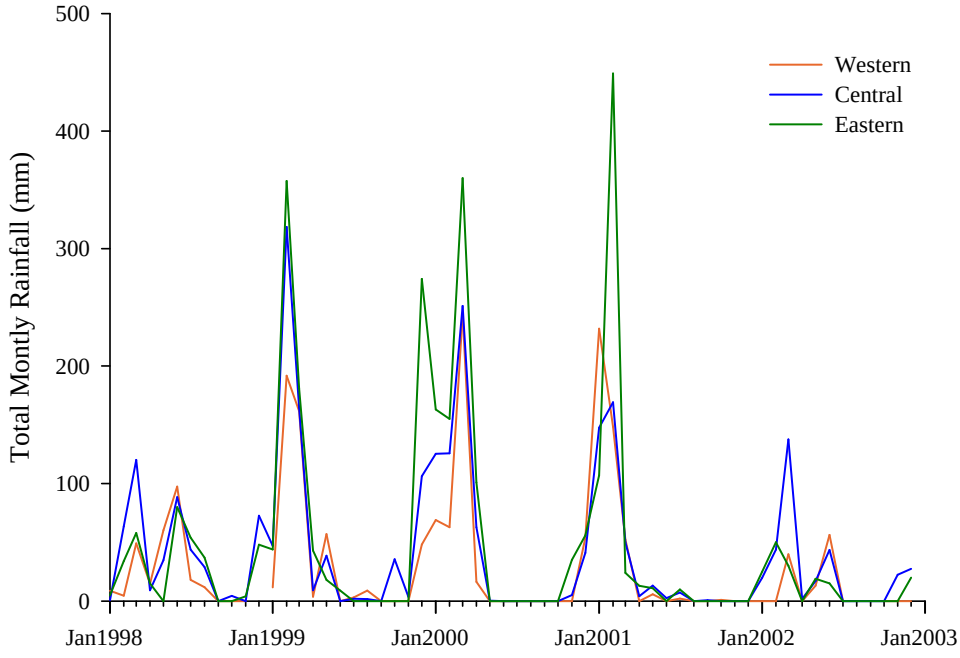


Figure 2.3. Total monthly rainfall for three sites on the Fortescue River, over a five year period. Data for the western site are from the Fortescue Roadhouse, adjacent to study sites 1 - 4. Data from central site are from Millstream National Park, adjacent to study site 7 (Palm Pool). Data from the eastern site are from Mount Florence Station, where study sites 11 - 14 were located.

contains water out of a total (see Capone and Kushlan 1991). Disadvantages of this measure include that it cannot separate pools that remained full over time from those that contained water but shrunk considerably. It also cannot distinguish between pools that remain relatively full over time from those which dry up considerably but were quickly refilled. Temporal variability in habitat volume describes changes in the volume of water within a pool (or section of stream) (see Schlosser 1987a), hence documents expansion and contraction of the aquatic habitat. Variation is described using the coefficient of variation (standard deviation divided by the mean), which removes the effects of differences in the sizes of the pools studied and provides a measure of relative variability (Zar 1999).

This study used variability in maximum pool depth over time as the preferred measure of stability. Depth, like volume, describes changes in the size of a pool (albeit with less accuracy), and the simplicity of this parameter meant that it could be monitored a greater number of times than volume. Instead of using the coefficient of variation to describe changes in pool depth, this study used the absolute value of the summation of all changes in maximum pool depth divided by mean depth (see Equation 2.1). This was done because standard deviation only describes the size of departures from the mean, whereas this study was interested in the frequency of departures from the mean. Small values indicate high stability and large values indicate low stability.

Equation 2.1 Pool Variability in Depth $= \left(\frac{\sum \left| X_{i+1} - X_i \right|}{\overline{X}} \right) * 10$

Where i = sampling date (between December 2000 and December 2002), and X is maximum pool depth (m)

Assessing a pool's stability using variation in depth could be done only for pools that were closely monitored through time (i.e. the primary pools, see the 'Study Sites' section below). Other pools had their stability determined using persistence. In this study, pool persistence equalled the number of months that a pool contained water during a 25-month period (December 2000 to December 2002). Values were

converted to a percentage to ease interpretation. Low values indicated that a pool was temporary and 100% indicated permanence during the study period.

Study Sites

Time constraints restricted sampling to the western catchment of the Fortescue River. Within this region six pools (primary pools) were sampled on a regular basis, and eight pools (secondary pools) were sampled opportunistically. The primary pools enabled an examination of temporal patterns in the fish communities. The secondary pools (by increasing the sample size) increased the power to examine the relationship between fish communities and physical factors. The location of each pool is shown in Figure 2.1. Pools were numbered in accordance with their position along the catchment; primary pools were also named. Where possible, names followed those provided on topographical maps (e.g. Bilanoo, Palm, and Mallina Pools), when a pool had not been named it was described according to its tributary or a prominent landscape feature (e.g. Railbridge, Portland, and Hooley Pools).

The study pools ranged in physical factors, from large permanent pools with connections to underground water sources and thick macrophytic growth, to small highly ephemeral pools with low habitat complexity. The physico-chemical characteristics of all pools are provided in Chapter 4; however, a detailed description of the six primary study pools, and their physico-chemical parameters through time is given below. Pools are introduced in order of decreasing stability.

Palm Pool (21º34’18”S, 117 º03’09”E) (Site 7, variability in depth value = 6)
This pool was located within the main channel of the river, within Millstream National Park (Figure 2.1). It is a relatively large, deep pool that has connections to the Millstream aquifer, as it is spring-fed it remains permanent over time (Masini 1988) (see Plates 2.1.A and 2.2.A). Its major substrate is gravel, but mud accumulates in deep water sections. The pool has a relatively complex aquatic habitat, with regions of high and low flow, shallow and deep sections, submerged macrophytes (*Najas marina, Vallisneria* sp, *Nitella* sp, *Chara* sp, *Potamageton tricarinatus*, and *Ruppia megacarpa*) and large woody debris. A diverse array of macroinvertebrates was present, and they were most abundant within the reeds. The pool was fringed by dense emergent macrophytes (*Schoenoplectus litoralis*, *Cyperus involucratus*, and *Typha*

orientalis) and shaded by cajeputs (*M. leucadendron*) (Plate 2.2.A). The wide channel means that while the littoral regions are well shaded, considerable light reaches the mid channel. A description of the physico-chemical properties of the pool is provided in Table 2.1.

Table 2.1. Physico-chemical properties of Palm Pool during sampling (December 2000-December 2002). DO refers to the concentration of dissolved oxygen. '--' = not available.

Date	Surface Area (m^2)	Length (m)	Width (m)	Maximum Depth (m)	Water Temp. (°C) AM	Water Temp. (°C) PM	Conductivity (µs/m)	pH	DO (mg/L) AM	Turbidity (ntu)
08/12/00	--	--	--	3.3		31.0	2275	--	--	5
04/05/01	>15000	>500	30	3.2	24.3	25.4	1960	8.4	7.7	3
21/08/01	>16000	>500	32	3.5	19.1	22.1	2208	8.1	8.1	4
30/11/01	>19000	>500	38	3.3	27.9	29.5	2300	7.6	9.3	10
08/02/02	--	--	--	3.3		34.5	1452	8.4	8.0	3
17/03/02	--	--	--	3.9	27.3	33.0	947	8.4	7.9	7
23/04/02	>17500	>500	35	3.3	22.5	25.5	1992	8.1	--	8
15/08/02	>17500	>500	35	3.3	18.6	20.0	2390	8.2	8.1	<1
28/11/02	--	--	--	3.2	28.8	32.2	2595	--	10.2	3

Bilanoo Pool (21º17'47"S, 116º08'46"E) (Site 2, variability in depth value = 17)
This is a lowland pool located within the main channel of the river (~40 km upstream from the river mouth). It has a shallow water table and bank storage, which keeps the pool in a semi-permanent state (Masini 1988). It is situated immediately north of where the North-West Coastal Hwy crosses the river, on Mardie Station (Figure 2.1). The main channel of the river is very wide (~800 m) and is surrounded by a large floodplain. However, the floodplain and the majority of the channel were dry for most of this study. The pool covered the lowest lying section of the main channel, being very deep at the meander bend and considerably shallower elsewhere (Plate 2.1.B, 2.2.B). Its major substrate is large cobblestones, but mud accumulates in the deep-water sections and backwaters. The pool has a relatively complex aquatic habitat, including: variation in depth, considerable stands of submerged macrophytes (*Myriophyllum* sp., *Vallisneria* sp., *N. marina*, *Potamageton crispus*, *R. megacarpa*), and large woody debris. Emergent macrophytes (*Eleocharis* sp. *S. litoralis*, and *T. orientalis*) were present but in low abundance. Macroinvertebrates were abundant,

particularly in amongst the macrophytes. The riparian zone overstorey consisted of cajeputs (*M. leucadendron*), river red gums (*E. camaldulensis*) and *Sesbania* sp. (see Plate 2.3.B). The understorey consisted of buffle grass, spinifex and Asteraceae thistle. The great width of the channel and the lack of vegetation on the floodplain side meant that the pool received a great deal of sunlight. A description of the physico-chemical properties of the pool is provided in Table 2.2.

Table 2.2. Physico-chemical properties of Bilanoo Pool during sampling (December 2000-December 2002). DO refers to the concentration of dissolved oxygen. '--' = not available.

Date	Surface Area (m^2)	Length (m)	Width (m)	Maximum Depth (m)	Water Temp. (°C) AM	Water Temp. (°C) PM	Conductivity (µS/m)	pH	DO (mg/L) AM	Turbidity (ntu)
05/12/00	--	--	--	2.8	30.6	--	1174	--	--	2
26/04/01	>40000	>500	80	4.0	27.2	29.1	864	8.3	6.6	1
14/08/01	>32500	>500	65	3.3	22.1	25.5	950	8.2	9.0	11
21/11/01	20210	430	47	2.5	21.5	--	1124	8.0	6.7	2
03/02/02	--	--	--	2.1	--	33.1	1160	7.4	3.0	5
15/03/02	--	--	--	1.8	28.2	31.0	1105	8.6	3.5	5
17/04/02	7200	225	32	1.7	22.4	--	1115	7.7	--	2
07/08/02	6600	220	30	1.5	18.9	21.5	1377	8.3	7.5	3
26/11/02	--	--	--	1.2	26.1	--	1527	--	7.2	1

Mallina Pool (21º43'37"S, 117º45'50"E) (Site 8, variability in depth value = 30)

This is a headwater pool located within an upland tributary of the river (Figure 2.1). This pool was much smaller and shallower than Palm and Bilanoo (Table 2.3, Plate 2.1.C). Local residents believed it to be permanent, and while considerably slower to dry than most of the surrounding pools, it shrank during the drought of 2002, hence cannot be connected to an aquifer (Plate 2.2.C). It is more likely that the pool has bank storage. Its major substrate was small to medium sized angular rocks, but there were patches of gravel and mud. The pool had lower habitat complexity than Palm and Bilanoo, with fewer species and coverage by submerged macrophytes (*Chara* sp. and *N. marina*). However, the pool did contain variation in depth and contained large woody debris. Dense emergent macrophytes (*S. litoralis, C. involucratus*) fringed the pool. The riparian zone was reasonably well developed, the dominant overstorey species being the river red gum (*E. camaldulensis*) and snakewood (*Acacia*

xiphophylla) (Plate 2.2.C). The dominant understorey species were buffle grass (*C. ciliaris*) and spinifex (*Triodia longiceps*). There were notable amounts of filamentous green algae in the shallow stagnant regions of the pool. A description of the physico-chemical properties of the pool is provided in Table 2.3.

Table 2.3. Physico-chemical properties of Mallina Pool during sampling (December 2000-December 2002). * = the original section of the pool that was sampled was dry, and sampling had to move to a section of the pool that still contained water. DO refers to the concentration of dissolved oxygen. '--' = not available.

Date	Surface Area (m^2)	Length (m)	Width (m)	Maximum Depth (m)	Water Temp. (°C) AM	Water Temp. (°C) PM	Conductivity (µS/m)	pH	DO (mg/L)	Turbidity (ntu)
14/12/00	--	--	--	1.4	29.2	33.5	1683	--	--	27
06/05/01	5220	290	18	2.0	23.3	25.6	1748	8.3	7.1	2
23/08/01	5040	280	18	1.6	17.7	21.8	1461	8.1	8.3	5
07/12/01	4480	280	16	1.4	27.7	31.1	1623	8.4	7.5	4
06/02/02	--	--	--	1.0	25.5	29.2	1904	8.6	6.2	3
19/03/02	--	--	--	1.3	27.9	32.9	738	7.9	2.3	14
26/04/02	4680	260	18	1.0	23.3	27.0	916	8.7	--	19
19/08/02	1350	90	15	1.4*	14.8	19.3	1464	8.3	9.5	80
30/11/02	--	--	--	0.2*	23.6	35.5	3800	--	4.0	56

Hooley Pool (21º52'50"S, 117 º59'50"E) (Site13, variability in depth value = 47)
This is a headwater pool located within an upland tributary (Hooley Creek) of the river (Figure 2.1). The pool was moderate in size and depth, being slightly larger than Mallina Pool (Table 2.4, Plate 2.1.D). Local residents suggest that it has bank storage, which when receiving good annual recharge allow the pool to remain in good condition. Masini (1988) classified it as a semi-permanent claypan. During this study the pool underwent great fluctuations in depth, finally drying in late 2002 (Plate 2.2.D). The pool had, in general, steep banks and a substrate of medium to fine-grained alluvium (Masini 1988). Habitat heterogeneity was lower than at most other sites; for while a large fraction of the substrate was covered by submerged macrophytes, this tended to be only one species, the stonewort (*Chara* sp.). The pool contained packs of leaf litter and woody debris, but had low abundance of macroinvertebrate fauna. The pool had a well developed riparian zone whose overstorey was dominated by the river red gum (*E. camaldulensis*), coolabah (*E.*

victrix), *Sesbana* sp and *Acacia cariacea* (Plate 2.3.D). These large trees shaded a large surface area of the pool keeping the water temperatures low. The understorey consisted of spinifex (*T. longiceps*), *C. involucratus* and buffle grass (*C. ciliaris*). Freshwater turtles were observed in August 2001. A description of the physico-chemical properties of the pool is provided in Table 2.4.

Table 2.4. Physico-chemical properties of Hooley Pool during sampling (December 2000-December 2002). DO refers to the concentration of dissolved oxygen. '--' = not available.

Date	Surface Area (m^2)	Length (m)	Width (m)	Maximum Depth (m)	Water Temp. (°C) AM	Water Temp. (°C) PM	Conductivity (µS/m)	pH	DO (mg/L) AM	Turbidity (ntu)
15/12/00	--	--	--	1.0	27.9	--	2270	--	--	1
09/05/01	7200	300	24	1.5	23.8	26.1	2040	8.1	8.2	3
28/08/01	5500	250	22	1.4	17.5	22.6	2016	7.8	8.1	14
03/12/01	4000	200	20	0.4	23.3	29.2	2743	7.3	3.6	3
05/02/02	--	--	--	0.3	24.1	--	3114	8.2	2.5	4
20/03/02	--	--	--	0.8	27.4	30.6	920	8.0	3.6	18
30/04/02	3900	195	20	0.3	21.3	25.1	1263	7.3	NA	7
21/08/02	0	0	0	0.0	pool dry					
02/12/02	0	0	0	0.0	pool dry					

Portland Pool (21º30'18"S, 117º02'52"E) (Site 6, variability in depth value = 61)
This is a headwater pool located within an upland tributary (Portland River) of the Fortescue (Figure 2.1). This pool was moderate in size and depth, being of similar dimensions to Hooley Pool (Table 2.5, Plate 2.1.E), but it was considerably more ephemeral; drying during the dry season of 2001 and 2002 (Plate 2.2.E). The pool had shallow banks and considerable heterogeneity of substrate types, which included fine-grained alluvium, mud, and bedrock. Submerged macrophytes included *Chara* sp., *Nitella* sp., *Myriophyllum* sp. and *P. tricarinatus*. Emergent macrophytes were rare. The riparian zone consisted of *C. involucratus*, buffle grass (*C. ciliaris*), *Sesbania* sp. and *Acacia* sp.. There were only a handful of river red gums (*E. camaldulensis*) and coolabahs (*E. victrix*) and consequently the pool received a large amount of sunlight (Plate 2.1.E). Freshwater turtles were found in April 2001. A description of the physico-chemical properties of the pool is provided in Table 2.5.

Table 2.5. Physico-chemical properties of Portland Pool during sampling (December 2000-December 2002). DO refers to the concentration of dissolved oxygen. '--' = not available.

Date	Surface Area (m^2)	Length (m)	Width (m)	Maximum Depth (m)	Water Temp. (°C) AM	PM	Conductivity (µS/m)	pH	DO (mg/L) AM	Turbidity (ntu)
10/12/00	--	--	--	1.0	27.4	--	18180	--	--	1
02/05/01	3000	150	20	1.5	24.9	29.3	2490	9.0	8.3	7
19/08/01	2030	70	29	1.0	19.7	--	4430	9.3	9.1	6
27/11/01	225	15	15	0.3	23.0	32.4	31560	8.3	2.1	37
07/02/02	0	0	0	0.0	pool dry					
16/03/02	--	--	--	2.2	27.6	30.8	366	8.4	5.8	252
20/04/02	6900	230	30	2.0	24.7	28.2	768	8.1	--	13
13/08/02	3390	113	30	1.0	18.9	21.9	1596	8.7	8.3	6
28/11/02	--	--	--	0.2	--	--	--	--	--	--

Railbridge Pool (21º27'21"S, 116º49'20"E) (Site 5, variability in depth value = 96)
This small pool was man-made. It was situated between the Pannawonica-Hamersley Iron Access Road and the Robe River railway, several kilometres north of the rail bridge over the Fortescue River (Figure 2.1). While its construction was anthropogenic its inhabitants were of natural origin, being sourced from a small headwater stream that lay on the other side of the road. This highly transitory pool provided an opportunity to examine the 'colonising' fish community. It was chosen over a natural pool because its greater depth enabled it to hold water for longer, hence allowing the sampling of a community which normally exists for only a brief period of time, and which is often difficult to access. The pool was considerably smaller than all other focal sites (Plate 2.1.F, Table 2.6), and although deep was considerably more ephemeral than Portland Pool (Plate 2.2.F). The pool had relatively steep banks and remarkable habitat heterogeneity considering its size. The substrate was rocky around the fringes and mud in the centre. Submerged macrophytes were dense and included *Chara* sp., *P. tricarinatus*, and *C. involucratus*. Macroinvertebrates were abundant and diverse. The riparian zone consisted of buffle grass (*C. ciliaris*) and snakewood (*A. xiphophylla*) (Plate 2.3.F). The pool received virtually no shading. The pool contained freshwater turtles, and while it contained fish in 2000 and 2001, the smaller amount of rain received in the summer of 2001/2002 meant that this site probably did not reconnect to the natural stream and in 2002 it contained only tadpoles. A description of the physico-chemical properties of the pool is provided in Table 2.6.

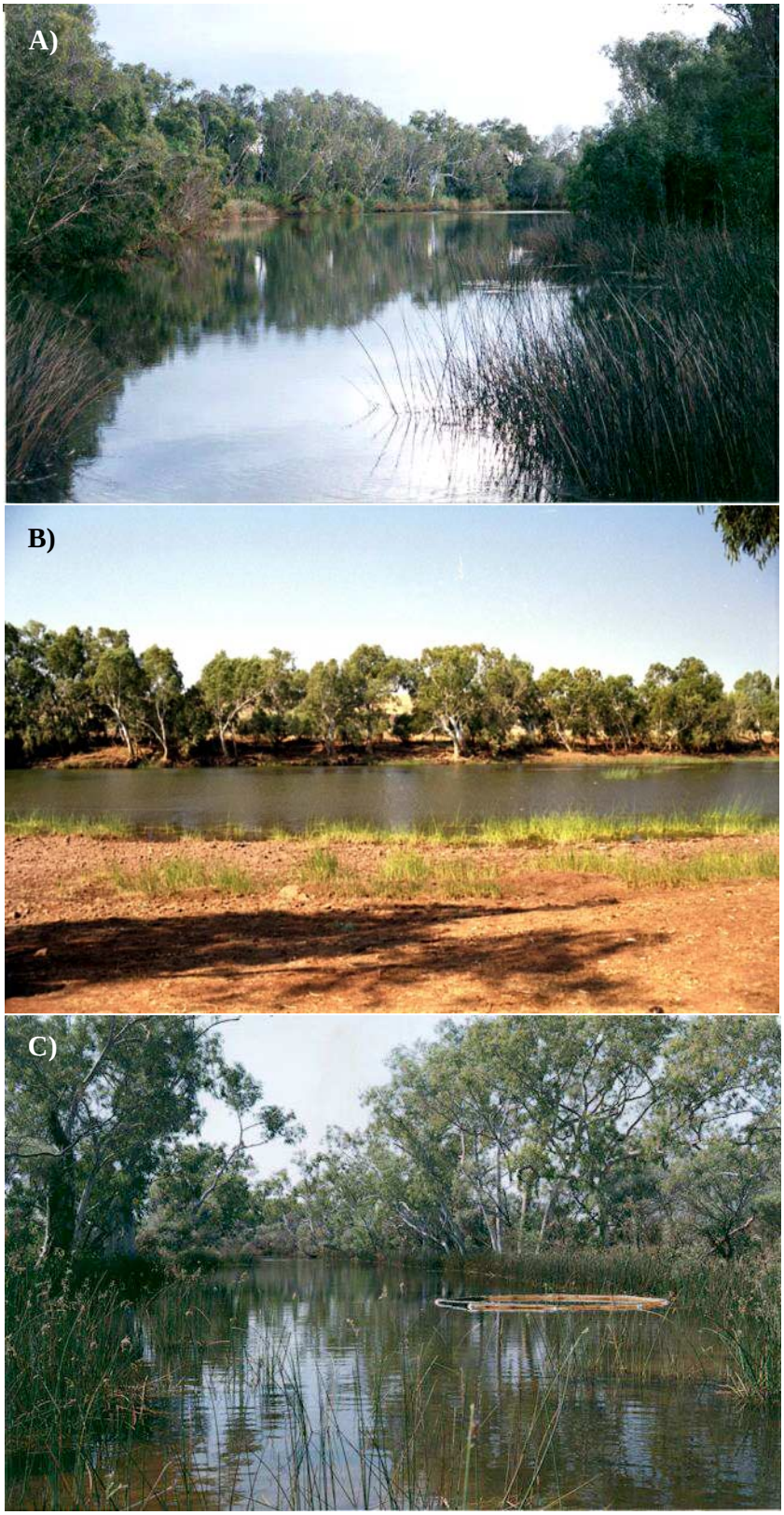


Plate 2.1. The six primary study pools in relatively full condition. Pools are displayed in decreasing order of persistence: Palm (A), Bilanoo (B), Mallina (C), Hooley (D), Portland (E), and Railbrige (F). The plate continues over the page.

Plate 2.1 (Continued). The six primary study pools in relatively full condition. Pools are displayed in decreasing order of persistence: Palm (A), Bilanoo (B), Mallina (C), Hooley (D), Portland (E), and Railbrige (F).

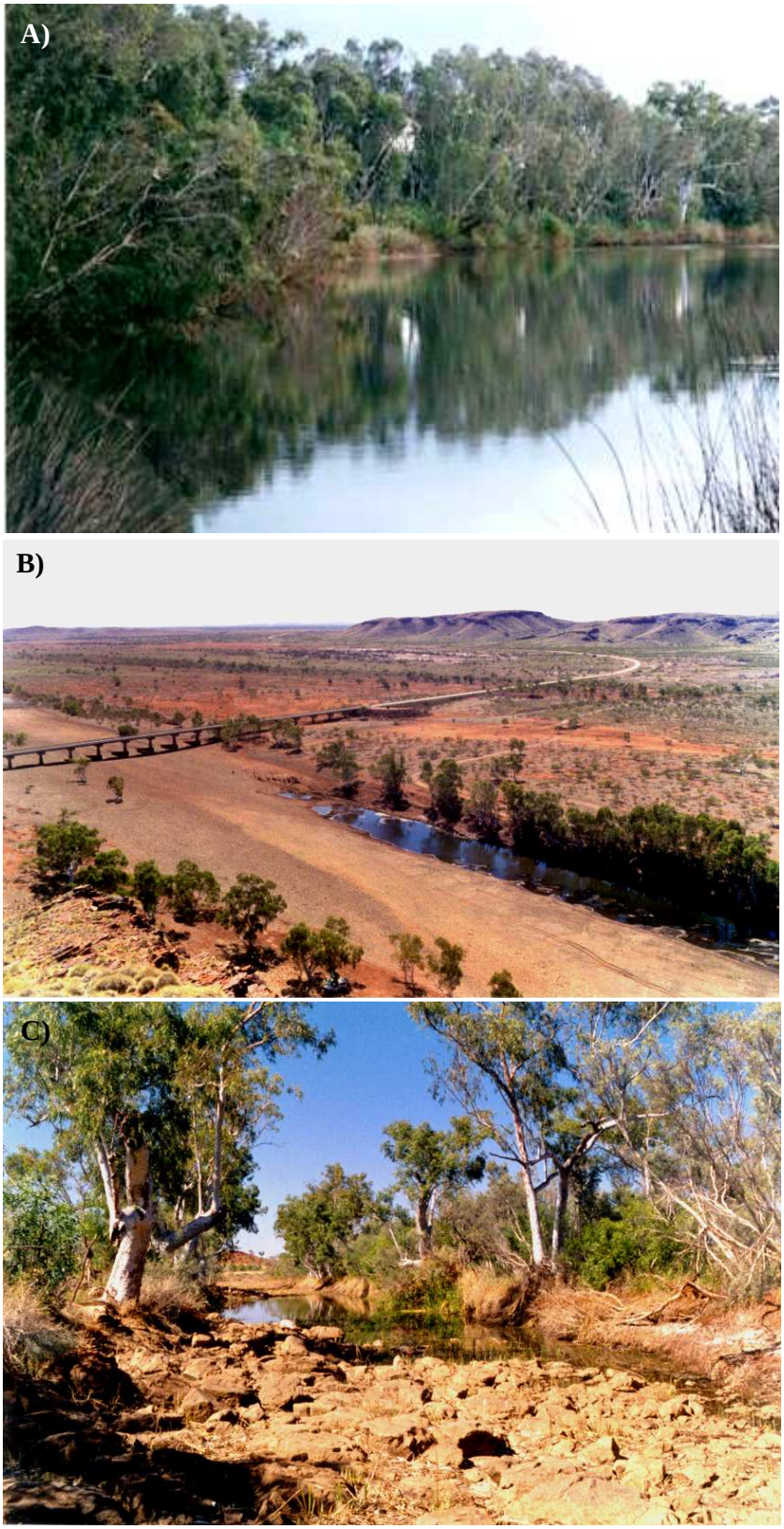


Plate 2.2. The six primary study pools following drought conditions. Pools are displayed in decreasing order of persistence: Palm (A), Bilanoo (B), Mallina (C), Hooley (D), Portland (E), and Railbrige (F). The plate continues over the page.

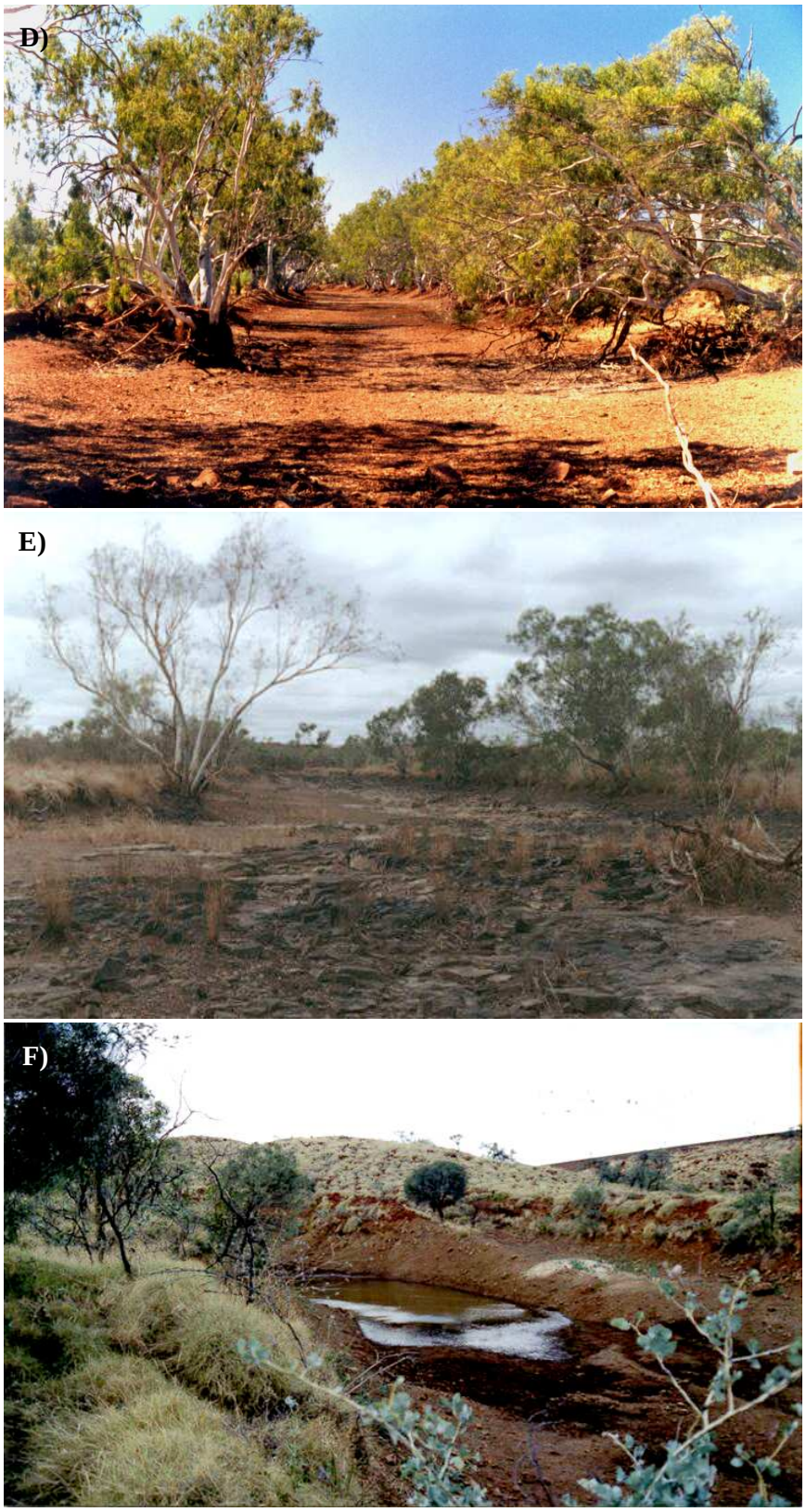


Plate 2.2 (Continued). The six primary study pools following drought conditions. Pools are displayed in decreasing order of persistence: Palm (A), Bilanoo (B), Mallina (C), Hooley (D), Portland (E), and Railbrige (F).

Table 2.6. Physico-chemical properties of Railbridge Pool during sampling (December 2000-December 2001). DO refers to the concentration of dissolved oxygen. '--' = not available.

Date	Surface Area (m^2)	Length (m)	Width (m)	Maximum Depth (m)	Water Temp. (°C) AM	PM	Conductivity (µS/m)	pH	DO (mg/L) AM	Turbidity (ntu)
07/12/00	330	30	11	0.7	28.2	31.6	650	--	4.2	21
30/04/01	1200	80	15	3.3	26.2	28.3	379	9.3	3.1	7
17/08/01	600	50	12	1.8	18.7	---	475	8.5	8.5	13
26/11/01	0	0	0	0.0	pool dry					

Sampling Regime

Pools were sampled on nine occasions between December 2000 and December 2002. Sampling was stratified through the year to incorporate seasonal changes; that is, the 'wet season' (December to April) and the 'dry season' (May to November). Sampling occurred during the late wet/early dry (late April early May), the mid-dry (August), and late dry/early wet season (late November early December) of 2001 and 2002. Additional sampling occurred during the wet season to provide extra information on breeding biology. Details of each sampling trip are provided below.

The first sampling trip was in the late dry/early wet season between the 5th to the 15th of December 2000. Pools were still relatively full at this time as there had been a massive amount of rain (1:100 year rainfall event) the preceding wet season due to tropical cyclones John and Steve, and pools remained relatively full. The first summer rains were also starting to fall. The second sampling trip was in the late wet/early dry season from the 26th of April 2001 to the 10th of May. Pools were very full at this time, as notable rain had fallen during the summer. The third trip was in the mid dry season between the 14th and the 20th of August 2001. The fourth trip was in the late dry/early wet season from the 21st of November to the 4th of December 2001. The ephemeral pools had shrunk considerably by this time; Railbridge Pool was completely dry and Portland pool was very close to disappearing. Sampling was concentrated over the 2001/2002 wet season, with the 6th and 7th trips in February (2nd–8th) and March (15th–20th) 2002. No rain fell in December or January, so pools were markedly shrunken for the February trip. Rain did fall in late February and March; however, it was a relatively small amount and was highly localised. Bilanoo Pool received no direct or indirect (via stream flow) inputs of water and continued to

shrink. Mallina, Hooley, and Railbridge Pools received small to moderate amounts of water, increasing in size but not filling. Portland and Palm Pool received considerable amounts of water, which refilled Portland Pool. The seventh trip was during the late wet / early dry season from the 14th of April – 1st of May 2002. Pools which had received rain had started to shrink again, and all pools except Portland and Palm Pool, where much smaller than they had been in April 2001. The eighth trip was during the mid dry-season from the 7th–21st of August 2002. By this time, Hooley and Railbridge Pools had dried completely and Mallina Pool was markedly shrunken. The ninth and final trip was during the late dry/early wet season from the 26th November – 1st December 2002. The summer rains had not started and pools were considerably shrunken. Portland Pool had overtaken Mallina Pool and was within days of drying. It contained only a small pool of stagnant water and no fish were present. Bilanoo Pool was markedly reduced from its former size, but Palm Pool remained relatively unchanged. Changes in the maximum depth of the six primary study pools through time are shown in Figure 2.4.

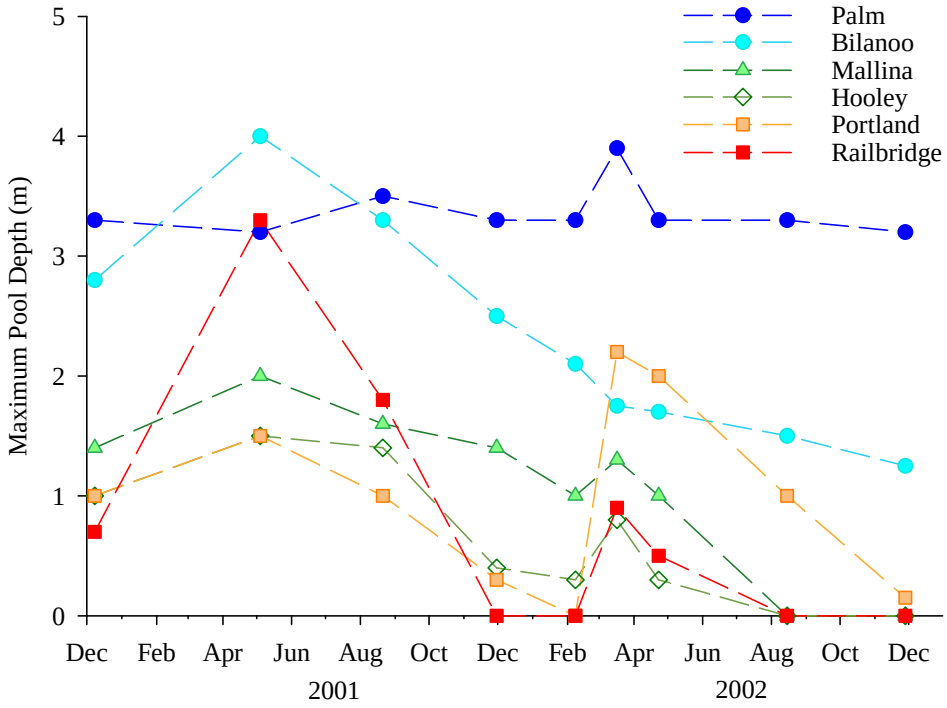


Figure 2.4. Variation in the maximum depth of the six primary study pools during the nine sampling occasions between December 2000 and December 2002.

The Fish Fauna

The Fortescue River contains 91% (10 of 11) of the surface-dwelling freshwater (and catadromous) fish species of the Pilbara region (Allen *et al.* 2002, Morgan and Gill 2004). Fishes include three species of terapontids: *Leiopotherapon unicolor* (spangled perch), *L. aheneus* (Fortescue grunter) and *Amniataba percoides* (barred grunter); one clupeid, *Nematalosa erebi* (freshwater herring); one ariid catfish, *Arius graeffei* (lesser salmon catfish); one plotosid catfish, *Neosilurus hyrtlii* (Hyrtl's tandan); one melanotaeniid, *Melanotaenia australis* (western rainbowfish); one gobiid, *Glossogobius giurus* (flathead goby); one eleotrid, *Hypseleotris compressa* (empire gudgeon); and finally one anguillid, *Anguilla bicolor* (Indian short-finned eel). Species not found in the Fortescue River include the Murchison River hardyhead, *Craterocephalus cuneiceps* (Allen *et al.* 2002, Morgan and Gill 2004).

Estuarine species were also found at sites near the river mouth and sometimes further upstream. These include: *Lutjanus argentimaculatus* (mangrove jack), *Megalops cyprinoides* (oxeye herring), *Elops hawaiensis* (giant herring), *Mugil cephalus* (mullet), *Gerres filamentosus* (threadfin silver biddy), *Caranx sexfasciatus* (bigeye trevally), and *Selenotoca multifasciata* (banded scat).

While this research recorded the presence and abundance of all freshwater species, it focused on the biology of the five most abundant species: *L. unicolor*, *L. aheneus*, *A. percoides*, *N. erebi*, and *M. australis* (Plate 2.3). Information on the biology of three of these species is available, but virtually all research had been carried out elsewhere in the country, principally in the wet-tropical regions of the Northern Territory (Bishop *et al.* 2001), and Queensland (Beumer 1979, Pusey *et al.* 1995, Pusey *et al.* 2004). Geographic variation in biology has been reported for some of these species (Pusey *et al.* 2004) and consequently their applicability to Fortescue populations was unknown. A general description of the biology of each species is provided below.

Leiopotherapon unicolor (Plate 2.3.A)

More is known of this fish species than any other living in the Fortescue River. This is probably because of its abundance and widespread distribution across the northern half of the continent (Allen *et al.* 2002). It is 30 cm (maximum length) (Allen *et al.* 2002), and capable of tolerating extremes in the aquatic environment (Llewellyn 1973, Beumer 1979, Glover 1982). It inhabits a wide range of aquatic habitats (Glover

1982, Bishop *et al.* 2001) and in some systems is found in greater abundances in tributary or upstream reaches (Bishop *et al.* 2001). It is an aggressive omnivore (Lake 1978, Merrick and Schmida 1984, Bishop *et al.* 2001), which is known to undertake rapid migrations (Bishop *et al.* 2001). It is thought to reach maturity within one year (Llewellyn 1973, Bishop *et al.* 2001) and typically spawns during the summer wet season (Llewellyn 1973, Beumer 1979, Bishop *et al.* 2001).

Amniataba percoides (Plate 2.3.B)

This species also has a wide distribution across northern Australia (Allen *et al.* 2002), but it has received relatively little attention. It is 18 cm (maximum length) (Allen *et al.* 2002), and occurs in pools with a wide range of pH and temperature (Bishop *et al.* 2001), but is thought to be adversely impacted by low oxygen levels (Pusey *et al.* 2004). It inhabits a wide range of aquatic habitats but is rarely found in high gradient streams (Pusey *et al.* 2004). Its diet is opportunistic but predominantly consists of aquatic insects (Bishop *et al.* 2001). It is thought to mature within a year and in Northern Territory populations it spawns during the summer wet season (Bishop *et al.* 2001).

Leiopotherapon aheneus (Plate 2.3.C)

This is a regional endemic, found only in the Fortescue, Robe and Ashburton Rivers (Allen *et al.* 2002). It is 13 cm (maximum length) (Allen *et al.* 2002), and feeds on small crustaceans and juvenile fish (Allen *et al.* 2002). Little else is known of its biology.

Nematalosa erebi (Plate 2.3.D)

This species is widely distributed, being common across northern Australia, and in inland rivers of south eastern Australia (Allen *et al.* 2002). It is 32 cm (maximum length) (Allen *et al.* 2002), and occurs in pools with a wide range of pH and temperature (Pusey *et al.* 1998, Bishop *et al.* 2001). However, it is susceptible to low oxygen levels (Bishop *et al.* 2001, Allen *et al.* 2002) and cold water (Lake 1971). It is a detritivore (Pusey *et al.* 1995), and is commonly found in deep water (Puckridge and Drewien 1988). The life history characteristics of this species vary considerably across the continent. In South Australia it grows relatively slowly, taking several years to mature, and breeds once a year, during the low-flow period of summer

(Puckridge and Walker 1990). In the Northern Territory it grows relatively quickly, reaching maturity in under one year, and is thought to breed several times during the year, but principally during the early wet season (Bishop *et al.* 2001).

Melanotaenia australis (Plate 2.3.E)

This rainbowfish occurs in the Pilbara and Kimberley regions of north Western Australia (Allen *et al.* 2002). It is 11 cm (maximum size) (Allen *et al.* 2002) and occupies a wide range of habitats (Allen *et al.* 2002). There have been few studies on this species, but data are available for other species within the same genus (Pusey *et al.* 2004). Rainbowfish are colourful and relatively hardy fish that breed throughout the year (Allen *et al.* 2002, Pusey *et al.* 2004).

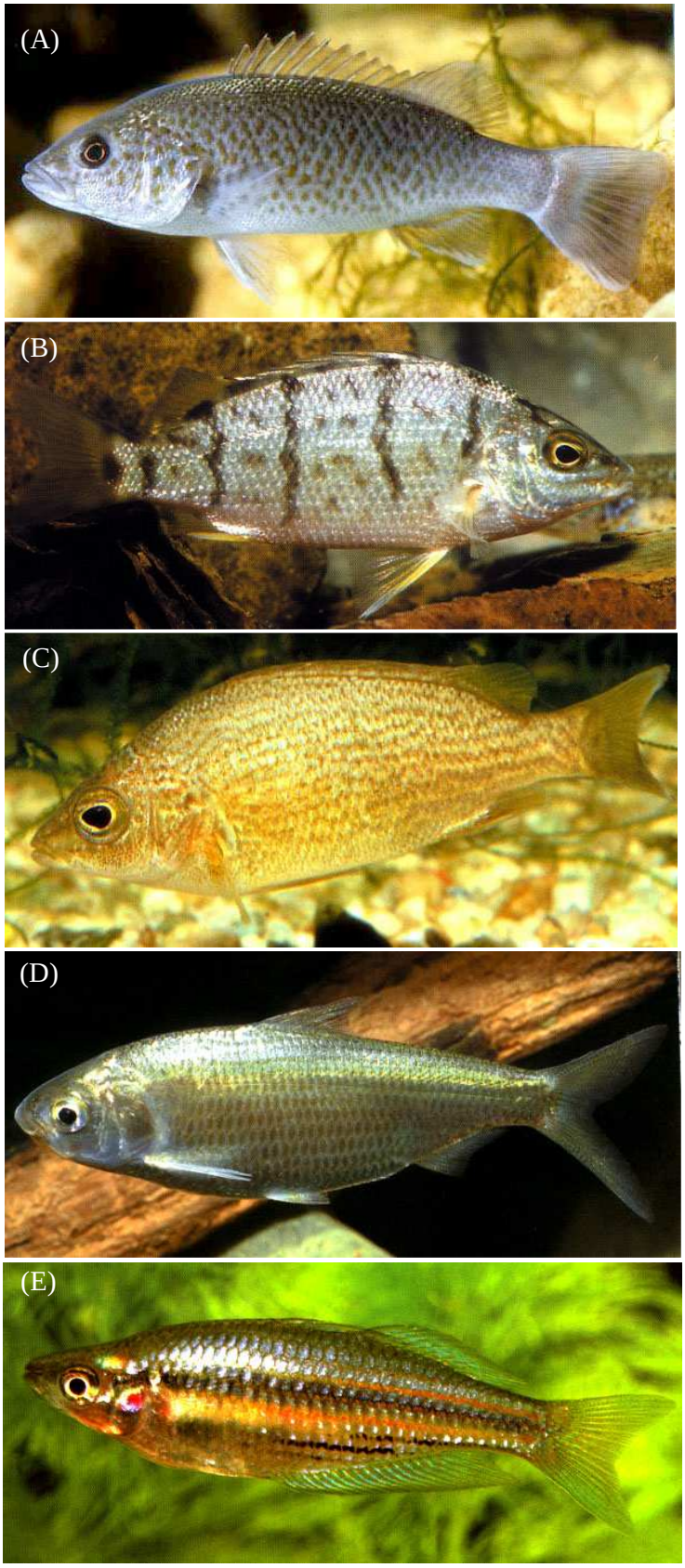


Plate 2.3. Focal species of the study: (A) *L. unicolor*, (B) *A. percoides*, (C) *L. aheneus*, (D) *N. erebi*, (E) *M. australis*. Photographs are courtesy of Allen *et al.* (2002), and are not to scale.

Chapter 3

Sampling the Fish Community

Introduction

Accurate sampling of fish communities is a necessity for ecological research and management programmes alike (Allen *et al.* 1999). Unfortunately, all methods of fish collection introduce some sort of bias into community and population estimates (Allen *et al.* 1999). Biases may be associated with the sampling design, but are commonly associated with the fishing technique used (Andrew and Mapstone 1987). Fishing techniques introduce bias when they do not catch a representative sample of the fish present. For example, gill nets tend to overestimate numbers of large pelagic fish (Knight and Bain 1996), and electrofishing also favours large individuals (Mahon *et al.* 1979, Reynolds 1983).

To minimize these biases researchers have devised different solutions. Some use block-nets to section off a segment of the stream, and make multiple passes using a seine net or backpack electrofisher (Mahon and Balon 1980, Lyons 1986, Copp and Penaz 1988, Knight and Bain 1996, Perrow *et al.* 1996). In this way, fish initially missed by the seine or electrofisher are eventually caught. Others use pop-nets or drop-nets to section off a small area of the stream, and then collect the fish within them (Hellier 1958, Kushlan 1974, Morgan *et al.* 1988, Espegren and Bergersen 1990, Trexler *et al.* 2000).

The above methods have the added advantage of producing an estimate of the number of fish per-unit-area (density), whereas other methods, such as gill netting or point source electrofishing provide a catch per-unit-effort (e.g. the number of fish collected in one hour of sampling effort). Density estimates can be extrapolated to provide estimates of the total abundance within a given area. This is particularly helpful when studying ephemeral water bodies, where catch per-unit-effort is likely to increase as the stream dries even though total abundance may fall.

When sampling is conducted in deep, complex, freshwater habitats, drop-nets are the preferred method to obtain density estimates (Kushlan 1974). This is because deep water makes it difficult to electrofish, and submerged aquatic vegetation and/or rocky substrates make it difficult to use a seine net (Perrow *et al.* 1996, Vaux *et al.* 2000).

Pop-nets are inappropriate as they sit over the complex substrate prior to deployment and benthic species are likely either to avoid or to be attracted to the sample area (Kushlan 1974).

In the freshwater environment, the most widely deployed drop-nets (and a modified version, drop-traps) are those based on a design by Kushlan (1974). While these nets are portable, most of them are small in area (1 m^2), and shallow in depth (Freeman *et al.* 1984, Jacobsen and Kushlan 1987, Chick *et al.* 1992, Trexler *et al.* 2000). The shallow depth of these nets precludes them from sampling deep-water habitats, and their small area may reduce their capacity to collect large fish (Jacobsen and Kushlan 1987). Larger and deeper drop-nets have been designed (Moseley and Copeland 1969, Kjelson and Johnson 1973) with a pursing mechanism at the base of the net which is activated after the net has fallen. This traps fish within the net, aiding in their collection. However, these nets were not designed to sample over the complex substrates that typify the pools of the Fortescue River, hence are unlikely to close correctly in such an environment.

To overcome this problem a modified drop-net was designed. This chapter provides a description of the net and evaluates its relative efficiency (catch per-unit-effort) by comparison with other standard fishing techniques (panel gill nets and a beach seine). The ability of the net to describe accurately the fish community of the Fortescue River was determined by comparing the fish it caught with those collected following the addition of a toxicant.

Methods

Drop net Description and Operation

The mobile drop-net consisted of three main components: a rigid aluminium frame, a detachable cylindrical net, and a pulley system (Figure 3.1.A, Plate 3.1.A). The octagonal aluminium frame had 2 m long sides made of 25 mm diameter piping with a 1.6 mm wall thickness. The sides of the frame were joined using T-pieces, enclosing an area of 19.3 m^2. The T-piece joins had horizontal arms with a 32 mm diameter, and a vertical arm with a 25 mm diameter. Both had a 1.6 mm wall thickness.

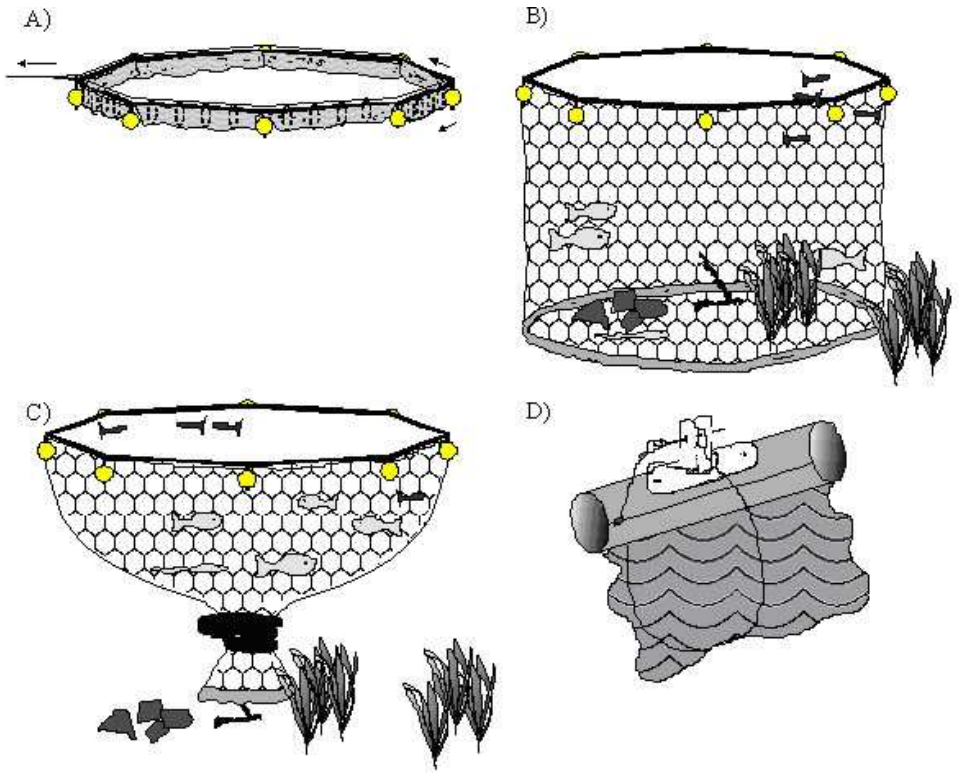
Two buoys (15 cm diameter) were attached to the vertical arm of each T-piece join, to provide positive buoyancy. The net (1.5 mm x 1.0 mm or 1/16″ mesh) had a fall of 4.5 m and was attached to the inside of the frame using clips of PVC piping. The base of the net was reinforced by gluing robust fabric (60 cm deep) to the skirting. An 8 mm chain was attached to the reinforced skirting of the net by a roll-up pocket, which was closed using Velcro. The net (with chain) was gathered to the frame and held in place using pieces of trace wire (1.5 mm diameter) that were attached to the frame. Each trace wire (four per side of the frame) circled the gathered net and was held to the frame using a pin. The pin joined the loop in the free end of the piece of trace wire to a horizontal double stay-put fastener that was riveted onto the frame (Figure 3.1.D). Two lengths of trace ran in opposite directions away from one corner of the frame, linking pins and meeting to join a 30 m rope that acted as a remote trigger (Figure 3.1.A). A sharp tug on the trigger pulled the pins, releasing the pieces of trace wire, allowing the chain to drop the curtain of mesh to the riverbed. The chain was flexible enough to adjust to the contours of the riverbed (Figure 3.1.B).

Prior to activation, the net was positioned using two anchors (dive weights attached to a rope) and left for half an hour. Field observations indicated that half an hour was sufficient for fish to resume normal activity. Once the net was activated, a diver using SCUBA gear swam the circumference of the net, pushing the chained skirting towards the centre. The skirting was quickly lifted over rocks and logs, while fish were scared inwards away from the curtain edge. After several circumnavigations the chain was bunched in the centre (Figure 3.1.C, Plate 3.1.B). A cord was tied around the net, just above the chain, trapping all fish. The anchors and chain were lifted and the net was moved into the shallow water. Two people then stood inside the net and pulled up the mesh from the centre to the edge and worked toward one another. Fish were collected with a dip net. Successive passes of the net were made, until three consecutive passes failed to find fish.

Study Areas

To minimize the impact of this study on local fish populations, three pools, which had a high chance of drying prior to the summer rains, were used. While all three pools were relatively small and shallow, they differed considerably in other physical aspects, incorporating many of the variations found in the region (Table 3.1). Two pools were located within the Fortescue River catchment (Pool A 21°17’46”S,

116°08’29”E, Pool C 21°43’46”S, 117°45’49”E), the other within the Harding River catchment (Pool B 21°19’33”S, 117°04’42”E). The Harding River lies adjacent to the Fortescue.



3.1. A diagram of the drop-net and its deployment; A: net prior to activation, B: net released, C: net gathered. D shows the way in which the curtain of netting is held in place prior to release. Trace wire encircles the mesh and is kept in place using a pin, which is pulled during the release of the net by a piece of trace wire which runs around the frame of the net (see A).

Table 3.1. The physical parameters of the three study pools. Surface area was estimated by measuring pool width in four locations along the pool, and multiplying the average width by pool length. Average depth was estimated from measurements taken every 3 m, along four transects which were laid across the width of the pool. Visibility and the level of habitat complexity were assessed visually and ranked. The amount of macrophytic cover was also estimated by eye.

	Pool A	Pool B	Pool C
Surface area (m^2)	315	522	675
Maximum depth (m)	1.3	1.5	1.5
Average depth (m)	0.9	0.7	0.5
Visibility	Good	Poor	Nil
Macrophyte cover (%)	80-90	<10	<5
Substrate	Rocks and cobbles	Bedrock and gravel	Rocks and mud
Level of habitat complexity	High	Moderate to Low	Low

Plate 3.1. The drop-net. (A) the net gathered ready to be triggered, (B) the net after it has been triggered, gathered and brought to shore for dip net collection of the fish.

Sampling procedure

At each pool the same sampling effort (3 h) was used for each technique, excluding the rotenone treatment. Effort included setting the device, using it and collecting all fish caught. The time required by each technique determined the number of

applications. The drop-net took one hour per application, hence was deployed three times at each site. Two monofilament panel gill nets (each with four 3 m panels and a drop of 1.3 m) took 1.5 h per application (set for 1 h), and were deployed twice at each site. One gill net contained large mesh sizes (50.8, 60.3, 76.2, and 101.6 mm) and was set in the deep-water section of the study pool. The other net contained small mesh sizes (12.7, 19.0, 25.4 and 28.6 mm) and was set within the shallow-water section. Gill nets were set perpendicular to the bank. The beach seine was deployed in various sections of the pool for a total of 3 one-hour bouts. The wings of the seine were 25 m long, 2 m deep, and made of 28.4 mm mesh. The centre panel was 5 m long and made of 3.2 mm mesh. Two people deployed the seine. One would stay close to the bank, holding the far side of the fine center panel, the other holding the end of the other wing would walk out into the pool (perpendicular to the bank) and circle back towards the bank. The wing mesh was gathered in as the operator approached the bank and fish were trapped in the fine mesh section. The lead line was kept as close to the substrate as possible.

The location of sampling (for each technique) within a pool was organized so that habitats were sampled in proportion to their relative abundance. Techniques were not employed sequentially during the day (0800 h to 1700 h); rather, the applications of each method were randomized. For example, a pool was sampled by one use of the drop-net, then a 1 h period of seining, then the drop-net, an application of the gill nets and so on. Following each sampling period fish were identified, measured (fork length), and returned to the pool. The pool was left for half an hour before commencement of the next sampling event. Once sampling was complete, rotenone, a fish toxicant, was added to the site to assess the accuracy of the different methods (Hockin *et al.* 1985, Jacobsen and Kushlan 1987). The rotenone was dissolved in a solution of soapy water and enough was dispensed around the pool to create an approximate concentration of 1-2 mg/L (for a discussion of sampling with rotenone see Davies and Shelton 1983). Affected fish were collected over the next 24 hrs. Snorkelling was used in deep-water sections to collect fish that had sunk.

Statistical analyses

A suite of community descriptors was used to assess the efficiency and accuracy of the various fishing techniques. Descriptors included: species richness (number of species caught), abundance (the total number of individuals caught), percentage

similarity index (PSI, the similarity in assemblage composition for fish collected by two different fishing techniques), and size selectivity (size-frequency distribution). The percentage similarity index used was PSI = $\Sigma\min(p_{1i}, p_{2i})$, where p_{1i} and p_{2i} are the % of individuals of the i^{th} species in samples 1 and 2 respectively (Krebs 1999).
Species richness and abundance were compared between fishing techniques (drop-net, gill nets, and seine net) using two-way ANOVA without replication, with techniques as the main effect and the sites as blocks (in the analysis). A disadvantage of a two-way ANOVA without replication is that it cannot examine the interaction between factors (i.e. techniques and sites), and any interaction will reduce the power of the test, particularly if both factors are fixed (Zar 1999). In this case site was considered a random factor because sites were not chosen specifically and this meant that it was possible to test the effect of fishing technique (Zar 1999). The effect of site was not investigated statistically; patterns were gleaned by examining the data directly.

Prior to the analyses data within each group were tested to see if they conformed to parametric assumptions of normality and homogeneity of variance (Zar 1999). Abundance data were $\log_{10}$ (n+1) transformed prior to analyses. The size selectivity of the various methods was examined using Kolomorogov-Smirnov two sample tests (Siegel and Castellan 1988).

Results

A total of 8021 fish were captured during the study: 990 fish were caught using the drop-net, 998 using the seine net, 42 using the gill nets, and 5991 using the rotenone. A total of 12 species (freshwater and estuarine) were collected during the study: 11 in pool A, 1 in pool B and 7 in pool C.

Efficiency
There was no statistical difference in the number of individuals caught by the drop-net, seine net, and panel gill nets during three hours of effort (Table 3.2). However, this result was largely due to limitations in sample size (ANOVA without replication) as the F-value for the effect of fishing technique was large (above 4) (Table 3.2). Examination of the raw data revealed that the drop-net and seine net caught many

more individuals than the panel gill nets (Figure 3.2.A). The effect of site could not be examined statistically, but the raw data suggested that there was an interaction between fishing technique and site. For example, the drop-net caught more than two times the number of fish as the seine at pool A, whereas the seine caught over three times more fish at pool C (Figure 3.2.A, Table 3.3). The drop-net caught many more *Melanotaenia australis* and *Hypseleotris compressa* at pool A, whereas the seine net caught more *Nematalosa erebi* and *M. australis* at pool C (Table 3.3).

There was no statistical difference in the number of species caught by the drop-net, seine net, and panel gill nets during three hours of effort (Table 3.4). This result was largely due to limitations in sample size (ANOVA without replication) as the F-value was large (above 4). The raw data revealed that the drop-net and seine net caught more species than the panel gill nets (Figure 3.2.B). The gill nets did not catch the small pelagic species such as *M. australis* and *H. compressa*, and did not catch the benthic species *Glossogobius giurus* and *N. hyrtlii* (Table 3.3). Once again, the effect of site could not be examined statistically; however, site differences clearly occurred. Pools A and C contained many more species than Pool B, which contained only one species, *Leiopotherapon unicolor* (Figure 3.2.B, Table 3.3).

Percentage similarity indices revealed that fish assemblages caught by the drop-net and the seine net were much more similar than those caught by the gill nets, particularly in pools A and B (Table 3.5). The gill nets failed to catch many of the benthic species, overestimating the contribution of large pelagic species such as *N. erebi*, *Megalops cyprinoids* and *Mugil cephalus* (Table 3.3).

The drop-net, seine net, and gill nets all caught different size distributions of fish (Table 3.5, Figure 3.3). The gill nets caught only the largest size classes (Figure 3.3). The drop-net and the seine caught a similar size range of fish, however size frequency distributions varied between sites. At pool B, where only one benthic species occurred (*L. unicolor*), and there were few macrophytes both techniques produced the same results (Table 3.5, Figure 3.3.B). At pools A and C where within-pool habitat and fish assemblage structure were more complex, the two techniques generated different results (Table 3.5, Figure 3.3.A, C). For example, pool A contained a great number of large rocks and dense vegetation, making it difficult to use the seine, hence the drop-

net collected more of the small fish (*M. australis* and *H. compressa*) (Table 3.3). In contrast, pool C did not contain many snags, and the seine caught more of the small fish (*M. australis* and juvenile *N. erebi*) than the drop-net (Table 3.3).

Table 3.2. Two-way ANOVA without replication comparing the abundance [$\log_{10}(n+1)$] of fish collected using 3 hours of effort with the drop-net, gill net, and seine net, for the three study pools. The remainder MS was used to test the significance of fishing technique and site as per Zar (1999). The $Fcrit_{2,4\ \alpha=0.05\ (2\ sided\ test)}$ = 10.6, NS = not significant. The effect of site was not examined due to constraints of the ANOVA.

	SS	df	MS	F
Fishing technique	4.923	2	2.461	10.007 NS
Site (random)	0.586	2	0.293	NA
Remainder	0.985	4	0.246	

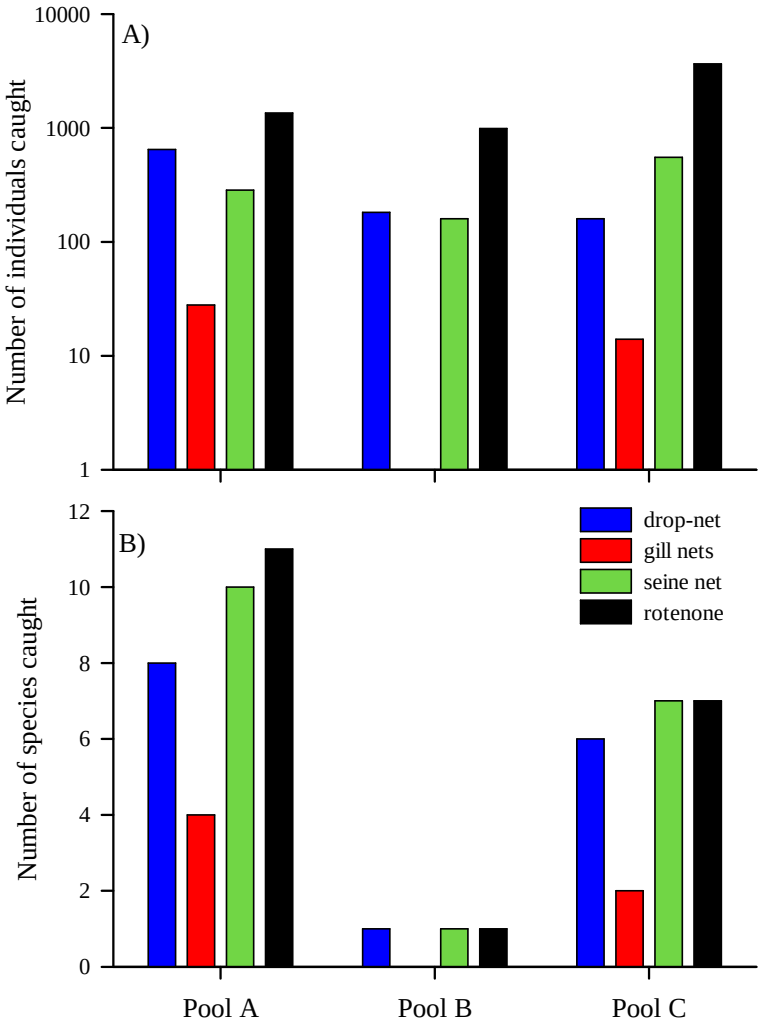


Figure 3.2. The number of individuals and number of species (of fish) caught using the various techniques at each pool. Fish caught using the drop net, gill nets, and beach seine were collected using the same amount of effort (3 h). Fish collected 'post-sampling' using rotenone are also shown.

Table 3.3. The number of individuals of each fish species collected from the study pools during three hours of effort with the drop-net, the beach seine net or the panel gill nets. The number of fish collected following the addition of the toxicant rotenone, have also been presented. * indicates estuarine species.

	Catch (number of fish)											
	Pool A				Pool B				Pool C			
Scientific name	Drop-net	Gill nets	Seine net	Rotenone	Drop-net	Gill nets	Seine net	Rotenone	Drop-net	Gill nets	Seine net	Rotenone
Amniataba percoides	10	9	9	25	0	0	0	0	57	0	32	460
Glossogobius giurus	20	0	17	388	0	0	0	0	1	0	1	34
Hypseleotris compressa	187	0	74	107	0	0	0	0	0	0	0	0
Leiopotherapon unicolor	4	0	2	44	182	0	160	988	15	1	18	733
Leiopotherapon aheneus	13	12	4	112	0	0	0	0	0	0	2	26
Melanotaenia australis	409	0	173	545	0	0	0	0	9	0	176	411
Nematalosa erebi	0	0	0	0	0	0	0	0	74	13	322	1260
Neosilurus hyrtlii	3	0	1	111	0	0	0	0	4	0	2	726
Anguilla bicolor	0	0	0	5	0	0	0	0	0	0	0	0
*Megalops cyprinoides**	2	3	2	4	0	0	0	0	0	0	0	0
*Selenotoca multifasciata**	0	0	1	3	0	0	0	0	0	0	0	0
*Mugil cephalus**	0	4	2	9	0	0	0	0	0	0	0	0
Total	648	28	285	1353	182	0	160	988	160	14	553	3650

Table 3.4. Two-way ANOVA without replication comparing the number of fish species collected using 3 hours of effort with the drop-net, gill net, and seine net, for the three study pools. The remainder MS was used to test the significance of fishing technique and site as per Zar (1999). The $Fcrit_{2,4\ \alpha=0.05\ (2\ sided\ test)} = 10.6$, NS = not significant. The effect of site was not examined due to constraints of the ANOVA.

	SS	df	MS	F
Fishing technique	26.000	2	13.000	4.727 NS
Site (random)	65.000	2	32.500	NA
Remainder	11.000	4	2.750	

Table 3.5. The percent similarity coefficient (PSI), of fish assemblages caught by any two of the sampling techniques are shown as a percentage above the diagonal. The observed 'D' value of the Kolomogorov-Smirnov two-sample tests which compare the size-distributions of fish caught by two sampling techniques are presented below the diagonal. * indicates that the two methods were significantly different at the alpha 0.05 level, ** indicates significance at the alpha 0.01 level. As no fish were caught using the gill nets at pool B, it was impossible to conduct Kolomogorov-Smirnov tests.

		Drop-net	Panel gill nets	Beach seine	Rotenone
Pool A	Drop-net		3.85	93.98	57.58
	Panel gill nets	0.93**		5.96	10.79
	Beach seine	0.15**	0.87**		60.94
	Rotenone	0.42**	0.52**	0.38**	
Pool B	Drop-net		0	100	100
	Panel gill nets	—		0	0
	Beach seine	0.10	—		100
	Rotenone	0.12*	—	0.16**	
Pool C	Drop-net		53.44	61.51	65.20
	Panel gill nets	0.69**		61.45	41.64
	Beach seine	0.65**	0.85**		55.71
	Rotenone	0.12*	0.56**	0.72**	

Accuracy

The addition of the toxicant, rotenone, to pools at the conclusion of sampling was undertaken to provide an accurate description of the fish present within each pool, thereby assess the accuracy of the drop-net. Unfortunately, while this method caught a large number of fish (n = 5991) it did have its own biases, which were made obvious by the fact that at pool A the drop-net collected nearly one-third as many fish as the

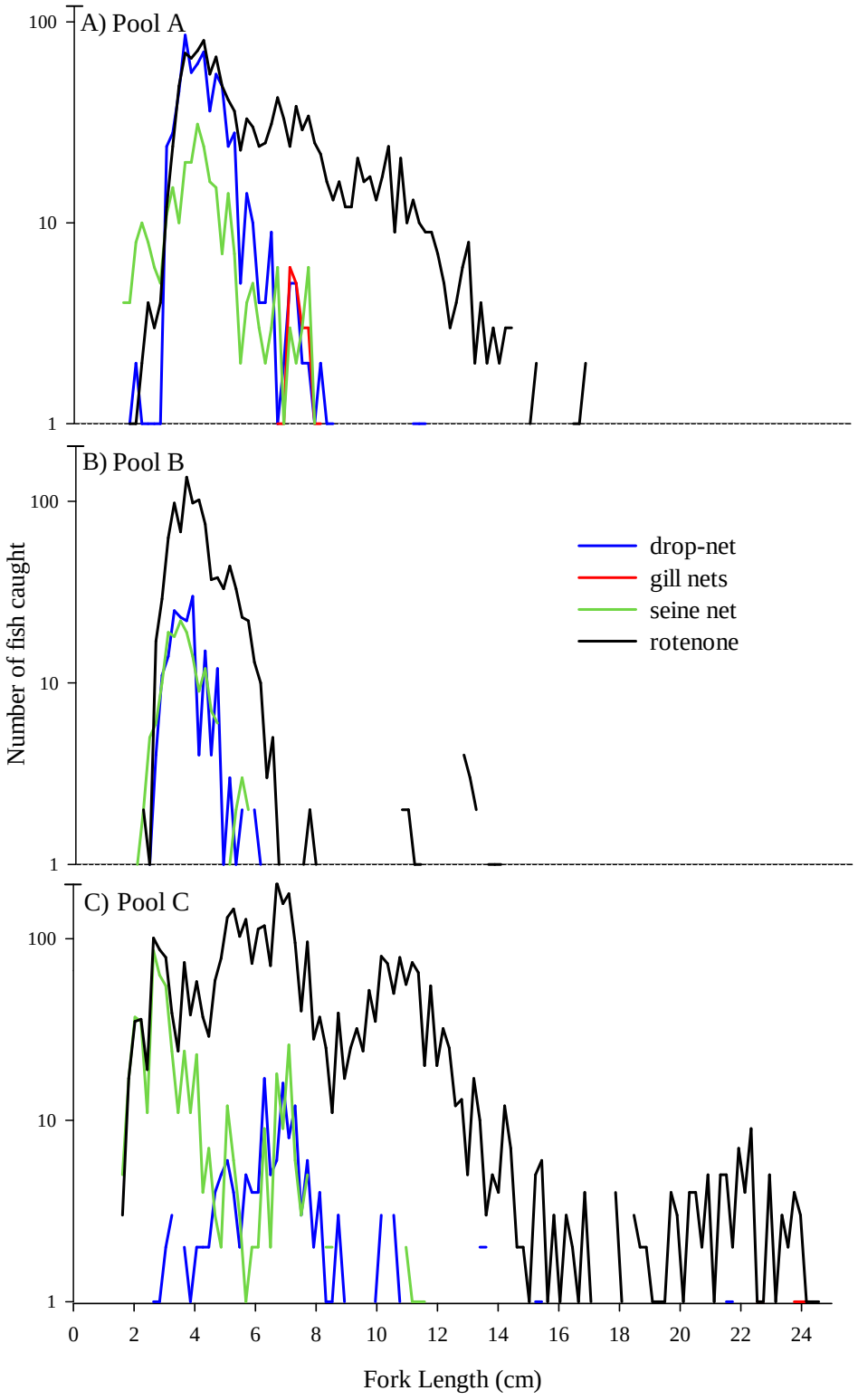


Figure 3.3. Size frequency distributions of the fish caught by the drop-net, the beach seine, and gill nets during 3 hours of effort. Fish collected following the addition of rotenone are also shown.

rotenone, even though it sampled one-sixth of the area. Bias associated with the rotenone was caused by poor collection of affected fish, rather than an inadequacy to affect fish, as all species except one, *H. compressa*, were disabled by the toxicant. The collection of fish was hampered at pool A by the dense weed, which although ensuring good visibility, made it very difficult to find fish, particularly small size classes. The collection of fish at pools B and C was severely hampered by poor visibility, and this was exacerbated in the deep-water sections. Fortunately, warm water temperatures accelerated gut fermentation and bloating, bringing many individuals to the surface.

Predation of affected fish was also noted (particularly at pools B and C), and would have further reduced the accuracy of this method. Predation of fish by other fish was associated with the presence of *L. unicolor*, an aggressive omnivore that was slow to succumb to the toxicant. Large individuals of this species were observed eating affected individuals of other species, and dissection revealed that many had stomachs packed with recently ingested fish. Predation by birds (cormorants, ravens, and kookaburras) was also observed, and the numbers of fish removed over the 24 h period of collection may be significant.

Although rotenone failed to provide a benchmark with which to assess the accuracy of the drop-net, it did collect a considerable number of fish (Table 3.5), and provided a 'better than most' means with which to assess the drop-net's ability to describe fish assemblages. In three hours of effort (sampling 16.5% of the surface area of pool A, 8.3% of pool B, and 4.3% of pool C) the drop-net did not collect all species present within the study pools (those collected by the rotenone) (Figure 3.2.B). However, species not collected were rare, representing <1% of all individuals collected (Table 3.5). The underestimation of species richness was most noticeable at pool A, which contained several estuarine species in low abundance. In three hours of effort, the drop-net caught fish assemblages that were on average 61% similar (Pools A and C), in terms of relative abundance, to those collected using rotenone (Table 3.6). At pool A the differences in similarity were caused by the drop-net underestimating the abundance of the benthic species, *G. giurus* and *N. hyrtlii*, and the rotenone underestimating the abundance of the pelagic species, *M. australis* and *H. compressa* (Table 3.5). At pool C the differences were caused by the drop-net underestimating

the abundance of *N. hyrtlii* (Table 3.5). In three hours of effort, the drop-net collected a truncated sub-set of the size classes caught using rotenone. In general, the drop-net failed to collect the large individuals, which were typically in low abundance (Figure 3.3). However, the drop-net was better at collecting small size classes in pools with considerable weed (pool A) (Figure 3.3). The failure of the drop-net to collect large fish was not due to a technique bias, as considerable numbers of large fish (>20 cm) have been caught using this method during other sampling trips, rather it was related to the low numbers of these fish. Hence the drop-net can adequately describe size frequency distributions when abundance is high.

Discussion

The specially modified drop-net worked well within the structurally complex pools of the Fortescue River and surrounds. Contrary to initial expectation, the beach seine also worked well. For the same time effort, the drop-net caught a similar sub-set of fish as the beach seine. In particular, they caught a similar number of individuals and species. They also caught species in a similar ratio (i.e. average relative abundance, 77.7 PSI). The high efficiency of the seine was unexpected as it is thought to be difficult to use in complex habitats (Casselman *et al.* 1990). However, while the seine often became snagged on rocks, or rolled up when used over thick weed, it still caught a considerable number of fish (in 3 hours of sampling effort). The better than expected collection of fish by this method was probably due to the large area that could be sampled by this technique, and the small size of the pools, which limited the escape of fish.

The drop-net and the seine were more efficient than the panel gill nets, which caught fewer fish, and displayed a strong bias towards large, pelagic individuals. This size related bias has been well documented (Knight and Bain 1996), and was potentially exacerbated in this study due to the small size of the native species.

The drop-net and the seine caught fish of a similar size range, but with different size frequency distributions. However, within each net type, size frequency distributions varied between sites, suggesting that differences in size frequencies of fish collected

between techniques were not due to inherent size-related biases, but were a consequence of variation in habitat type and/or species composition. For example, the most notable variation in size frequency distributions occurred at site C where the pelagic species *N. erebi* was present. The drop-net caught relatively few individuals of this species when compared to the seine net, and also caught few individuals of *M. australis*, another schooling species, at this site. It is suggested that the discordant collection of fish at site C was due to both the improved efficiency of the seine net at this site, and the reduced efficiency of the drop-net.

The seine net was easier to use in pool C than in pools A or B. Pool C had a relatively smooth substrate and had little habitat complexity compared to pool A, which contained considerable amounts of rocks, snags and weed, and pool B, which was quite rocky. Increased ease and efficiency of use of the seine net at pool C, meant that the pool was seined a great number of times during the 3 hours of sampling effort. Pelagic species that were readily collected by this method such as *N. erebi* and *M. australis* were caught in great numbers, and were probably collected more than once, due to the replacement of fish between sampling applications.

Reduced collection of schooling fish by the drop-net in Pool C was probably caused by the larger size of this pool, which reduced the fraction of the pool sampled by the drop net in 3 hours of effort. Difficulties collecting fish that aggregate, such *as N. erebi* and *M. australis*, are likely to have also contributed. The drop-net has the potential to underestimate or overestimate the abundance of schooling species if too few drops are made.

The results of this study indicate that if fish need to be sampled from within a complex habitat, and if estimates of fish density are required, the drop-net should be used. However, if fish are to be sampled from within a relatively simple habitat, and if density estimates are not required, that the beach seine should be used due to its minimal gear requirements and ease of use. It should also be stressed that while this study did not examine the relative efficiency of these methods in deeper water, that field trials revealed that the seine became increasingly difficult to use. The drop-net was effective at sampling water up to 2.5 m depth and would be the preferred method for studies in deeper pools.

The ability of the drop-net to provide accurate estimates of total fish abundance could not be determined because the toxicant (rotenone) did not provide a good estimate of the total number of fish within the pools studied. Although rotenone affected 11 out of the 12 fish species found within the pools, the collection of fish was significantly hampered by the presence of: macrophytes, muddy and rocky substrates, deep water, and especially by poor visibility. Small size classes (i.e. fish <3 cm) were the hardest to collect. Poor collection of small fish following the application of a toxicant has been reported elsewhere (Henley 1967, Shireman *et al.* 1981, Bayley and Austen 1988), and is thought to be linked to their reduced buoyancy and increased likelihood of entanglement in vegetation (Shireman *et al.* 1981). Furthermore, the collection of fish for only 24 hours after the application of the rotenone, probably accentuated its inaccuracy. Other authors (Henley 1967, Pot *et al.* 1984, Jacobsen and Kushlan 1987) suggest that at least three days are required to collect most of the fish. Yet, while prolonged gut fermentation and its associated bloating may bring many fish to the surface (Shireman *et al.* 1981), this may not free the small fish trapped in aquatic vegetation. Another source of error that has received little attention in the literature is piscivory. Small fish may succumb to the toxicant before larger fish, increasing the rate of piscivorous predation. Such a pattern was very evident in this study and would contribute to underestimations of total fish abundance. Although the biases associated with toxicants have been discussed by many authors, many still use rotenone to quantify the accuracy of other methods (Mahon 1980, Pot *et al.* 1984, Hockin *et al.* 1985, Jacobsen and Kushlan 1987, Capone and Kushlan 1991). Unless considerable care is taken, erroneous conclusions about the accuracy of a method or the abundance of larval/juvenile fish may be drawn.

Although rotenone failed to provide a benchmark with which to assess the accuracy of the drop-net, it provided a 'better than most' means with which to assess the drop-net's ability to describe fish assemblages. A comparison with fish collected with rotenone, revealed that sampling (between 4.3 to 16.5% of a pools surface area, in 3 hrs) with the drop-net collected all species, except those that were rare (<1 % of the individuals collected using rotenone). It also collected a similar proportion of the various species (an average of 60% PSI). However, it underestimated the abundance of the benthic species, *G. giurus*, and in particular *N. hyrtlii. N. hyrtlii* is particularly active at night, and while active during the day, commonly occupies deep-water,

muddy habitats at this time (Allen *et al.* 2002, Pusey *et al.* 2004, personal observation). It may have escaped capture during daylight hours by resting or burying within the mud. Observations in aquaria reveal that individuals of this species stay close to the substrate and "feel" their way along, and may escape under the skirting of the net. Alternately, it is possible that congregation in an area or habitat not sampled by the drop-net may be the cause. Poor collection of *G. giurus* may be related to its tendency to freeze when danger is nearby. This behaviour may have resulted in these gobies being left behind when the skirting of the net was lifted over obstructions on the substrate. However, the fact that gobies were not underestimated at one pool, and that they were commonly captured during other sampling excursions, suggests that a failure to sample their preferred habitat was responsible. Comparison with rotenone also revealed that the drop-net did not collect many of the relatively large (>10 cm) fish. Failure to collect large size classes was not due to a technique related bias, but was related to the rarity of these fish. Hence, if certain size classes are in low abundance then they are likely to remain undetected. It is suggested that gill nets be used in conjunction with the drop-net to document the upper size range of fish.

Summary

In conclusion, the modified drop-net provided a non-destructive technique with which to sample fish assemblages that inhabit complex habitats. The technique provided density estimates that were relatively accurate (in comparison with rotenone) and of similar efficiency to the beach seine net. The discrete and mobile nature of the drop-net allowed the sampling of specific habitat types. However, if too few drops of the net are made rare species and size classes may not be caught, and the abundance of schooling species may be under- or over-estimated. Certain sedentary species may also be underestimated by this method.

Chapter 4

Community Structure: The Importance of Pool Stability

Introduction

Variation in the composition of fish communities (or assemblages) along the lengths of rivers is well documented (Sheldon 1968, Horwitz 1978, Ostrand and Wilde 2002, Hoeinghaus *et al.* 2003). Upland or headwater reaches typically contain fewer species and smaller fish than lowland or downstream reaches (Sheldon 1968, Gorman and Karr 1978, Meffe and Minkley 1987, Gilliam *et al.* 1993). Many freshwater fish ecologists believe that the changes in the physical in-stream environment (habitat) that parallel this headwater to lowland (longitudinal) progression are responsible for this pattern, because most species have habitat requirements (physiological or dietary) which limit the areas where they can live (Gorman and Karr 1978, Angermeier and Karr 1983, Gelwick 1990, Pusey and Arthington 1993, Pusey *et al.* 1995, Brown 2000, Hoeinghaus *et al.* 2003).

Headwater reaches typically are shallow and relatively uniform (Schlosser 1987a). The reduced size of the water body means that it undergoes relatively large diurnal fluctuations in water temperature and, if algal or plant life is present and water flow is low, relatively large fluctuations in oxygen levels (Matthews and Styron 1981, Boulton and Brock 1999). Hence, species (or size classes) that are susceptible to extremes of temperature or low oxygen levels cannot survive (Capone and Kushlan 1991, Smale and Rabeni 1995). Large species or size-classes may also not be suited to survival within the headwaters because the shallow water increases their vulnerability to terrestrial and avian predators (Lowe-McConnell 1975, Schlosser 1987a). Species that require certain food sources may be absent as well; for example, detritivorous fish are most abundant in the middle and lower reaches of rivers where there is substantial build up of fine-particulate detritus on the riverbed (Lowe-McConnell 1975).

In contrast, lowland reaches are typically deeper and relatively heterogeneous (Schlosser 1987a). The increased size of the water body buffers against diurnal fluctuations in water temperature and oxygen levels, allowing more vulnerable species to persist (Capone and Kushlan 1991). Deep water also provides cover from predators for large species or size-classes (Lowe-McConnell 1975, Schlosser 1987a). The increasing physical heterogeneity of lowland reaches, that is, the presence of deep and shallow water, slow and fast water, smooth and rougher substrates, and vegetated and

non-vegetated areas, makes it more likely that species with specific habitat requirements will be accommodated and allows for spatial segregation of species and size classes. This will then minimise competitive interactions between fish and allow a greater number of species and size classes to coexist (Schlosser 1987a).

Changes in the stability of the environment also take place between the headwaters and the lowlands, and may therefore play a part in creating the longitudinal changes in community structure (Horwitz 1978, Grossman *et al.* 1982, Meffe and Minkley 1987). Headwater reaches, due to their shallow depth, undergo greater fluctuations in water depth through time, and are more likely to dry up than lowland reaches (Matthews 1987, Schlosser 1987a, Spranza and Stanley 2000). Consequently, extermination from unstable headwater habitats and re-colonisation from stable downstream sites (refuges or sources) may be responsible for the longitudinal changes in community structure (Horwitz 1978, Osborne and Wiley 1992, Taylor 1997).

The importance of within-stream physical characteristics (such as pool size, depth, water chemistry, substrate type, and heterogeneity), versus the importance of environmental stability (persistence or variability of water) for fish community structure is likely to vary with the stability of the river system as a whole (Grossman *et al.* 1982). Rivers that receive a large or constant supply of water (e.g. glacier fed, or tropical systems) do not dry out, and will be shaped more by within-stream physical environment than stability. Rivers that receive a small amount or a varied supply of water, particularly those in hot environments, are likely to dry out (i.e. be intermittent). In rivers such as these, the stability of the within-stream environment may be as important, if not more, than its physical characteristics.

If survival within stable pools and dispersal to unstable pools are important factors shaping community structure along an intermittent river, then community structure should be related to factors that affect dispersal (Dunning *et al.* 1992, Schlosser 1995b, Snodgrass *et al.* 1996). Such factors include: the distance of a pool to a source (Pulliam 1988, Schlosser 1995a), a pool's location within the catchment (i.e. stream order) (Osborne and Wiley 1992, Taylor 1997), and barriers to dispersal (i.e. waterfalls or dams) (Pusey *et al.* 1998). For example, unstable pools that are distant

from sources are expected to contain fewer species than pools that are close, as only those species with good dispersal will be able to colonise them (Horwitz 1978).

Climatic patterns (large-scale patterns of flow) should also alter community structure in intermittent rivers (Schlosser 1995a, Medeiros and Maltchik 2001). For example, sequential years of high rainfall should facilitate dispersal, increasing the species richness of pools (except source pools), whereas consecutive years of low rainfall will limit dispersal, reducing the species richness of all pools (except source pools).

The stability of a river reach or pool should also affect the way in which a community persists over time (Ross *et al.* 1985, Schlosser 1987a, Matthews *et al.* 1988). Populations inhabiting unstable environments are expected to vary in numbers (abundance) through time as the environment passes through periods of optimal and suboptimal condition. Populations inhabiting stable environments are expected to change relatively little through time (Schlosser 1987a).

This chapter documents changes in the community structure of the fish populations of the Fortescue River main-channel and its tributaries. The main goal was to determine the relative importance of: within-pool physical characteristics (i.e. pool area, depth, water chemistry, habitat heterogeneity), pool stability (measured by persistence of water), and landscape factors (i.e. stream order, distance to source pool); providing an insight into the importance of habitat associations versus dispersal from stable (source) pools on the fish community. The chapter also examines the extent to which pool stability (measured by variation in depth through time) was associated with temporal changes in total fish abundance and intra-specific numerical abundance.

Methods

Site Selection

Fourteen pools situated within the catchment of the Fortescue River were chosen to assess the relationship between community structure and within-pool physical characteristics, pool persistence, and landscape factors. Pools were not all sampled at the same date, but this was not deemed to be critical as the study was aimed at the general association between a pool's characteristics and its fish community and not

how the relationship may change over time. Furthermore, it was impossible to standardise pools with regard to their state of drying, or time since connection to a permanent pool, because of localised rainfall within the catchment and variable rates of desiccation. Certain pools were sampled more than once (see the following paragraph), so for these pools one date was chosen at random and used in this analysis. The location of the pools is shown in Figure 2.1, Chapter 2.

Six of the pools (#2, 5, 6, 7, 8 & 13) were used to assess temporal changes in community structure. They were monitored five times over a 17-month period; April, August, and December 2001, and April, and August 2002. Significant rain fell during the summer of 2000/01, but only a small amount of localised rain fell during the summer of 2001/02. Consequently, the majority of sites were dry by December 2002. A detailed description of the physical characteristics of these pools: Bilanoo, Railbrige, Portland, Palm, Mallina and Hooley, is provided in Chapter 2.

Sampling methodology

Fish communities were sampled using a combination of techniques, whose efficiency and accuracy were discussed in Chapter 3. When species presence was required, seine nets, gill nets, snorkelling and visual surveys at night with a torch were employed. When abundance estimates were required (i.e. for the temporal analysis of community structure) the drop-net was used.

To provide a 'best estimate' of total fish abundance within a pool the number of fish collected using the drop-net was standardised relative to habitat abundance. A map of the different habitats present within the pool was constructed, and for each deployment of the net the habitat sampled was recorded. When replicate samples were taken from within one habitat, the number of fish were averaged and multiplied up to the area of that habitat within the pool. Habitat delineations tend to be subjective and, in this study, two-dimensional areas were separated using depth, littoral margin, substrate type, macrophyte type and density. Habitats were sampled in proportion to their relative abundance, however deep water (>2 m) and minor habitats were not sampled due to sampling difficulties and time constraints. When a habitat was not sampled its area was not included in estimates of total abundance. For five out of the six pools sampled for abundance these habitats contributed, on average, 22% of the total pool area, and although not ideal, it is assumed that a good representation of

community structure was still gained. Palm Pool was difficult to sample due to its considerable depth and steep edges. The description of the fish community for this pool was made up from collections in habitats that contributed only 16.6% of the pool surface area. So, while the fish community of Palm Pool was of interest due to the pool's high stability, the results for this site should be interpreted with caution. In addition, if a pool exceeded 100 m in length, a 100 m section that was representative of the pool as a whole was chosen and fish abundance was estimated for this section. At the start of the study all pools except Railbridge exceeded 100 m in length, but at the close of the study only two pools, Palm and Bilanoo Pools, exceeded 100 m.

Within-Pool Physical Factors

Within-pool physical factors were measured each time a pool was sampled and included: pool surface area (length* average width) (m^2), maximum pool depth (m), conductivity (µS), turbidity (ntu), and habitat heterogeneity. Habitat heterogeneity was estimated using an index generated according to variety in: substrate type, water depth, the number and density of macrophyte species present, and the density of large woody debris (Table 4.1). pH was measured and varied between 7.8 to 8.6 across the sites. Technical difficulties prevented comprehensive monitoring; hence it was not included in analyses.

Pool Stability

Pool stability was described using two measures: pool persistence, and pool variability in depth (for a detailed description and discussion of these measures see Chapter 2). Pool variability in depth was the preferred measure but could only be used for investigations involving pools that were monitored through time, that is, the primary pools (Palm, Bilanoo, Mallina, Hooley, Portland, and Railbrige Pools). Pool persistence was used for all other investigations and equalled the number of months that a pool contained water during a 25-month period (December 2000 to December 2002). Values were converted to a percentage to ease interpretation. Low values indicated that a pool was temporary and 100% indicated permanence during the study period. Accurate estimates of persistence were available for all but two of the small pools (#1 & 12) that were sampled in December 2000. These pools dried up soon after the sampling date, giving them low persistence scores yet the pools had been inundated since the 1:100 year flood nine to twelve months earlier. Consequently, these two pools were omitted from analyses involving pool persistence.

Landscape Factors

Landscape factors included: distance to nearest permanent water (km), and stream order. Topographic maps (1:50 000) were scanned and the free-line distance from study sites to the nearest permanent pool was measured using Image Pro Plus (Media Cybernetics).

Table 4.1. Index of habitat heterogeneity. Each pool received a score for the level of complexity of its depth, substrate, macrophyte species, macrophyte cover, and amount of woody debris. Scores increased with the level of diversity, and were summed for the five categories to provide the index score. High index scores described high levels of habitat heterogeneity.

Feature	Level of Complexity	Score
Depth	uniform shallow <0.3m	0
	uniform moderate 0.3-1.5m	1
	shallow + moderate, or moderate + deep	2
	shallow, moderate and deep	3
Substrate	uniform	0
	two types	1
	three types	2
	> three types	3
Macrophyte species	absent	0
	1 species	1
	2 or 3 species	2
	≥ 4 species	3
Macrophyte cover	absent	0
	sparse < 10% of pool	1
	moderate 10-40%	2
	dense >40%	3
Woody debris	absent	0
	sparse	1
	moderate	2
	dense	3

Statistical Analyses

Multivariate ordination and linear regression were used to examine trends in the data. Multivariate ordination provided a graphical description of community structure, and was based on dissimilarity measures (association measures) constructed using the Bray-Curtis coefficient. The normality of the association measures was assessed and considered acceptable if the frequency histogram was not skewed towards values of one (complete dissimilarity) (Belbin 1992). Ordination of the dissimilarity matrix was achieved using multi-dimensional scaling (semi-strong hybrid multi-dimensional scaling). This method is highly flexible and makes few assumptions about the nature

and quality of the data (Clarke and Warwick 2001). The stress involved in the ordination was assessed and was considered acceptable if it was below 0.20. If the stress associated with a 3-D ordination was less than 0.05, a 2-D ordination was used as it is easier to interpret (Belbin 1992). The co-occurrence of physical parameters and/or species with the ordination of sites was examined using correlation in ordination space. Correlations were considered significant when their critical value was greater than the 95^{th} value generated by 100 Monte Carlo randomisations (Belbin 1992). Significant species and physical parameter gradients were plotted on the ordination to reveal trends in the data. Multivariate ordinations were conducted using PATN (Belbin 1992). When a species' presence at a site was equivocal the default missing value (-9999) was used.

Multivariate ordinations examining the relationship between community structure and: within-pool physical factors, pool stability, and landscape factors, used only the presence/absence data. However, the ordination examining temporal changes in community structure used abundance data. Abundance data were standardised for habitat type and fish less than 3 cm were excluded. This was done because the mesh used on the drop-net changed during the study. The first two sampling periods (April and August 2001) used a 5 x 5 mm mesh, which did not catch fish less than 3 cm; consequently, the mesh size was reduced to 1 x 1.5 mm in December 2001. Excluding small fish also reduced the effect of recruitment on temporal changes. The data were $\log_{10}$ (n+1) transformed as abundance data often differed by several orders of magnitude. This transformation helped to homogenise the spread of data. Abundance data were separated into species groups (intra-specific abundance) prior to the analysis. Total abundance was preferred over relative abundance as it documented changes in both community composition and community size. Additionally, declines in the abundance of one species did not affect scores of the other species, as is the case for relative abundance data. To compare variation in species abundance through time between sites, the Euclidean distance between consecutive sampling dates on the ordination (i.e. in 2 or 3-D space) were determined.

Ordination is affected by rare species, those that occur at less than 10% of sites (or sampling times) (Belbin 1992). No species were rare in the species presence data, but one species, *Arius graeffei*, was rare in the species abundance data. *A. graeffei* was

omitted from the data set. *Neosilurus hyrtlii* was known to be underestimated by the drop-net (see Chapter 3) and was also omitted.

Simple linear and multiple linear regression analyses were used to examine the relationship between species richness and: within-pool physical factors, pool persistence, and landscape factors. Simple linear regression was also used to examine the relationship between pool variability in depth and variance in total abundance (pooled across all species) through time. Total abundance data were $\log_{10}(n+1)$ transformed and the coefficient of variation was used as a measure of the variance in total abundance within each pool.

Prior to regression analyses, the assumptions of the models were tested. Assumptions of normality were investigated by constructing normal quantile-quantile plots and testing the goodness of fit of a straight line using the Shapiro-Wilk W test (Sall *et al.* 2001). Assumptions of homogeneity of variances were investigated by plotting the residuals versus x. Prior to multiple regressions, x values (physical and landscape factors) were checked to see if they were correlated, hence could cause problems associated with collinearity (Quinn and Keough 2002). Regression analyses were performed using JMP statistical software (Sall *et al.* 2001). Estuarine species were omitted from all analyses.

Results

Variation in Within-pool Physical Factors, Pool Persistence and Landscape Factors

Study pools differed considerably in their within-pool physical factors, persistence and landscape factors (Table 4.2). Pool surface area varied by three orders of magnitude (24 to 87500 m^2), while most other variables varied by approximately one order of magnitude. Depth ranged from 0.15 to 3.5 m, conductivity from 379 to 2690 µS, turbidity from 0.3 to 30 ntu, habitat heterogeneity from 1 to 11 (rank score), pool persistence from 4 to 100 (as a percentage), distance to permanent pool from 1.5 to 25 km, and stream order from 1 to 7.

Table 4.2. Within-pool physical factors, pool persistence, and landscape factors. Sampling date between 2000 and 2002 is provided. '---' indicated data not available.

		Within-pool Physical Factors					Pool Persistence	Landscape Factors	
Pool number and (name)	Date	Surface Area (m^2)	Maxi-mum depth (m)	Conduc-tivity (µS)	Turb-idity (ntu)	Habitat hetero-geneity	(%)	Stream order	Distance to permanent pool (km)
1	Dec00	600	0.19	868	7	1	---	7	2.0
2 (Bilanoo)	Dec01	20210	2.50	1124	2	11	100	7	2.5
3	Aug02	500	1.40	---	16	13	96	7	2.0
4	Feb02	2535	0.40	1196	<1	8	64	7	1.5
5 (Railbridge)	Dec00	1200	3.30	379	7	10	36	1	3.5
6 (Portland)	Aug02	3390	1.00	1596	6	10	80	3	3.7
7 (Palm)	Aug02	87500	3.50	2390	<1	11	100	5	0.0
8 (Mallina)	Dec01	4480	1.40	1623	4	7	96	2	25.0
9	Dec00	65	0.40	2530	---	3	4	2	25.0
10	Dec00	860	1.05	2690	30	5	56	2	25.0
11	Apr02	24	0.15	---	---	1	4	4	15.5
12	Dec00	200	0.20	2168	4	1	---	4	15.0
13 (Hooley)	Apr01	7200	1.50	2040	3	7	80	4	15.0
14	Mar02	525	0.40	1506	19	4	12	4	14.7

The Number and Type of Species within a Pool and their Relationship to Within-pool Physical Factors, Pool Persistence and Landscape Factors

All species (n=10) of freshwater fish known to exist within the Fortescue River were collected or observed (Table 4.3). Species richness within a pool was related to pool persistence (Figure 4.1.A) and habitat heterogeneity (Figure 4.1.B), but not to pool surface area, maximum depth, conductivity, turbidity, stream order, or distance to the nearest permanent pool (Table 4.4). Pool persistence was a better predictor of species richness, explaining 85% of the variation, than habitat heterogeneity, which explained only 57% (Table 4.4).

Estimating the number of species within a pool was improved by 5.8% when the landscape factor, stream order, was used in conjunction with pool persistence (Table 4.6). The other landscape factor, distance to permanent water, did not explain any additional variation (Table 4.7). Similarly, habitat heterogeneity did not improve the predicative power of the regression (Table 4.8). This was not a great surprise as habitat heterogeneity was correlated with pool persistence (Table 4.5). The insignificant result meant that problems associated with collinearity did not have to be addressed (Quinn and Keough 2002).

Pool persistence was also associated with the type of species present within a pool (Figure 4.2, Table 4.9). Physical and species gradients through the multivariate ordination of species presence/absence at the various sites, revealed that pools with good persistence were more likely to contain *N. erebi* and to a lesser extent, *Leiopotherapon aheneus, Glossogobius giurus, Amniataba percoides* and *N. hyrtlii* (Table 4.10). Species found within stable and unstable pools alike included: *L. unicolor* and *Melanotaenia australis*. Other species such as *A. graeffei, Anguilla bicolor* were only found within the stable pools on the main channel and *Hypseleotris compressa* was only found in stable pools in lowland sections of the main channel.

Table 4.3. Species present within the pools of the Fortescue River, 1=present, 0=absent, ~=inconclusive.

Pool number and (name)	*Leiopotherapon unicolor*	*Leiopotherapon aheneus*	*Amniataba percoides*	*Nematalosa erebi*	*Arius graeffei*	*Neosilurus hyrtlii*	*Melanotaenia australis*	*Glossogobius giurus*	*Hypseleotris compressa*	*Anguilla bicolor*	Total
1	1	1	1	1	0	0	0	1	0	0	5
2 (Bilanoo)	1	1	1	1	1	1	1	1	1	1	10
3	1	1	1	1	0	1	1	1	1	1	9
4	1	1	1	1	0	1	1	1	0	0	7
5 (Railbridge)	1	0	0	0	0	1	1	0	0	0	3
6 (Portland)	1	1	1	1	0	1	1	1	0	0	7
7 (Palm)	1	1	1	1	1	1	1	1	0	1	9
8 (Mallina)	1	1	1	1	0	1	1	1	0	0	7
9	1	0	0	0	0	0	0	0	0	0	1
10	1	~	1	1	0	1	1	1	0	0	6
11	0	0	0	0	0	0	1	0	0	0	1
12	1	0	1	0	0	0	1	0	0	0	3
13 (Hooley)	1	1	1	1	0	1	1	1	0	0	7
14	1	1	1	0	0	0	1	1	0	0	5

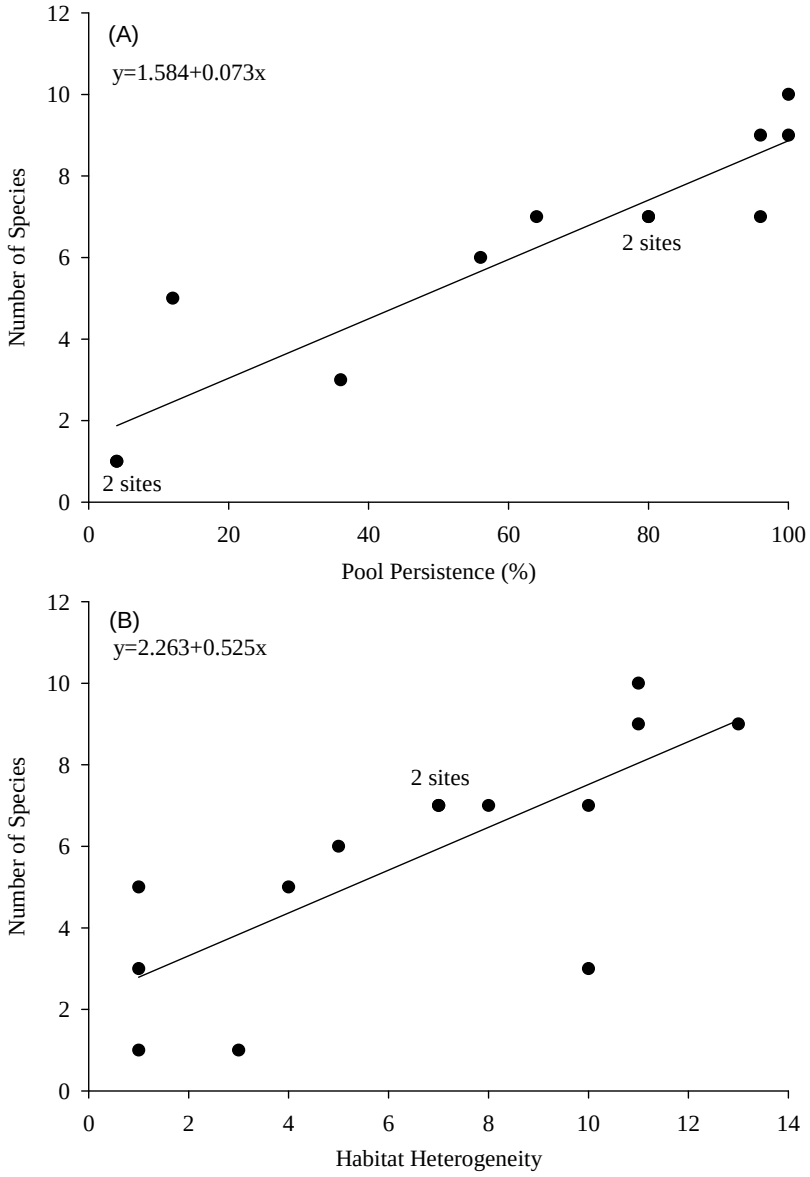


Figure 4.1. Linear regressions of the number of species within a pool versus (A) pool persistence n=12, and (B) habitat heterogeneity, n=14.

Table 4.4. Linear regressions between species richness (y) and pool persistence, within-pool factors and landscape factors (x). Significant relationships are indicated by *. The equation of the line-of-best-fit, and the coefficient of determination (r^2) is only provided where the relationship was significant.

Factor (x)	Equation	r^2	df	F value	p-value
Pool Persistence	y=1.584+0.073*x	0.853	11	57.899	<0.0001*
Within-pool					
Habitat heterogeneity	y=2.263+0.525*x	0.571	13	16.005	0.002*
Surface area (m^2)			13	3.155	0.101
Maximum depth (m)			13	3.541	0.084
Conductivity (µS)			11	0.035	0.855
Turbidity (ntu)			11	0.303	0.594
Landscape					
Stream order			13	4.387	0.058
Distance to permanent water (km)			13	3.489	0.086

Table 4.5. Correlation coefficients between all factors (within-pool, pool persistence and landscape factors). Values are only provided when the correlation was significant.

	Habitat hetero-geneity	Surface area (m^2)	Maximum depth (m)	Conduct-ivity (µS)	Turbidity (ntu)	Stream order	Distance to permanent pool (km)
Pool persistence	0.650	—	—	—	—	—	—
Habitat heterogeneity		—	0.741	—	—	—	0.540
Surface area (m^2)			—	—	—	—	—
Maximum depth (m)				—	—	—	—
Conductivity (µS)					—	—	—
Turbidity (ntu)						—	—
Stream order							0.649

Table 4.6. Multiple linear regression of species richness (y) versus pool persistence (x_1) and stream order (x_2). * indicates a significant relationship at the alpha = 0.05 level. The r^2 was 0.911.

ANOVA					
Source	df	SS	MS	F	p-value
Model	2	89.327	44.663	46.348	<0.001*
Error	9	8.673	0.964		
Parameter Estimate					
Term	Estimate	SE	t-ratio	p-value	
Intercept	0.631	0.676	0.93	0.375	
Persistence	0.064	0.009	7.37	<0.001*	
Stream order	0.375	0.154	2.44	0.037*	

Table 4.7. Multiple linear regression of species richness (y) versus pool persistence (x_1) and distance to permanent pool (x_2). * indicates a significant relationship at the alpha = 0.05 level.

ANOVA					
Source	df	SS	MS	F	p-value
Model	2	84.984	42.492	29.382	<0.001*
Error	9	13.016	1.446		
Parameter Estimate					
Term	Estimate	SE	t-ratio	p-value	
Intercept	2.296	0.988	2.32	0.045	
Persistence	0.068	0.010	6.44	<0.001*	
Distance to permanent pool	-0.039	0.040	-0.99	0.348	

Table 4.8. Multiple linear regression of species richness (y) versus pool persistence (x_1) and habitat heterogeneity (x_2). * indicates a significant relationship at the alpha = 0.05 level.

ANOVA					
Source	df	SS	MS	F	p-value
Model	2	83.878	41.939	26.728	<0.001*
Error	9	14.122	1.570		
Parameter Estimate					
Term	Estimate	SE	t-ratio	p-value	
Intercept	1.372	0.851	1.61	0.141	
Persistence	0.067	0.017	3.96	0.003*	
Habitat heterogeneity	0.077	0.173	0.45	0.667	

Table 4.9. Correlation coefficients for the regression of within-pool physical factors, pool persistence, and landscape factors against the multivariate ordination of species presence. The critical value used was the 95th highest from 100 Monte Carlo randomisations, * indicates a significant relationship at the alpha = 0.05 level.

Factors	Correlation coefficient (r)	Critical Value
Within-pool		
Habitat heterogeneity	0.586	0.621
Surface area (m^2)	0.373	0.839
Maximum depth (m)	0.314	0.699
Conductivity (µS)	0.361	0.703
Turbidity (ntu)	0.124	0.770
Pool Persistence	0.859*	0.730
Landscape		
Stream order	0.563	0.670
Distance to permanent pool (km)	0.512	0.628

Table 4.10. Correlation coefficients for the regression of species against the multivariate ordination of species presence. The critical value used was the 95th highest from 100 Monte Carlo randomisations, * indicates a significant relationship at the alpha = 0.05 level.

Species	Correlation coefficient (r)	Critical Value
Leiopotherapon unicolor	0.844	0.844
Leiopotherapon aheneus	0.955*	0.644
Amniataba percoides	0.862*	0.708
Nematalosa erebi	0.893*	0.585
Arius graeffei	0.437	0.712
Neosilurus hyrtlii	0.645*	0.598
Melanotaenia australis	0.712	0.751
Glossogobius giurus	0.953*	0.663
Hypseleotris compressa	0.434	0.717
Anguilla bicolor	0.538	0.573

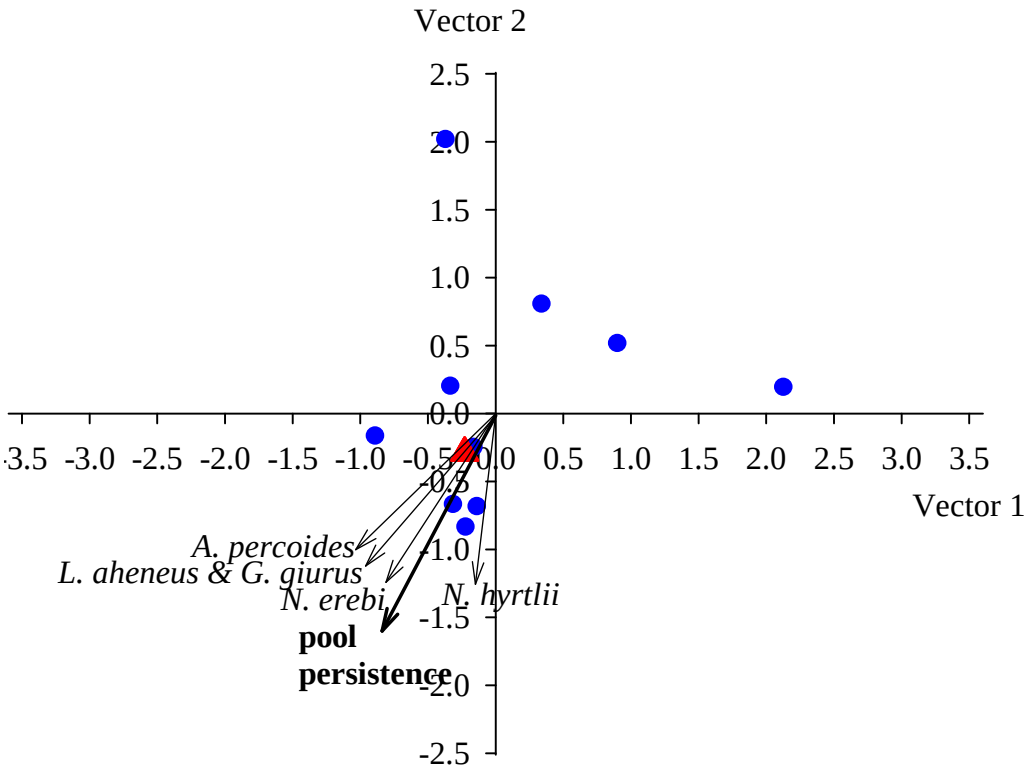


Figure 4.2. A two-dimensional ordination of sites using species presence/absence, n=14. The stress associated with this ordination was 0.09, which is considered to be very good. Significant correlations between species and physical factors and the ordination of sites are shown. The red triangle represents 4 sites.

Temporal Changes in Community Structure

A total of 7133 fish greater than 3 cm in length were collected from the six primary pools over the five sampling dates (Table 4.11, Appendix II lists them separated into species). The total number of fish within all pools changed though time (Table 4.11). Fluctuations (coefficient of variation of log total abundance) appeared to be greater within the more unstable pools (Figure 4.3). When this relationship was examined statistically the result was not significant (Table 4.13); however, the high F-value (>4.0) suggested that lack of significance at the 5% level was due to the small number of study sites (low power). Increased variation in total abundance within the unstable pools (Hooley and Railbridge) was caused by the eradication of fish during periods when the pools dried completely (Table 4.11).

The multivariate ordination of intra-specific numerical abundance (i.e. total fish abundance separated into species groups) at each site through time provided greater detail of the temporal shifts occurring within the community. Marked changes in assemblage structure through time were clear for the two pools with the greatest instability (Portland and Railbridge) (Figure 4.4). Portland Pool showed on average the greatest temporal changes (Euclidean distances between consecutive sampling dates on the ordination), the largest of which was associated with re-colonisation of the pool (Table 4.13). Although there was a trend towards increasing temporal shifts in total species abundance (using average Euclidean distance in multivariate space) with a decrease in pool stability (Figure 4.5), the relationship was insignificant (Table 4.14). Once again, the high F-value (>4) suggested that that the lack of significance, at the 5% level, was due to the small number of study sites (low power).

Changes in community structure (intra-specific numerical abundance), expressed in multivariate two-dimensional space, did not appear to be related to the progression of the drought, as communities moved in different directions (Figure 4.4). Species presence within unstable pools also changed relatively little as they dried. For example, Mallina Pool contained virtually the same number of species in its drastically shrunken state (August 2002) as it did in all prior sampling events (Table 4.15). Similarly, Portland Pool contained a similar number of species when in a drastically shrunken state (December 2001) as it did when it was full (April 2001) (Table 4.15). Note that small changes in species presence through time (see Table 4.15) were typically associated with the difficulties involved in collecting rare species using the drop-net.

Table 4.12. Fish collected during each deployment of the drop-net, at each site, at each time. Fish <3 cm are not included. Log (n+1) TPA (total abundance of fish within a pool or 100 m section of pool) is also shown. This value was standardised for habitat area.

Pool	Date	Drop number										Log
		1	2	3	4	5	6	7	8	9	Total	(n+1) TPA
Palm	April 01	17	27	28	12						84	2.86
	August 01	15	40	22	12	34	7				130	2.85
	Dec. 01	33	45	34	72	92					276	3.23
	April 02	71	77	53	63	49	88				401	3.29
	August 02	32	36	40	16	10					134	2.98
Bilanoo	April 01	22	5	35	7	8	16				93	3.37
	August 01	1	1	2	9	16	35	1	3	12	80	2.89
	Dec. 01	9	18	7	30	40	25	16	10		155	3.44
	April 02	131	10	21	21	173	10	30	34		430	3.82
	August 02	11	17	9	107	45	28	18	9	38	282	3.78
Mallina	April 01	234	128	160	218						740	4.05
	August 01	2	8	128	11	39	51	521	14		774	3.82
	Dec. 01	26	24	38	61	62					211	3.52
	April 02	40	42	38	136	84	54	70			464	3.77
	August 02	11	109	15	37	39					211	3.20
Hooley	April 01	71	20	53	17						161	3.73
	August 01	0	0	0	0						0	0
	Dec. 01	94	117	75	89						375	3.84
	April 02	46	18	46	7	34	34				185	3.47
	August 02	pool dry									0	0
Portland	April 01	25	27	41	17						110	3.58
	August 01	15	1	7	20	9	14				66	2.80
	Dec. 01	482	234								716	2.88
	April 02	3	15	13	74	36	49	10	52		252	3.56
	August 02	86	69	14	6	59	5	41	27		307	3.81
Rail-bridge	April 01	10	18	9							37	2.68
	August 01	131	100	128	100						459	3.59
	Dec. 01	pool dry									0	0
	April 02	pool contained water but no fish									0	0
	August 02	pool dry									0	0
										∑	7133	

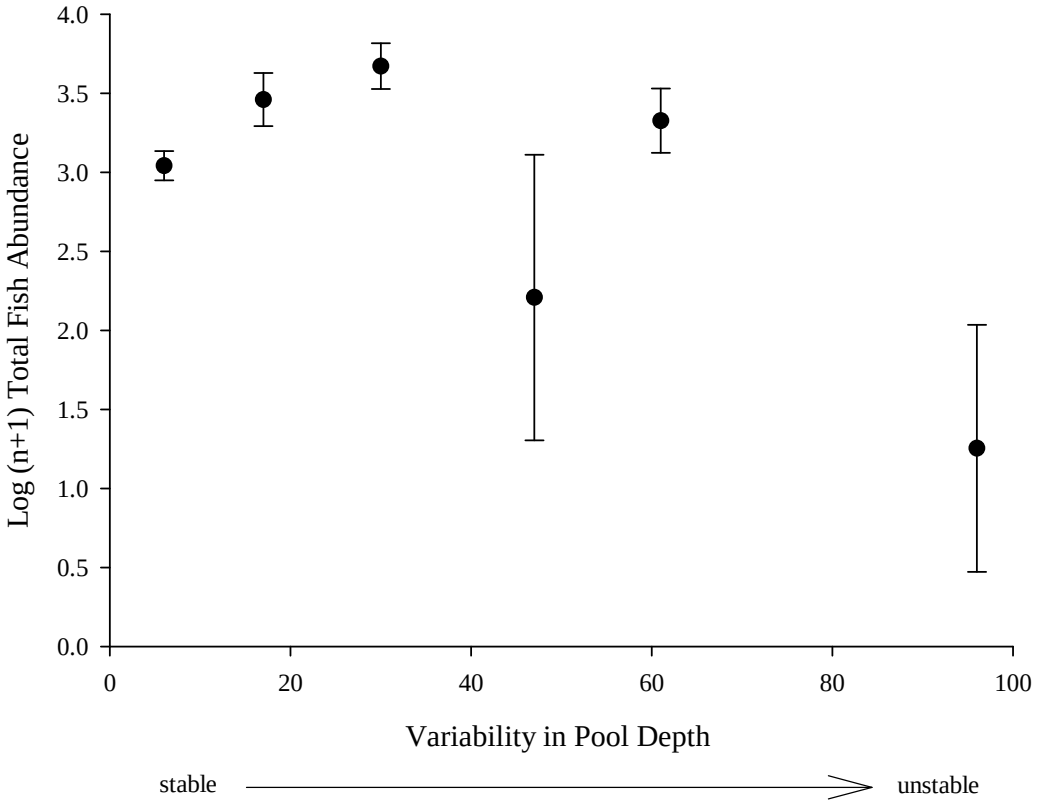


Figure 4.3. Average (± SE) log (n+1) total abundance of fish within a pool versus variability in pool depth (a measure of pool stability). Sampling times were April, August and December 2001, and April and August 2002. Total abundance estimates did not include fish less than 3 cm in length and were standardised for habitat abundance. In pools greater than 100 m in length, total abundance refers to fish within a 100 m section.

Table 4.13. Linear regression of variation in pool depth (x) versus the coefficient of variation of log (n+1) total fish abundance within a pool over time (y). Estimates of total fish abundance were standardised for habitat and did not include fish <3 cm.

Source	df	MS	F	p-value
Model	1	10189.9	7.05	0.057
Error	4	1444.8		

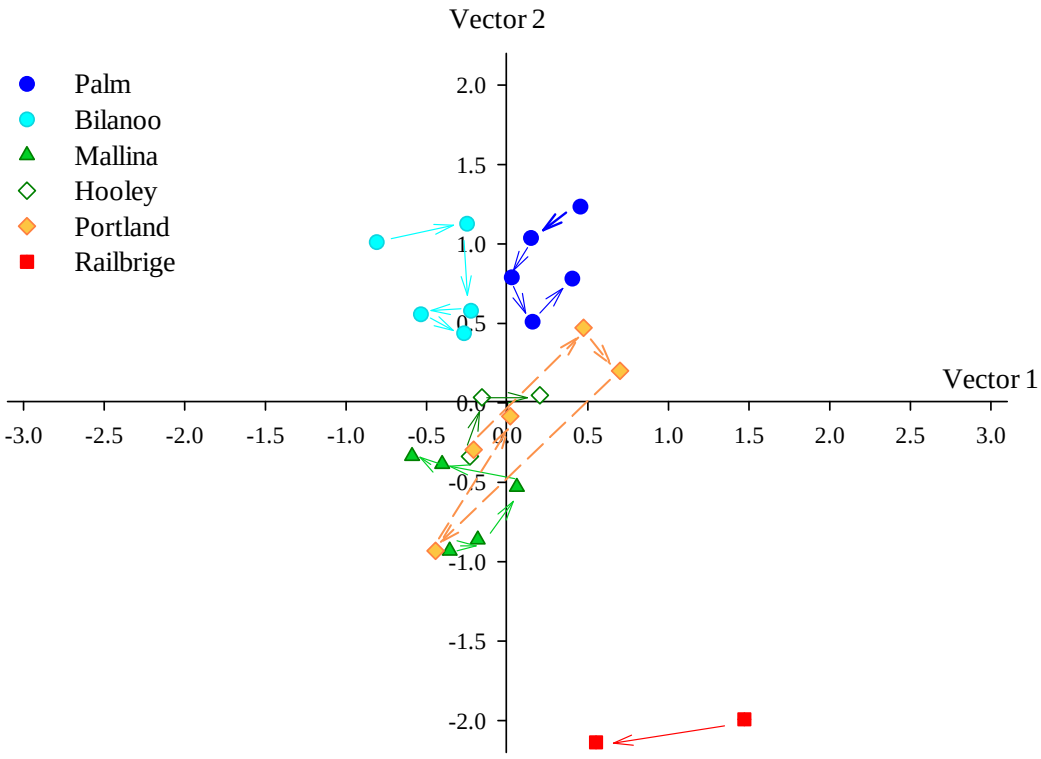


Figure 4.5. A two-dimensional ordination of $\log_{10}(n+1)$ total intra-specific abundance for the six focal pools through time (April, August and December 2001, April and August 2002). Fish were collected using the drop-net, and species abundances were standardised for habitat and extrapolated to provide estimates for the total number within a pool. All estuarine species were omitted from the analysis, and so was *A. graeffei*, which was collected in < 10% of sampling events, *N. hyrtlii*, which was known to be poorly collected by the drop-net. Fish <3 cm were also omitted, to reduce the effects of periods of recruitment on community structure and because the mesh size changed through time. Arrows link adjacent sample periods through time.

Table 4.14. The Euclidean distance between consecutive sampling dates from the multivariate ordination of $\log_{10}(n+1)$ total species abundances (Figure 4.3). Distances are shown for the six primary study pools, which have been ordered in terms of their stability, which is shown in parentheses; smaller numbers indicate higher stability. * indicates that total species abundances at Hooley Pool were compared between April 2001 and December 2001 because no fish were collected in August 2001.

	Apr01 – Aug01	Aug01 – Dec01	Dec01 – Apr02	Apr02 – Aug02	Mean	SE
Palm (6)	0.275	0.308	0.366	0.456	0.351	0.040
Bilanoo (17)	0.573	0.548	0.312	0.293	0.432	0.075
Mallina (30)	0.187	0.411	0.485	0.193	0.320	0.076
Hooley (47)	0.380*		0.359		0.369	0.010
Portland (61)	1.026	0.353	1.611	0.965	0.989	0.257
Railbridge (96)	0.930				0.930	0.000

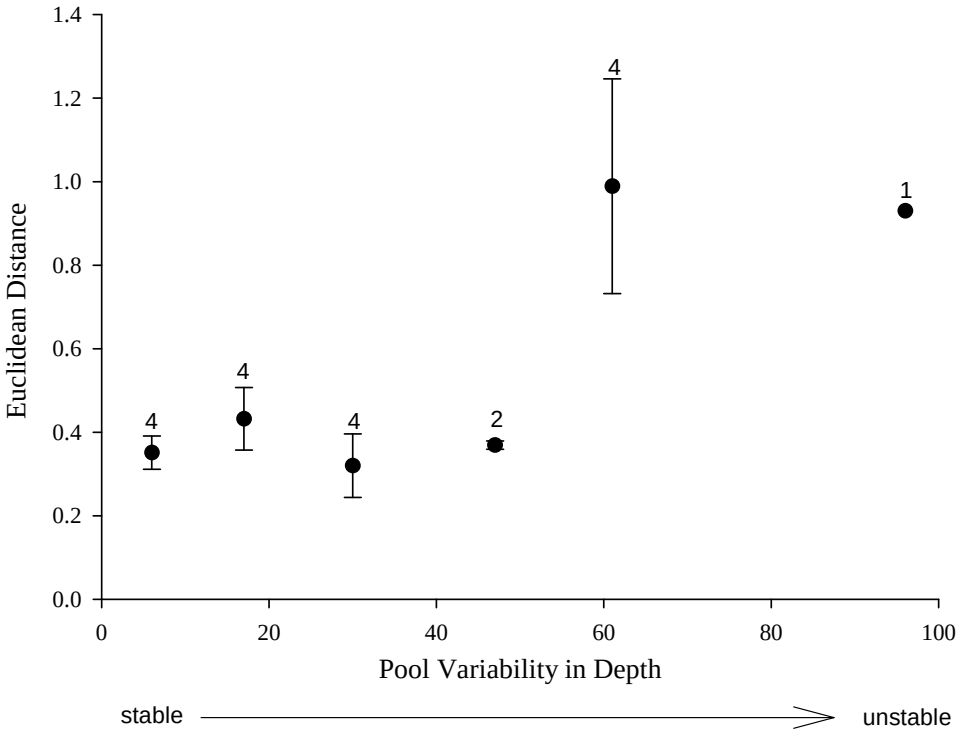


Figure 4.6. The average Euclidean distance (± standard error bars) between consecutive sampling dates on the ordination of $\log_{10}$(total species abundance) within a pool through time, versus pool variability in depth (a measure of pool stability). The sample size is shown above each mean.

Table 4.15. Linear regression of variation in pool depth (x), a measure of pool stability, versus the average Euclidean distance between consecutive sampling dates in the multivariate ordination of total species abundance (y).

Source	df	MS	F	p-value
Model	1	0.310	7.50	0.052
Error	4	0.041		

Table 4.16. The total number of each species (total intra-specific abundance) estimated to be at each site during the five sampling periods. Estimations were based on the fish collected using the drop-net and were standardised for habitat area and extrapolated to pool area. Pool area was constrained to a 100 m section when pools were longer than this. The data were $\log_{10}(n+1)$ transformed. * indicates species that were not included in the multivariate ordination as they were collected on too few occasions (*A. graeffei*), or known to be underestimated by the drop-net (*N. hyrtlii*). Note that *A. bicolor* is not included in this table, because although it was observed in Palm and Bilanoo Pools (see Table 4.3) it was not collected by the drop-net.

Site	Date	Species								
		L. unicolor	*L. aheneus*	*A. percoides*	*N. erebi*	*A. graeffei**	*N. hyrtlii**	*M. australis*	*G. giurus*	*H. compressa*
Palm	April 01	0.00	1.95	1.32	2.53	0.00	0.00	2.27	1.95	0.00
	August 01	0.88	2.10	1.80	2.50	0.00	0.00	1.72	2.17	0.00
	December 01	1.04	1.83	2.10	2.29	0.00	0.00	2.84	2.80	0.00
	April 02	0.69	2.64	2.08	1.48	0.00	1.48	2.75	2.88	0.00
	August 02	0.00	2.18	1.41	1.32	0.00	0.00	1.99	2.82	0.00
Bilanoo	April 01	0.00	2.38	2.73	3.14	0.00	3.02	0.94	1.31	1.68
	August 01	0.00	2.02	2.41	2.30	0.00	0.00	1.18	2.22	1.58
	December 01	1.40	2.46	2.96	2.39	0.00	0.00	1.93	2.98	2.39
	April 02	1.57	2.63	2.63	3.69	2.20	0.00	1.55	2.75	1.59
	August 02	1.77	3.02	2.29	2.89	1.80	1.68	2.51	3.10	3.36
Mallina	April 01	3.16	0.00	2.92	3.29	0.00	0.98	3.84	0.00	0.00
	August 01	2.42	0.00	2.77	2.82	0.00	1.41	3.70	0.00	0.00
	December 01	2.76	1.58	2.94	2.96	0.00	1.11	2.97	0.00	0.00
	April 02	2.68	0.00	3.05	3.47	0.00	2.23	3.04	1.91	0.00
	August 02	2.25	0.00	2.77	2.74	0.00	2.09	2.18	1.23	0.00
Hooley	April 01	3.41	0.00	2.94	2.69	0.00	2.27	3.00	2.50	0.00
	December 01	3.46	2.23	3.15	2.50	0.00	2.12	3.25	2.48	0.00
	April 02	2.90	1.80	1.77	2.27	0.00	1.04	3.21	2.34	0.00
Portland	April 01	2.68	0.00	2.83	2.72	0.00	0.00	3.27	2.45	0.00
	August 01	1.32	1.48	2.12	1.32	0.00	1.00	2.38	2.26	0.00
	December 01	0.78	0.30	1.58	2.43	0.00	0.00	2.59	1.74	0.00
	April 02	3.18	0.00	1.93	3.25	0.00	0.00	2.42	0.00	0.00
	August 02	3.55	1.45	3.24	2.26	0.00	0.00	2.92	2.34	0.00
Railbridge	April 01	2.36	0.00	0.00	0.00	0.00	1.26	1.42	0.00	0.00
	August 01	3.38	0.00	0.00	0.00	0.00	0.85	2.25	0.00	0.00

Discussion

Community Structure and Within-pool Physical Factors, Pool Persistence, and Landscape Factors

The fish communities existing within the pools of the Fortescue River were structured predominantly by the stability of their local environment. In other words, of all the factors measured, pool persistence (a measure of pool stability) was the best predictor of the number and type of species present within a pool. Pools that were more persistent contained additional species not found in the ephemeral pools.

Importantly, this study allowed a separation of the effects of environmental stability (pool persistence) from those of within-pool physical factors on species richness. This was because, unlike many other systems (see Schlosser 1987a, Capone and Kushlan 1991), most of the within-pool physical factors (e.g. pool area, maximum depth etc.) were not correlated with pool persistence. This is unusual, as typically the size and depth (or volume) of a pool is related to how quickly a pool will dry (i.e. its persistence). Indeed, many researchers assume that pool size provides a good indication of pool persistence and, in turn, the probability of extermination (MacArthur and Wilson 1967, Schlosser 1987a, Capone and Kushlan 1991, Taylor 1997). The Fortescue River appears to be, like the pools studied by Fausch and Bramblett (1991), an exception to this general rule. In this system, pool persistence was linked to the presence of underground water storages. These water storages may be connections to an aquifer, or bank storage (Masini 1988), and it was the uneven distribution of these storages across the catchment, which broke down the longitudinal associations (i.e. increasing pool size, depth, and stability downstream) which typify most temperate systems.

Although pool stability (measured as persistence) was the dominant factor shaping the community, the number of species within a pool was still related to habitat heterogeneity. This may indicate that habitat associations still play a role, albeit somewhat reduced, or it may have been a consequence of the fact that habitat heterogeneity was correlated with pool stability. Arthington *et al.* 's (2005) study of the fish in arid central Australia found that local habitat features (in conjunction with landscape features) were correlated with community structure. The lack of an association between the types of species (as distinct from number) within a pool and

habitat heterogeneity within the communities of the Fortescue River suggests that habitat heterogeneity is of secondary importance in this system. A reduced role for habitat in the structuring of fish communities has been reported in other systems (Angermeier and Schlosser 1989, Bart 1989, Schlosser 1995a, Taylor 1997, Pusey *et al.* 1998, Marsh-Matthews and Matthews 2000, Pusey *et al.* 2000), and may occur in the Fortescue River because many of the fish species are habitat generalists (Pusey *et al.* 1998). It is also possible that the high frequency of disturbance events within the Fortescue River have eroded the relationship between habitat heterogeneity and species distributions (Angermeier and Schlosser 1989).

The importance of stability (measured as persistence) to community structure, and the fact that pool persistence reflects the likelihood that a community will be exposed to extermination, suggests that the fish communities within the river as a whole are shaped by processes of extermination and re-colonisation. However, if this is so, then landscape factors that affect dispersal (the process of re-colonisation) should have been related to community structure. Interestingly, this study found mixed evidence to support this; for while there was no relationship between the species richness of a pool and its distance to the nearest source pool, the position of a pool within the catchment (stream order) did explain some (6%) of the variation in species richness not accounted for by pool stability. For example, pools with more species than expected by their stability were in lowland sections, whereas pools with fewer species than expected were in headwater sections.

Proponents of the extermination/re-colonisation model may find the fact that stream order helped to predict species richness but distance to source pool did not contradictory. This is because the model assumes that the distance from a pool to its source is correlated with stream order (Horwitz 1978). In the Fortescue River, the dissociation of pool persistence and position within the catchment no doubt erodes this relationship. Furthermore, the re-colonisation/extermination model proposed by Horwitz (1978) was formulated using catalogued studies, and researchers were likely to have concentrated their sampling in persistent sections of a river (see Stanley *et al.* 1997). If this was so, then it would have strengthened the idea that a gradual decline in persistence exists as one travels away from source pools. This may be suitable for rivers with continual flows, but will be inappropriate for intermittent systems such as

the Fortescue River, where persistent and ephemeral pools abut one another. In the Fortescue River, pool persistence, the dominant shaping force, makes the distance of a pool to its source irrelevant.

If factors associated with dispersal seemed unimportant, why were there more species in the stable lowland pools than anywhere else? Examination of the species only present in the stable lowland pools (*A. graeffei*, *A. bicolor* and *H. compressa*) suggests that species habitat preferences may play a role. For example, all of these species are known to have an affinity for brackish water. For example, anguillids in other rivers have been restricted to lowland reaches (Pusey *et al.* 1998). This is thought to be due to their oceanic life history phase (Pusey *et al.* 1998). *H. compressa* is known to prefer brackish water (Allen *et al.* 2002), and *A. graeffei* is thought to be an estuarine vagrant (Pusey *et al.* 1998).

Appraisal of the other species that inhabit the Fortescue River suggested that their distribution was determined primarily by physiological or life history constraints. For example, the most ephemeral pools generally contained *L. unicolor* and/or *M. australis*. These species have high tolerances of environmental extremes (Bishop *et al.* 2001, Allen *et al.* 2002, Pusey *et al.* 2004), and life histories suited to variable environments (Chapter 7, Bishop *et al.* 2001, Pusey *et al.* 2004). In addition to these species, the more persistent pools were likely to contain *N. erebi* and to a lesser extent, *A. percoides, L. aheneus*, *G. giurus* and *N. hyrtlii*. *N. erebi* may not be able to survive within the most ephemeral pools as it has poor tolerance of low oxygen concentrations (Bishop *et al.* 2001, Allen *et al.* 2002). An unsuitable life history strategy may account for the absence of *N. hyrtlii* from the most unstable pools (Chapter 7), as it is thought to have good tolerance of physico-chemical extremes (Bishop *et al.* 2001, Pusey *et al.* 2004). It is unclear what factors prevented *A. percoides* and *L. aheneus* from surviving within the highly ephemeral pools, for, while nothing is known of *L. aheneus*, research conducted on *A. percoides* in northern Australia (and see Chapter 7) indicates that it has a similar life history strategy to *L. unicolor*, and can tolerate similar water temperatures and oxygen concentrations (Bishop *et al.* 2001). However, field observations during this study suggested that neither species was as robust as *L. unicolor*.

Dispersal capability may also have affected species' distributions. For example, *L. unicolor*, one of the most widespread species within the Fortescue River is known to have a remarkable tendency to swim into newly inundated reaches (Unmack 2001, pers. obs.). That said, most of the fish that inhabit the unstable section of the catchment are thought to have good dispersal capacities (Pusey *et al.* 1998).

Although the distribution of species across the catchment appeared to be related more to their physiological tolerance than to their ability to re-colonise pools, there was evidence to suggest that flow history may alter this relationship. For example, one site (Railbridge Pool) contained three species of fish prior to drying out; however, upon re-filling the pool contained no fish. This suggested that the renewing rains were not heavy or long enough to facilitate re-colonisation. This finding highlights the complexity of the system and indicates that the importance of a species' re-colonising ability (to its distribution) is likely to differ depending on climatic patterns. Large floods should push species around the catchment, and open connecting links between pools for longer time periods, reducing the importance of re-colonising ability. Sustained periods of drought and small floods should mean that species' distributions will be related to their own dispersal capacities - only species with rapid migration will travel up connecting channels before pools become isolated. It is suggested that the apparently minor importance of re-colonising ability in this study may be explained by the fact that this study was conducted in the wake of a large (1:100 year) flood.

The impacts of flow history on fish community structure have been noted by other researchers (Fausch and Bramblett 1991, Pusey and Arthington 1993, Arthington *et al.* 2005). Floods and drought may erode the association between physical factors (such as pool stability) and community structure (e.g. species richness) and result in the seemingly stochastic 'regulation' of the community as described by Grossman *et al.* (1982). Long-term temporal studies need to be carried out in this system to address this potential.

Temporal Variability in Community Structure and Pool Stability

Pool stability (as measured by pool variability in depth) was a relatively good indicator of temporal changes in community structure. Most fish communities in unstable pools underwent greater changes in total fish abundance, and greater changes

in the abundance of the different species (intra-specific abundance) than communities in more stable pools. Increased variation in community structure within unstable pools was expected, and is thought to be associated with the greater changes in the within-pool environment that characterise unstable pools (Ross *et al.* 1985, Schlosser 1987a). For example, Taylor *et al.* 's (1996) study of the fish assemblages of the upper Red River Basin (Oklahoma, USA) found that "temporal variability in environmental variables correlated with variability in assemblages through times". The study by Arthington *et al.* (2005) of the fish communities of the Cooper Creek (central Australia) during a spate of drying found that changes in community structure were related to habitat loss. In the Fortescue River, it was difficult to determine what within-pool factors were important because, as pools shrank, the structure of the fish communities within the study pools went in different directions, suggesting that the effects of drought on community structure were complex and site specific.

The relatively short-term nature of this study and the fact that only two pools dried and were recolonised, made it difficult to assess the extent to which stochastic events during re-colonisation may contribute to temporal changes in community structure. Furthermore, these two pools produced contrasting results. One pool (Railbridge) contained no species after it was refilled, indicating extreme temporal instability. The other (Portland Pool) had similar total abundances and species abundances when it was full in April 2001 and April 2002 (after drying up in December of 2001), indicating a high level of community resilience. This suggests that temporal changes in climate can affect community structure by altering colonising ability.

Summary

The freshwater fish communities of the Fortescue River were structured principally by the stability of their environment. Pool stability was related to: the number and type of species within a pool, the magnitude of changes in total fish abundance and intra-specific abundance through time. Specifically, stable pools contained more species and underwent smaller fluctuations in total and intra-specific numerical abundance than unstable pools. The meta-community appears to be shaped by extermination of fish from intermittent pools and their re-colonisation from source pools; however this does not occur in a longitudinal manner. Species' physiological tolerances, rather than dispersal capacity, appeared to determine their distribution across the catchment.

This page has been left blank intentionally.

Chapter 5

The Relationship between Pool Stability and Population Size Structure

Introduction

The stability of the environment is thought to affect the size and/or age structure of fish populations. Populations inhabiting stable environments should be dominated by large (typically adult) size classes, whereas populations inhabiting unstable environments should be dominated by small (typically juvenile) size classes (Werner and Gilliam 1984, Schlosser 1987a).

Large fish should dominate stable environments because: (1) they are better competitors for limited resources in what is a relatively saturated habitat, and (2) they are less vulnerable to fish predation (Jobling 1995). In other words, survival in stable environments should be a function of size (Wilbur 1980).

Small fish should dominate unstable environments because: (1) mortality in this environment type is determined primarily by the physical environment, i.e. the competitive advantage of size is relatively unimportant (Dobzhansky 1950, Pianka 1970, Closs and Lake 1996, Ostrand and Marks 2000), (2) fish are highly fecund, i.e. juveniles are abundant, (3) the greater age of large fish (i.e. adults) increases their exposure to potentially fatal environmental conditions, and (4) the shallow depths that often typify unstable environments may adversely affect large fish because there may not be enough space to support them, and/or it may increase their exposure to avian predators (Schlosser 1987a, Power *et al.* 1990).

The pools of the Fortescue River differ widely in their stability (see Chapter 4) and provide a good opportunity to test the above theory. It was predicted that fish populations in relatively stable pools would contain a greater fraction of larger, and older, fish than populations in relatively unstable pools.

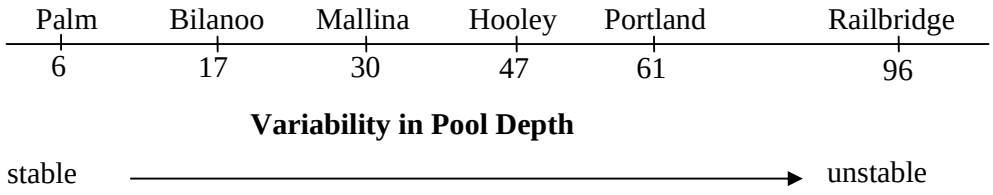
Although the stability of a habitat is predicted to affect both the age and size structure of a fish populations, it is extremely time consuming and often difficult to age fish (Pannella 1974, Campana and Neilson 1985). Nonetheless, substantial efforts were made to age numerous individuals of all dominant fish species of the Fortescue River; however, this was largely unsuccessful (see Appendix VII). Consequently, this chapter examines the relationship between habitat stability and population size structure rather

than age structure. It does so for five of the most abundant species within the Fortescue River: *Leiopotherapon unicolor, L. aheneus, Amniataba percoides, Nematalosa erebi* and *Melanotaenia australis*. The size structure of each population was viewed in terms of large versus small fish, with size at maturity used as the boundary to separate these groups. Size at maturity was chosen for two reasons: (1) it has ecological consequences for the maintenance (reproductive capacity) of populations, and (2) the growth rate of fish is relatively linear before maturity, allowing a coarse appraisal of the effects of age (time) on population structure.

Methods

Study Sites

Population size structures were examined in each of the six primary pools (Palm, Bilanoo, Mallina, Hooley, Portland and Railbridge), for each of the five sampling dates (April, August and December 2001, April and August 2002). These pools varied considerably in their stability; quantified as variation in maximum pool depth through time (see Chapter 2 for details). The relative stability of the pools is shown below.



Sampling Methodology

Fish were collected using a specially designed drop-net, the accuracy of which is described in Chapter 3, and method of placement within a pool described in Chapter 4. The raw data from drop-net collections are provided in Appendix II. It is important to note that the mesh used on the drop-net changed during the study period. The first two sampling periods (April and August 2001) utilised a mesh size of 5x5 mm and field observations revealed that small individuals, particularly *M. australis*, were

falling through the net during collection. The mesh was changed to 1x1.5 mm mesh for all subsequent sampling.

Gill nets and light traps were also deployed at each sampling period in order to catch the very largest and smallest size classes. This was done, not because the drop-net did not catch these size classes, but because their low abundance meant that they may be missed by the drop-net (see Chapter 3). Fish caught using the gill nets and light traps were not used in the construction of the size frequency distributions, but were used to extend the size range. A description of the gill nets used is provided in Chapter 3. The light traps were quatrefoil in style and used chemical light sticks (white light, 13.3 cm) for illumination (Secor *et al.* 1992a). Light traps were set in the various habitats of the littoral zone after dark (7-9 pm) and retrieved at dawn (~6 am). At each site, four light traps were set each night for two nights. Light traps were not used in the August 2002 sampling trip as they had caught few fish in all previous trips.

Analyses

For each species, a size frequency distribution was constructed for each site at each sample time. Different interval sizes (0.25 mm, or 0.5 mm, or 10.0 mm) were used for different species, according to which one best delineated cohorts; generally, smaller interval sizes were used for small or slow-growing species. Distributions composed of less than 20 individuals were omitted from the analysis. All results from April and August 2001 had the 0-2 cm section shaded out to represent the inaccuracy of the larger mesh used during these sample periods.

To summarise the size frequency distributions and aid in the identification of patterns between pool stability and population structure, size frequency data were pooled for all sampling times at each site (unpooled data are available in Appendix IV). One pool, Railbridge, was sampled on only two occasions (April and August 2001) which coincided with the use of the larger mesh type, hence size frequency distributions for this pool were biased against small size classes. This affected only *M. australis* and *L. unicolor*, as the other species did not occur in this pool. *M. australis* appeared to be more affected than *L. unicolor* for several reasons: (1) small *M. australis* are thin and were commonly observed falling through the larger mesh, whereas small *L. unicolor* were much wider and rarely seen falling through the mesh, (2) sampling of *M. australis* using the smaller mesh collected much smaller size classes (increased size

range), whereas the size range of *L. unicolor* collected did not change with mesh types (see Appendix IV, Figure IV.2 and IV.10), (3) the small size of *M. australis* (maximum size 8.4 cm) meant that the underestimation of the smallest size classes affected a significant proportion of fish sizes, whereas the larger size of *L. unicolor* (maximum size 26.5 cm) meant that this bias effected a proportionally smaller section of fish lengths. Consequently, Railbridge Pool was omitted from all analyses involving *M. australis* but included for those involving *L. unicolor*.

To simplify the comparison of small versus large size classes, only two size classes were examined; that is, fish of adult size and fish of juvenile size. Size at maturity was chosen as the boundary because it has ecological consequences; that is, adult size classes have the potential to reproduce and expand the population whereas juveniles do not. The method for determining size at 50% maturity is provided in Chapter 7, and was: 6.2 cm for *L. unicolor*, 2.7 cm for *L. aheneus*, 4.0 cm for *A. percoides*, 10.4 cm for *N. erebi*. *M. australis* was not examined for 50% maturity and a value for this parameter (3.5 cm) was assigned based on the results of ad hoc field data collected during this study, and research on closely related species (see Table 7.6). Size at maturity values rarely fell on the size frequency intervals used to constructing the graphs; hence the closest interval was used. These were: 6.1 cm for *L. unicolor*, 3.1 cm for *L. aheneus*, 4.1 cm for *A. percoides*, 11.1 cm for *N. erebi* and 3.4 cm for *M. australis*.

Data were converted to % as it standardised differences in total numbers caught, enabling a direct comparison between groups. This approach also removed any variation associated with uneven sampling effort at each study site. Simple linear regressions were used to investigate the relationship between pool stability and population structure (proportion of the population that were above adult size) for each species. Prior to the analysis the data were arcsine transformed to normalise the spread of the data (proportion data have a binomial distribution) (Zar 1999). All statistical procedures were carried out using JMP (SAS Institute 2001).

Results

A total of 8424 fish were collected using the drop-net at the six pools over the five sampling dates. This included: 1429 *L. unicolor*, 457 *L. aheneus*, 864 *A. percoides*, 4927 *N. erebi* and 3166 *M. australis*. The December 2001 collection of *N. erebi* included a large school of recruits (n=2667). The high fecundity of this species and the schooling nature of its larvae meant that this collection distorted the shape of the population. To reduce the distortion this cohort was capped at 250; this large number showed the dominance of small size classes in this pool, but still allowed less frequent size classes to be observed. All figures and analyses were carried out using the capped data (i.e. the total number of *N. erebi* equalled 2510).

Pool Stability and the Relative Survivorship of Large (adult) versus Small (juvenile) Size classes

Population size frequencies differed between pools (Table 5.1, Figure 5.1). Three of the five species showed a noteworthy change in the proportion of large fish (those that were of adult size) with pool instability (variability in pool depth) (Figure 5.2, Table 5.2). The term 'noteworthy' was used to denote a trend which was not significant at the 5% level, yet had a high F-value (> 4.0), which suggested that insignificance at the 5% level was due to the small number of study sites (low power). All of these species (*L. unicolor*, *A. percoides* and *N. erebi*) showed, as expected, a decreasing proportion of adult sized fish with increasing pool instability (Figure 5.1). *L. aheneus* and *M. australis* showed no relationship between the proportion of the population that was of adult size and pool variability in depth (Figure 5.1, 5.2; Table 5.2).

Table 5.1. The number (n) and percentage (%) of fish that were of adult size for each study pool. Data were pooled across sampling times, and are presented for each species. — indicates sample size of < 20, data were not included, NA indicates that a species absent from site, and ~ indicates that a data are unreliable due to an artefact of methodology (see Methods).

	L. unicolor		*L. aheneus*		*A. percoides*		*N. erebi*		*M. australis*	
	n	%	n	%	n	%	n	%	n	%
Palm	—	—	140.0	51.1	43.0	68.2	182.0	79.8	209.9	36.5
Bilanoo	—	—	128.0	92.1	111.0	82.8	333.0	87.9	21.0	13.9
Mallina	134.0	63.5	—	—	248.0	74.9	36.2	3.6	1287.6	94.4
Hooley	105.0	35.2	9.0	40.9	70.0	64.2	2.0	0.6	177.9	63.1
Portland	33.0	5.7	3.4	16.7	60.8	26.8	41.0	7.5	442.7	70.5
Railbridge	17.0	5.1	NA	NA	NA	NA	NA	NA	~	~

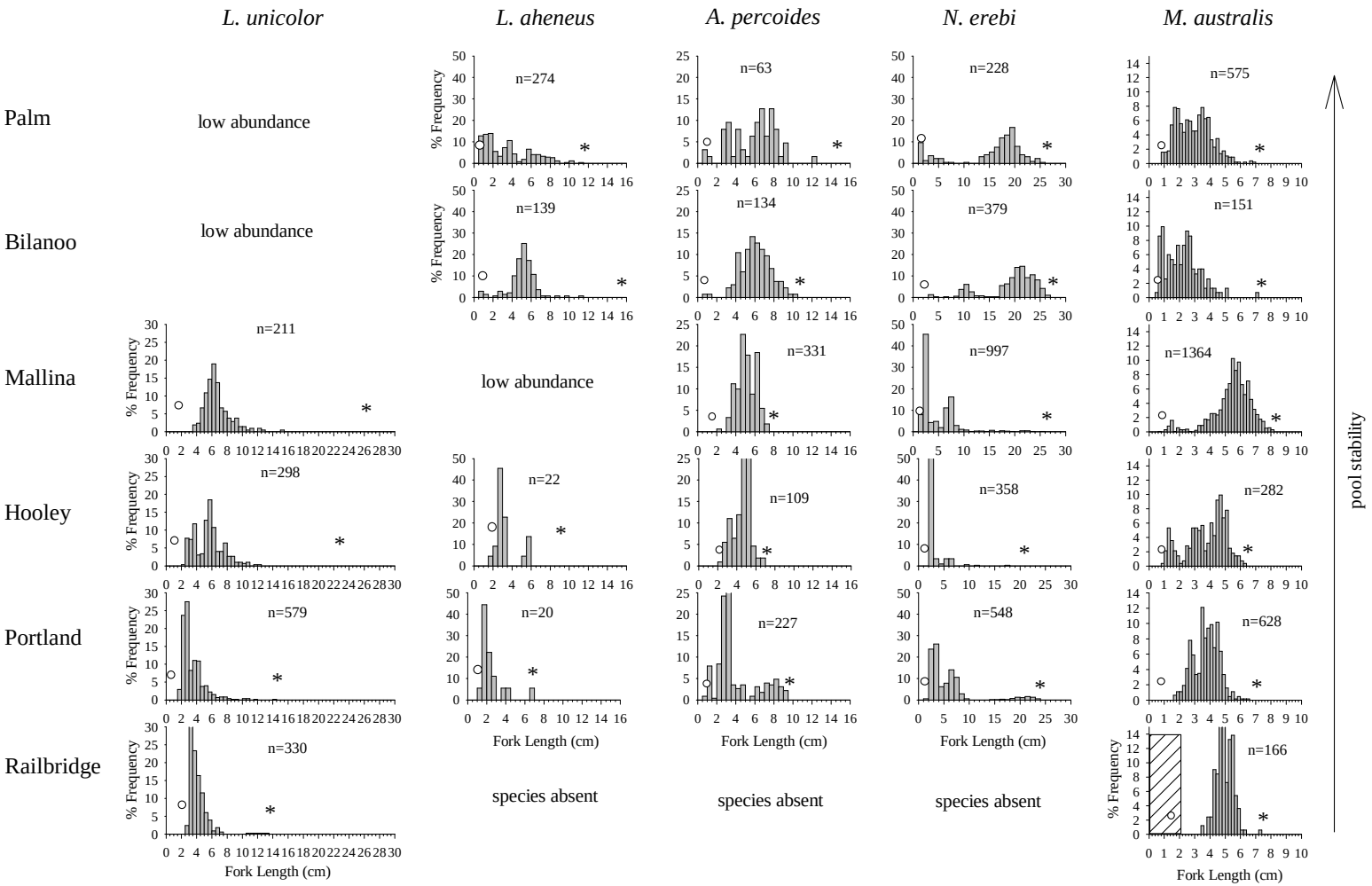


Figure 5.1. Size frequency distributions (as a percentage) for *L. unicolor*, *L. aheneus*, *A. percoides*, *N. erebi* and *M. australis*, for the six study pools. Pools are ordered in decreasing stability, and data for each pool have been pooled for the five sampling dates. Data are based on collections using the drop-net, but the maximum (*) and minimum (o) size classes of fish collected using all methods (drop-net, gill nets and light traps) are indicated on each graph. Sample size (n) is shown, and when fewer than 20 fish were collected from a pool no graph is provided. The hatched rectangles on the distribution of *M. australis* from Railbridge Pool indicate that small size classes were underestimated due to an interaction between the mesh size used on the drop-net, sampling dates, and this species' body shape (see Methods).

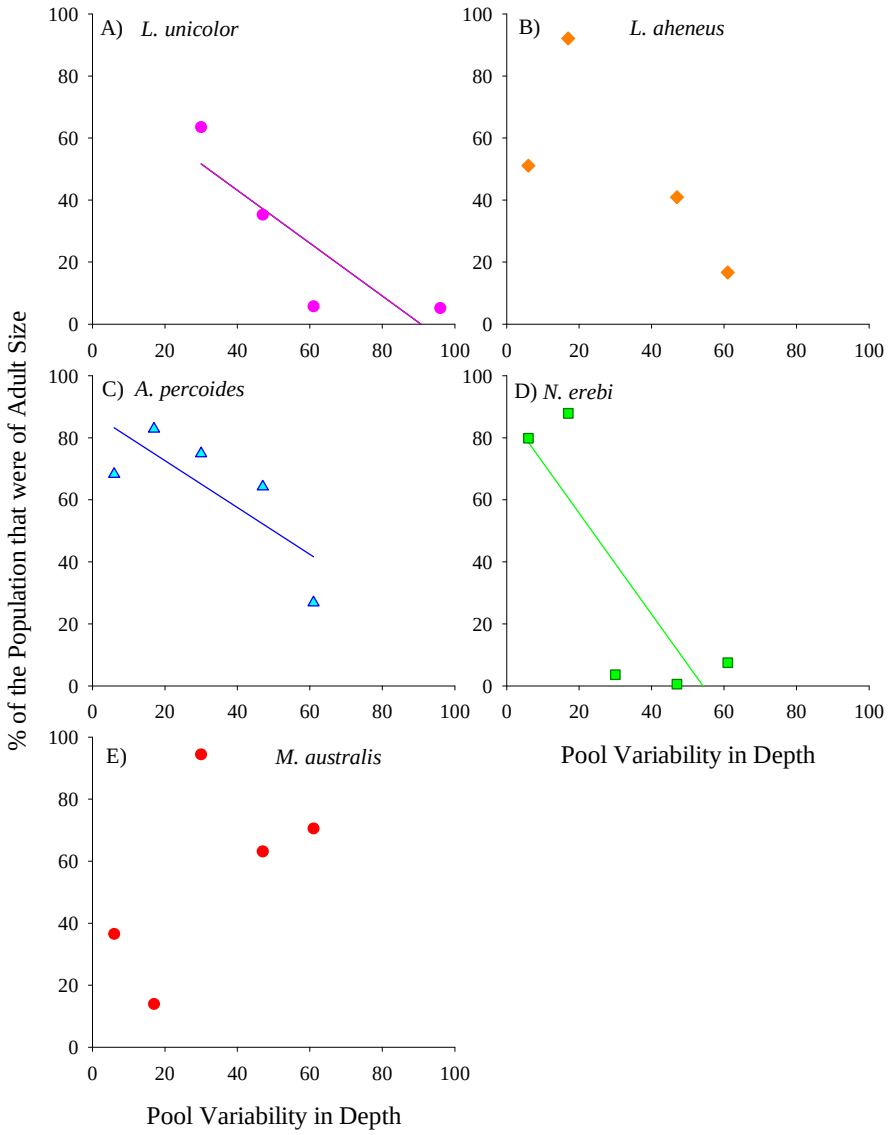


Figure 5.2. The percentage of a population that were of adult size versus pool variability in depth. Each point on the graph represents data that have been summed for all five sampling periods (April, August and December 2001, April and August 2002). Data are provided for the five species. Significant patterns (i.e. F>4) are shown with a line-of-best-fit.

Table 5.2. Linear regressions between variability in pool depth (x) and the arcsine transformed proportion of the population that were of adult size (y). A separate linear regression analysis was performed for each species. * indicated that the F-value was > 4, and the trend was considered significant (see Results).

Species	r^2	n	F-value	p-value
L. unicolor	0.75	4	5.996*	0.134
L. aheneus	0.51	4	2.074	0.286
A. percoides	0.60	5	4.467*	0.125
N. erebi	0.65	5	5.519*	0.104
M. australis	0.27	5	1.102	0.371

Discussion

The fish populations of the Fortescue River provided mixed support for the proposal that the stability of the local environment is an important determinant of the size structure of a population. Only three of the five species studied showed a change in the proportion of large (adult sized) and small (juvenile sized) fish with pool stability. However, all species showing a change (*L. unicolor, A. percoides,* and *N. erebi*), showed the trend predicted by theory, that is, the proportion of the population that was of large size (adult sized) increased with pool stability.

An increase in the proportion of older fish (adults) within the more stable pools was expected because these pools are buffered against the potentially lethal effects of drought (Schlosser 1987a). For example, the three most unstable pools dried at least once during the 16 month sampling period, killing all fish within the pools (see Chapter 2 Figure 2.4).

Increasing depth within stable pools may also have played a role. Studies conducted elsewhere report that deep-water protects fish during periods of flood (Schlosser 1987a), and protects large fish from avian predators (Angermeier and Karr 1983, Power *et al.* 1990). Such benefits may have contributed to the findings of this study, as pool depth increased with pool stability for all pools bar one, Railbridge Pool being the exception (see Chapter 2). Railbrige Pool affected only one species, *L. unicolor*, because the results from this pool were not included in the analyses of all other species (generally because they were absent from this site). If the shelter associated with deep-water did contribute to the results, then it was probably more important for *N. erebi*, which grew to a larger maximum size (~27 cm), than for *A. percoides* (maximum size 14.5 cm). It is important to note that maximum pool depth was not correlated with pool stability (measured by persistence of water) for the river at large (Chapter 4), hence any benefits associated with it are likely to be of minor importance at a larger scale.

An increase in the number of large (adult) fish within the more stable pools could also be a consequence of faster growth rate within these pools. However, this is unlikely as Chapter 6 revealed that the growth rate of adult *N. erebi* was slowest within the most

stable pools, and differed little between stable and unstable pools for adult *L. unicolor*.

A decline in the proportion of small fish within the more stable pools was expected. Small fish may be eaten by the large fish present within these pools. Alternatively, if they escape this fate, and seek shelter within a common refuge, their high density and overlapping diet (due to their small gape size - Jenkins *et al.* 1993) may increase competitive interactions and thus mortality (Moyle and Vondracek 1985, Schlosser 1987b, Gelwick 1990, Schlosser 1991 & 1995a). Interestingly, increased fish predation in the most stable pools appeared unlikely in the Fortescue River. This was because the most aggressive species, *L. unicolor*, was present in very low numbers in these pools (see Appendix V). It is of course possible that the additional species that occurred within the most stable pools (*Arius graeffei* and *Anguilla bicolor*) increased the level of predation on small fishes. However, this appears an unlikely scenario because: (1) food web analysis revealed that *A. graeffei* was not a top predator (Appendix VI), and (2) *A. bicolor*'s large size (and gape) means that it should prey on large as well as small size classes.

The decoupling of increased fish predation with increasing pool stability within the Fortescue River may have contributed to the fact that some of the species studied did not display the expected change in community structure with pool stability. This appeared to be the case for *M. australis*. This species is the smallest in the river, attaining a maximum size of less than half that of all other species, and as such, should be the most vulnerable to fish predation. Not surprisingly, the demography of this species was related to the presence and size range of the most aggressive species, *L. unicolor*. For example, populations of *M. australis* that co-occurred with *L. unicolor* (in notable abundance), had relatively few small size classes. Mallina Pool, which contained the greatest number of large *L. unicolor,* supported a population of *M. australis* with the greatest skew towards large size classes (relatively few small fish). Predator-mediated variation in population demography has been reported for other small freshwater-fishes (Gilliam *et al.* 1993, Rodd and Reznick 1997), and requires further investigation in the Fortescue River.

Small size classes (especially larvae) may also suffer higher mortality than large size classes in stable pools if food is limiting. This is because slow growth means that fish will "remain vulnerable to a larger suite of predators for a longer time interval" (Winemiller pers. comm.). While it is hypothesised that food is a limiting factor within stable environments (Schlosser 1987a, Jobling 1995) no information was available on pool productivity, or juvenile survivorship in this study system. However, the fact that juvenile *L. unicolor* grew at a slower rate as pool stability increased (and this did not appear to be a function of water temperature) (Chapter 6) provides indirect support for this suggestion.

If larval competition for food was in someway responsible for the changing proportion of large versus small size classes with pool stability, it is not surprising that the species with high fecundity (*L. unicolor*, *N. erebi*, and *A. percoides*) showed the expected trend, whereas species with lower fecundity (*L. aheneus* and particularly *M. australis*) did not.

Summary

The fish populations of the Fortescue River provided mixed support for the hypothesis that the stability of the local environment is an important determinant of the size structure of a population; only three of five species showed a change. However, all of the species that did show a change in population structure with pool stability showed the trend predicted by theory, that is, the proportion of the population that was of large (adult) size increased with pool stability. This pattern was probably caused by the eradication of large (adult) fish from unstable pools during periods of drought. In the Fortescue River, the abundance of fish that preyed on other fish did not increase with pool stability, and this may have contributed to the fact that not all species agreed with expectation.

This page has been left blank intentionally.

Chapter 6

Growth Rate: Relations with Fish Density/Biomass per-unit-area and Pool Stability

Introduction

Growth rate has important ecological consequences for fish populations because: (1) the survival of larval (and juvenile) fish is thought to be positively linked to size (Werner and Gilliam 1984, Hutchings 1993, Cargnelli and Gross 1996, Hutchings 1997, Schlosser 1998, Post *et al.* 1999); (2) fish fecundity increases at an increasing rate with fish size (Stearns and Koella 1986, Weatherley and Gill 1987, Reznick and Yang 1993, Hutchings 1997); and (3), the onset of reproduction in many species of fish is determined by size (Weatherley and Gill 1987). Consequently, a population whose individuals are growing quickly should increase in number more rapidly, due to increased reproductive output and improved recruitment, than a population (if all other things are equal) whose individuals are growing slowly (Jenkins *et al.* 1993).

The stability of the environment should affect the growth rate of fish. This is because environmental stability will affect the density and size classes (biomass) of fish within a system, and consequently the strength of competition for food (Pianka 1970, Schlosser 1987a, Jobling 1995, Goto 1998, Schlosser 1998). In stable environments, the number of fish within a population is thought to be relatively close to the maximum number that the environment can support (i.e. the carrying capacity) (Pianka 1970). Consequently, food is in relatively short supply and individuals have to spend energy searching and competing with one another for limited food resources. As a result, growth rates are relatively low (Jobling 1995).

In contrast, the number of fish within unstable environments is thought to be far from the carrying capacity of the environment (Pianka 1970). Low fish density is also accompanied by reduced fish biomass, as the fish in unstable environments are smaller than those in stable environments (Schlosser 1987a). These factors together mean that food should be relatively plentiful. Individuals do not have to spend energy searching or competing for food and so growth rates are relatively high (assuming equal productivity between stable and unstable environments) (Jobling 1995).

However, the notion that food is always plentiful within unstable environments is overly simplistic. Unstable environments will fluctuate between periods of optimal and sub-optimal conditions. For example, fish density (and fish biomass per-unit-area)

is likely to increase within a drying pool (Matthews 1998, Matthews and Marsh-Matthews 2003). As fish density increases, food availability should decrease and competition for food should increase, slowing growth (Zaret and Rand 1971, Goto 1998, Schlosser 1998).

Furthermore, fish inhabiting unstable environments will be exposed to severe fluctuations in the physico-chemical environment (Ostrand and Marks 2000, Matthews and Marsh-Matthews 2003). Some species may display behavioural or physiological adaptations to minimize the stress associated with the fluctuating environment (Lewis 1970, Matthews and Maness 1979, Matthews and Styron 1981, Smale and Rabeni 1995). However, those that do not may have to spend a great amount of energy to maintain internal homeostasis and may have reduced growth rates as a result.

While recent climatic patterns and species tolerances may affect whether unstable environments are associated with faster fish growth, patterns of growth will be also complicated by the physical and biological characteristics of the system. Fish growth rate has been found to alter with: water temperature (Wooton 1992, Sogard and Olla 2001), system productivity (Weatherley and Gill 1987, Schlosser 1991, Jenkins *et al.* 1993), and the presence/abundance of piscivorous predators (Rodd and Reznick 1997). The complexity of growth rate in natural systems is outlined by the following examples.

Spranza and Stanley (2000) studied the fishes in an intermittent prairie stream in Oklahoma (USA), and found that central stonerollers, *Campostoma anomalum*, occupying the more unstable (headwater) sections of the stream had elevated growth rates and body condition when compared with conspecifics inhabiting relatively stable (downstream) sections. They also found that two other trophically distinct species, the orangethroat darter, *Etheostoma spectabile*, and the bigeye shiner, *Notropis boops*, also had elevated body conditions in the unstable sections of the stream. While the reduced density and biomass of fish in unstable reaches of the river could have been responsible for this result, Spranza and Stanley (2000) did not measure these traits. Instead, they attributed the increased growth in the headwaters to the increased water temperature and primary productivity in this section of the stream. They also

suggested that the reduced abundance of predators in the headwater reaches might have reduced the amount of energy spent or lost in negative interactions, aiding growth rate.

Oliva-Paterna *et al.* (2003) studied Sclater's barbel, *Barbus sclateri,* in the semi-arid streams of Spain and found that fish condition (a ratio of weight to length) was higher in streams with greater stability (i.e. continuous flow) than in relatively unstable streams (i.e. intermittent flow). Increased condition was attributed to a greater variety of habitats and food availability within the stable streams. Poor condition was attributed to the high densities of fish, and presumably stronger biological interactions, within the shrinking pools of the unstable streams.

This chapter examines the relationships between pool stability, fish density/biomass per-unit-area, and fish growth rate in the Fortescue River. It was predicted that growth rate would be negatively correlated with fish density and fish biomass per-unit-area. It was also predicted that fish density and fish biomass per-unit-area would vary with pool stability, but that the nature of this relationship would change with climatic conditions. Specifically, that following periods of high rainfall, when unstable pools were swollen, fish density and fish biomass per-unit-area would be at their lowest, and fish growth rate would be fastest. At this time, changes in growth rate between stable and unstable pools would be most obvious. Following periods of drought, when unstable pools were shrunken, fish density and fish biomass per-unit-area would be higher, and fish growth rate would be slower. At this time, changes in growth rate between stable and unstable pools would be negligible, or growth in unstable pools may be the slowest. Growth rate in unstable pools was predicted to decrease as they shrank and increase as they expanded. Growth within stable pools was expected to remain relatively constant over time.

Essential to this investigation was the ability to estimate a fish's growth rate accurately. Estimating growth rate is difficult and requires the researcher to choose and validate the most appropriate method. For this study, otolith weight-at-size was used as a correlate of growth rate (for a discussion and validation of this method see Appendix VII). Light otoliths (at size x) indicate fast growth rate and heavy otoliths (at size x) indicate a slow growth rate (Templeman and Squires 1956, Marshall and

Parker 1982, Reznick *et al.* 1989, Secor and Dean 1989). As otolith weight provides a description of a fish's growth rate over its whole life (i.e. its average growth) (Jenkins *et al.* 1993), fish were separated into adult and juvenile size classes. Juvenile fish were used to examine the relationships between present (and recent) pool conditions and fish growth. Adult fish were used to examine long-term relationships.

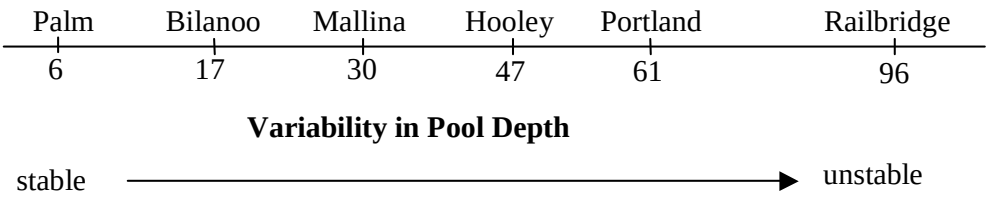
The relationships between pool stability, fish density/biomass-per-unit-area, and fish growth rate were examined for two widespread fish species of the Fortescue River: *Leiopotherapon unicolor*, and *Nematalosa erebi*. This study commenced one year after a large flood. All study pools were full at this time, and conditions for growth were considered to be optimal. As the study progressed, the system passed through a period of drought. The drought lasted two years and provided an opportunity to examine the effects of seemingly increasingly unfavourable conditions on fish growth rate.

Although this study was not directly interested in the role of water temperature on the growth rate of fish within the pools of the Fortescue River, the importance of water temperature of fish growth rate cannot be overstated. Consequently, this chapter also examined the relationship between growth rate and water temperature.

Methods

Study Sites and Sampling

Fish (adults and juveniles) were sampled from the six focal pools (Palm, Bilanoo, Mallina, Hooley, Portland and Railbridge) on eight occasions (April, August and December 2001, February, March, April, August and December 2002). The pools varied considerably in their stability, which was quantified as variation in maximum pool depth through time (see Chapter 2 for details). The relative stability of the pools is shown below.



Fish Density and Fish Biomass

Estimates of fish density and fish biomass per-unit-area were only possible when the drop-net was used during sampling. This meant that estimates were confined to five dates: April, August and December 2001, April and August 2002. Density estimates were based on estimates of the total abundance of fish within a pool. This involved standardising the fish caught by the drop-net for the relative abundance of the different habitat types present within a pool. A detailed description of this procedure is given under the '*Sampling Methodology'* heading within the methods section of Chapter 4. Estimates of fish density are presented as the number of fish/100 m^2.

Estimates of fish biomass were as for fish density; the only difference was that fish weight (g) rather than number was used. Not all fish were weighed, and fork length, the distance (cm) from the snout to the fork in the tail, was used to predict weight. Weights were estimated by fitting a line to scatterplots of $\log_{10}$(fork length) (x) versus $\log_{10}$(weight) (y) for each species, and solving these equations [logWt=gradient*log(fork length) + y intercept] for y, and inverse logging the results. The equations used for each species are shown in Table 6.1. Estimates of fish biomass were presented as the weight of fish g/m^2.

Water Temperature

Water temperature was measured using a portable dissolved oxygen meter (Nester portable meter). Measurements were taken at 10 cm below the waters surface within the littoral margin of each pool (1 m in from the edge). Temperature was measured after dawn (6 to 8 am) and in the late afternoon (4 to 5 pm) to document diurnal extremes.

Table 6.1. The relationship between weight (g) and fork length (cm) for each of the freshwater fish species of the Fortescue River except *Anguilla bicolor*. Gradients and y-intercepts are shown for lines-of-best-fit for the scatterplot of $\log_{10}$(fork length) (x) versus $\log_{10}$(weight) (y). The sample size (n) and coefficient of determination (r^2) of each line is also provided.

Species	Gradient	Y-intercept	n	r^2
Leiopotherapon unicolor	3.207	-2.015	968	0.96
Leiopotherapon aheneus	3.233	-1.937	607	0.97
Amniataba percoides	3.407	-2.113	923	0.91
Nematalosa erebi	3.209	-2.047	1464	0.99
Melanotaenia australis	3.428	-2.301	1022	0.85
Glossogobius giurus	2.822	-2.019	283	0.89
Arius graeffei	2.877	-1.656	39	0.96
Hypseleotris compressa	5.036	-3.593	44	0.74
Neosilurus hyrtlii	3.174	-2.351	30	0.96

Otolith Collection and Processing

Most otoliths were removed in the field, following the methods of Secor *et al.* (1992b). They were dried and stored in eppendorf containers. Small fish were stored in 70% ethanol and their otoliths removed in the laboratory under a dissecting microscope.

Otoliths were examined under a dissecting microscope at 6 and 12x magnification to check for chips and to remove any foreign bodies. Otoliths were weighed (mg), one at a time, using a Sartorius 4503 microbalance (d=0.001 mg). Chipped otoliths were excluded, and the average weight of the two otoliths of each fish was used for all analyses.

Statistical Analyses

Analysis of Covariance (ANCOVA) was used to examine if otolith weight (adjusted for the covariate fish size) varied over time within-pools and among-pools. To prevent within-pool fluctuations from affecting among-pool comparisons, time was held as constant as possible. If the sample size was low, such as in the case of large adults, then multiple sampling dates were pooled, but only if no temporal variation was detected. If temporal variation was present at a pool, the two most different data sets from that pool were included in among-pool analyses as separate entities. This made it possible to examine the magnitude of temporal variation in growth rate within a pool and determine if it could alter growth rate comparisons among-pools.

ANCOVA has several assumptions. To test the assumption of similar spread of the covariate (x value), groups were compared using one-way ANOVA. The range of the comparison was narrowed if the uneven spread of one group caused this assumption to be violated. On one occasion, low sample sizes meant that reducing the size distribution for one group would exclude another group. In this case, the analysis was allowed to proceed because the group that had heavier otoliths had also, on average, smaller individuals. The positive relationship between fish size and otolith weight meant that, if anything, the uneven spread of the x variable (size) would bias the adjusted-least-squares mean to be smaller (hence lighter), reducing significance and so making the test more conservative.

To test the assumption of homogeneity of variances, the residuals of the model were plotted against the predicted (fitted) y values of the model, and against the category groups under study. If the first method showed that the scatter of the residuals was wedge shaped (variance in residuals increased with the fitted value) then the data were reciprocal transformed $(1/y)$[1]. If the second method suggested uneven variation in the residuals between groups then the data were also reciprocal transformed and re-analysed. To ensure that the transformation had resolved the problem, the residuals were viewed again graphically, and compared using several tests provided by JMP IN® (SAS Institute 2001) to investigate homogeneity of variance: including O'Brien's, Brown-Forsythe, Levene and Bartlett.

Another assumption of ANCOVA is that the slopes of the lines-of-best-fit are homogeneous (Quinn and Keough 2002). If the slopes varied, the range of the comparison (fish size) was restricted until this assumption was met.

Post-hoc comparisons were conducted to determine statistical significance. If a visual examination of the adjusted least squares means (and their errors) displayed an obvious gradient of separation then planned contrasts of the adjusted means were conduced using t-tests (Quinn and Keough 2002). However, if the separation of means was not obvious then unplanned multiple comparisons were conducted using Tukey tests (Quinn and Keough 2002). All statistical analyses were performed using the JMP IN® statistical package (SAS Institute 2001).

[1] See www.basic.nwu.edu/statguidefiles/linreg_ass_viol.html

Results

Pool Stability and Fish Density and Biomass/m^2

A total of 12584 fish were collected using the drop-net from the six study sites over the five sampling dates. Where and when they were collected are shown in Table AII.1 of Appendix II (note this table provides information for only the freshwater species, whereas density and biomass estimates include all species).

Fish density (# fish/100m^2) and fish biomass (g/m^2) were not related to pool stability. The exact relationships between fish density/biomass and pool stability were difficult to define due to temporal variation in density/biomass (Figure 6.1.A, B). It was predicted that at the commencement of the sampling period (April and August 2001) fish density/biomass would be greatest within the unstable pools, but this was not the case. For example, in April and August 2001, the relatively unstable pools contained communities with both higher and lower densities of fish than the most stable pool (Palm) (Figure 6.1.A). Similarly, at these times, the most stable pool (Palm) had the highest fish biomass and the second most stable pool (Bilanoo) had the lowest biomass (Figure 6.1.B).

The magnitude of temporal fluctations in fish density/biomass was not related to pool stability. It was predicted that unstable pools would display greater variation in density/biomass than the stable pools, but this was not the case. For example, large changes were observed in unstable (e.g. Portland Pool) and stable pools alike (e.g. Bilanoo Pool) (Figure 6.1.A). Increasing fish density was often associated with pool drying, for example Railbrige Pool in December 2001, Portland Pool in December 2002, and Bilanoo Pool in December 2001 (Figure 6.1.A), but not always. For example, fish density decreased as Mallina Pool shrunk throughout 2002 (Figure 6.1.A). Fish biomass increased in some pools as they shrunk, for example: Railbridge Pool in August 2001, Portland Pool in December 2001 and Bilanoo Pool in April 2002 (Figure 6.1.B). However, other pools showed relatively little change in biomass even through they shrunk considerably, for example Mallina Pool (Figure 6.1.B). One unstable pool (Portland) received notable rainfall during the summer of 2001/02, this pool showed the expected increase in fish biomass as it shrank and then the decrease in biomass after it was refilled and re-colonised (Figure 6.1.B).

An interesting result was that fish density (#/100 m^2) within the study pools converged as the drought progressed (Figure 6.1.A). Density converged toward that shown by the most stable pool (Palm). Fish biomass (g/m^2) showed no such trend (Figure 6.1.B).

Differences in fish density and fish biomass/m^2 among pools and through time were difficult to examine statistically because there was only one replicate per pool*time combination, and because there were missing values (pools dried). Non-parametric statistics using times as replicates were also avoided because graphical representation of the data suggested that interactions occurred between sites and times. Consequently, patterns are interpreted from graphs.

Water Temperature

Water temperature showed obvious seasonal trends, being greater in summer (December sampling period) than winter (August sampling period). There was no consistent pattern between water temperature and study pools (Figure 6.2.A, B). For example, Bilanoo Pool was warmer (in the morning) than Palm, Hooley and Mallina Pools in April 2001, but was the coolest pool in December 2001 (Figure 6.2.A). However, some differences among pools lasted for several sampling periods. For example, in April and August 2001, Bilanoo Pool had warmer morning water than Portland Pool, which was warmer than Palm Pool, and Mallina and Hooley Pool respectively (Figure 6.2.A).

The varying degree of diurnal fluctuations between small and large pools no doubt contributed to the complicated relationship between study pools and water temperatures. Small, shallow pools underwent greater daily fluctuations in water temperature than large, deep pools (see Appendix VIII). This meant that one pool could be warmer than another in the late afternoon but cooler in the morning. For example, in December 2001 the severely shrunken Portland Pool was warmer than Palm Pool in the late afternoon, but was colder in the morning (Figure 6.2. A, B).

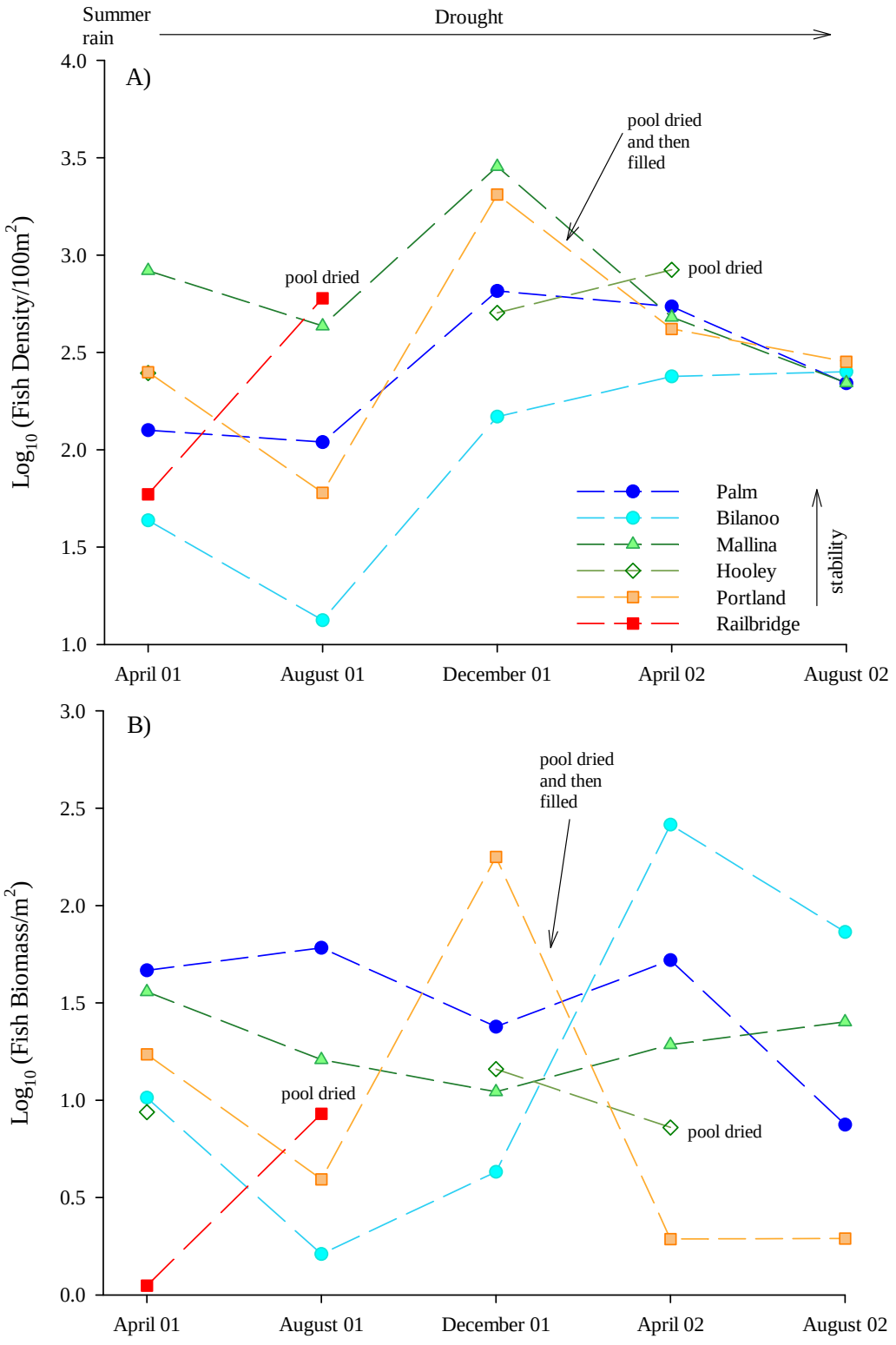


Figure 6.1. The density of fish (abundance/100 m^2) (graph A) and the biomass of fish (g/m^2) (graph B) at each of the six study pools at each of the five sampling dates between April 2001 and August 2002. Density and biomass estimates included all fish species and all fish sizes. Data used for the estimates were gathered using the drop-net, and were standardised according to the habitat types present within a pool.

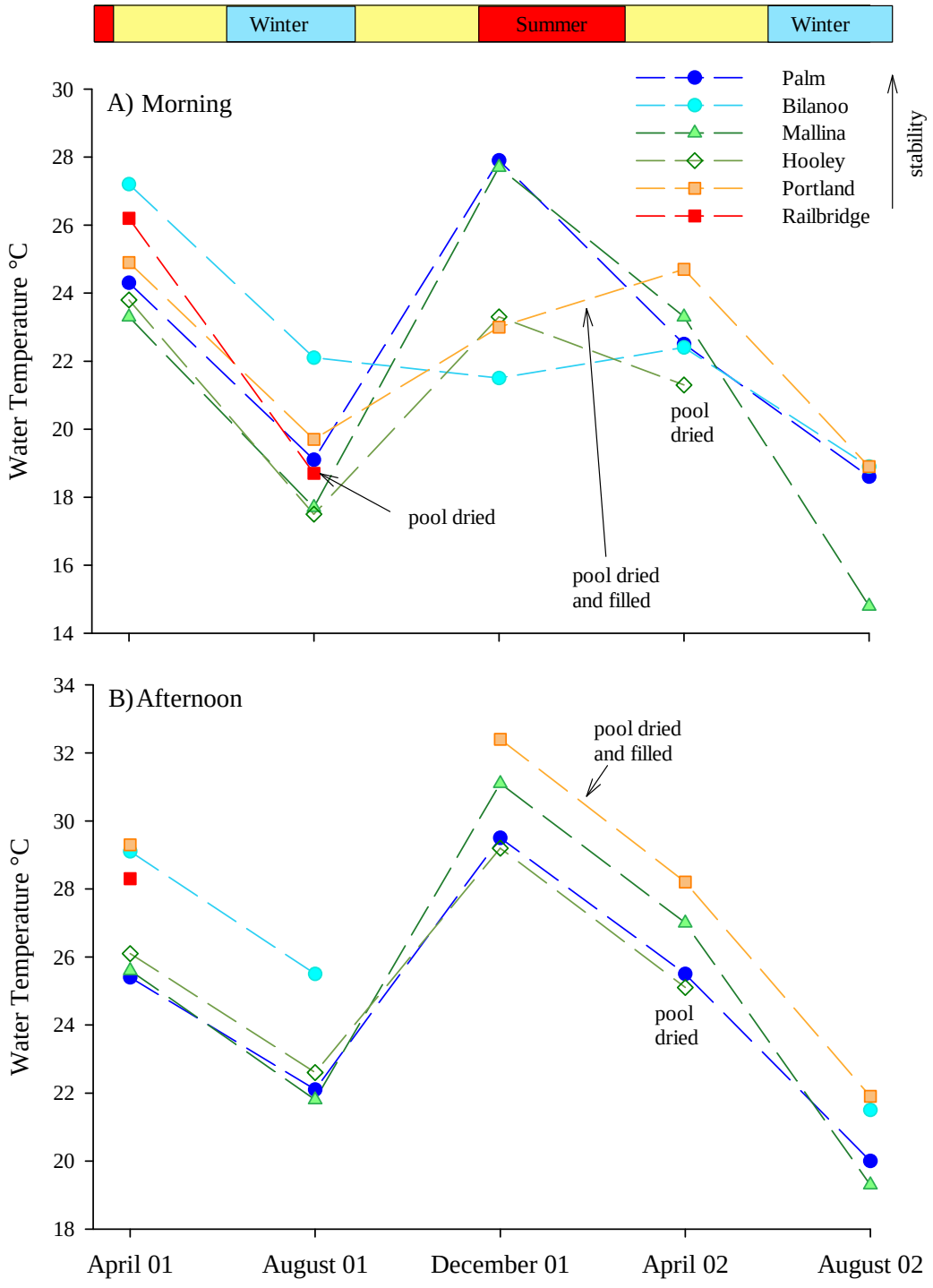


Figure 6.2 Morning (graph A) and afternoon (graph B) water temperature at the six study pools during the five sampling dates (April 2001 – August 2002). Times when pools dried are indicated on the graphs. The afternoon graph is missing several data points, including: Railbridge pool in August 2001, and Bilanoo pool in December 2001 and April 2002.

Otolith Weight and Fish Size

A total of 1485 pairs of otoliths were collected: 631 from *L. unicolor*, and 854 from *N. erebi*. The relationship between otolith weight and size differed between *L. unicolor* and *N. erebi*; *L. unicolor* had heavier otoliths for a given size than *N. erebi* (Figure 6.3.A, B).

L. unicolor had a relatively uniform scatter in otolith weight with fish size (Figure 6.3.A), whereas *N. erebi* showed considerably more scatter in otolith weight in the large size classes (Figure 6.3.B). Increased scatter within large size classes was expected, as the otoliths of fish should continue to grow even though somatic growth has ceased. The reduced scatter in *L. unicolor* suggested either that fish had not reached their maximum size (i.e. their growth was still indeterminate), or that all large individuals were of a similar age.

Growth Rate

Growth rate (otolith weight-at-size) varied not only among pools and within pools over time, but among size classes and between species. Changes in growth rate through time are presented before differences among pools because variation in the former had the potential to affect the way comparisons of the latter were carried out.

Changes in Growth Rate through Time

Leiopotherapon unicolor

Temporal comparisons were conducted for only four of the six study pools due to low abundances of this species in the two most stable pools (see Appendix V). Temporal changes in growth rate were associated with pool shrinkage at three of these pools (Mallina, Hooley and Railbridge). Portland Pool received rainfall during the summer of 2001/02, hence temporal changes in growth were complicated.

Changes in growth rate as pools shrunk were not consistent, varying not only among pools, but also between size classes within a pool. At Mallina and Hooley Pools the growth rate of juveniles increased as the pools shrank, as shown by the lighter otolith weight at any given size (Figure 6.4.A, 6.5.A; Table 6.2, 6.4), whereas the growth rate of large adults decreased as the pools shrunk, as shown by the heavier otolith weight at any given size (Figure 6.4.C, 6.5.C; Table 6.3, 6.5). In contrast, the growth rate of

juveniles (3 to 5.5 cm) decreased as Railbridge Pool shrank (Figure 6.6, Table 6.6). Large size classes could not be investigated in this pool due to low abundances.

Changes in growth rate at Portland Pool were not associated with pool shrinkage, as the pool shrunk but was refilled. Juveniles (4 to 5 cm) and adults (7 to 8.5 cm) collected from this pool in August 2002 had grown faster than those collected in April 2001 (Figure 6.7.A, B; Table 6.7, 6.8).

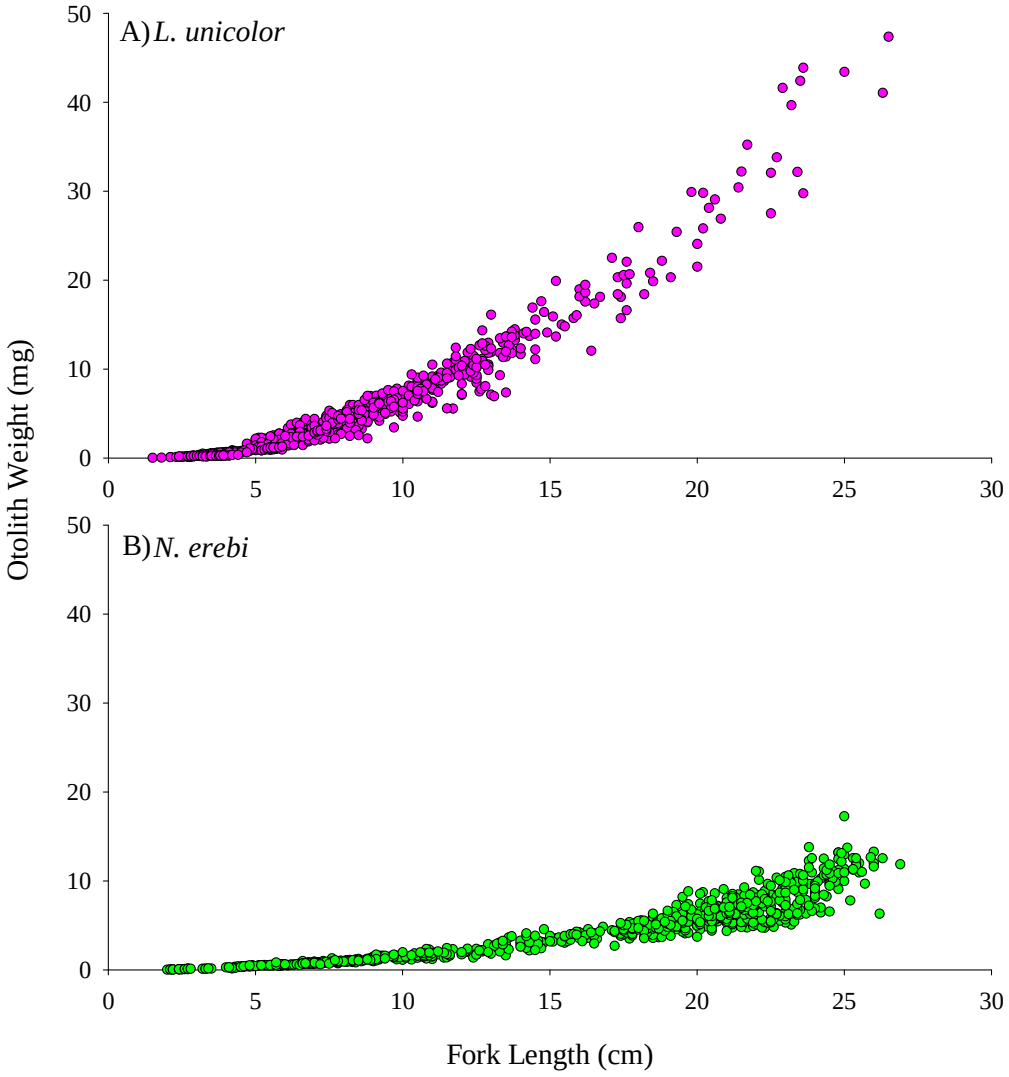


Figure 6.3. Otolith weight (mg) versus Fork Length (cm), a measure of fish size. A) *L. unicolor*, B) *N. erebi*. The data displayed are from all sites and all times.

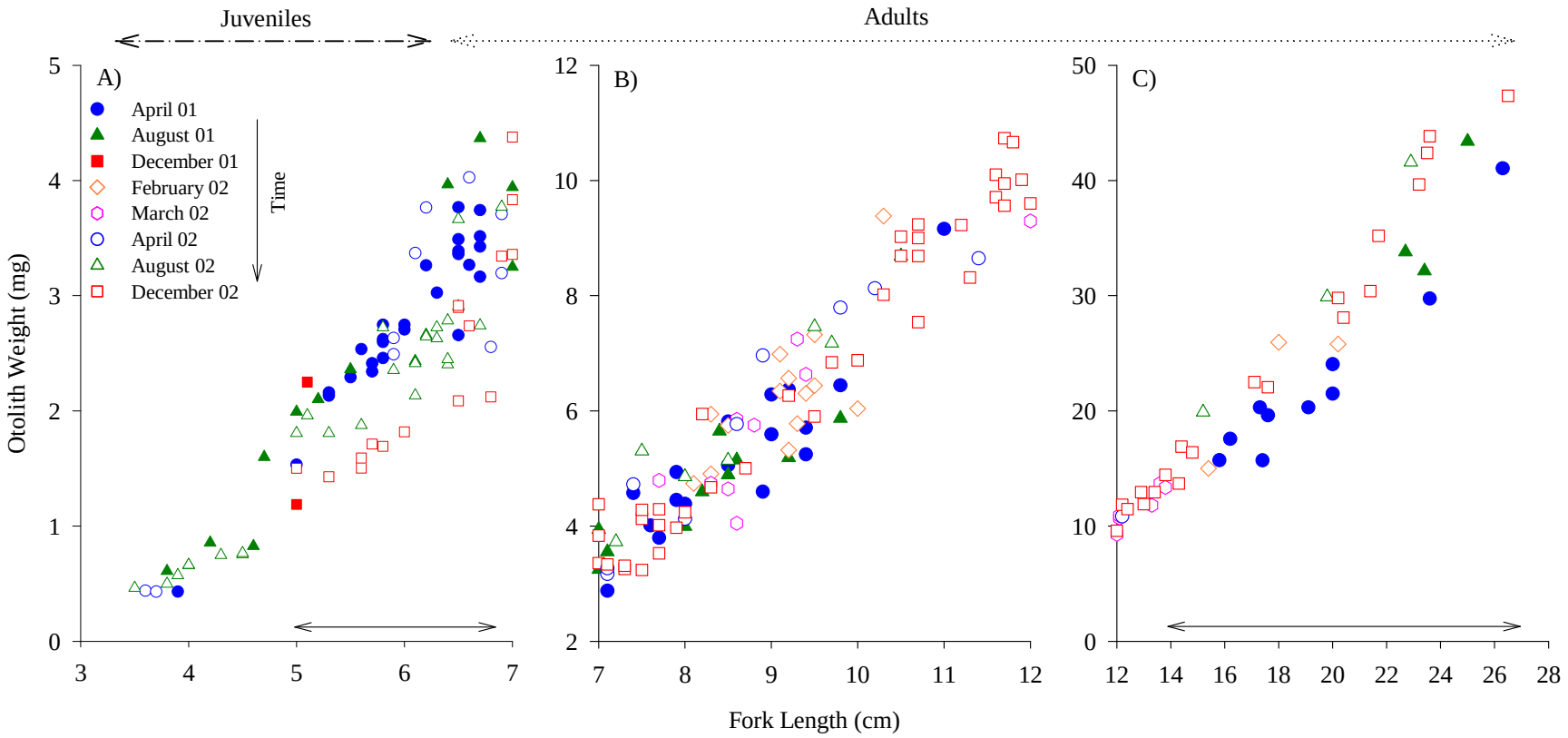


Figure 6.4. Temporal comparisons of otolith weight (mg) versus fork length (cm) for *L. unicolor* at Mallina Pool. Fish size (fork length) has been separated into three graphs to improve visual depiction. Juvenile and adults are shown. Sampling times spanned from April 2001 to December 2002. Size classes where times have been compared using ANCOVA have been identified using double-sided arrows.

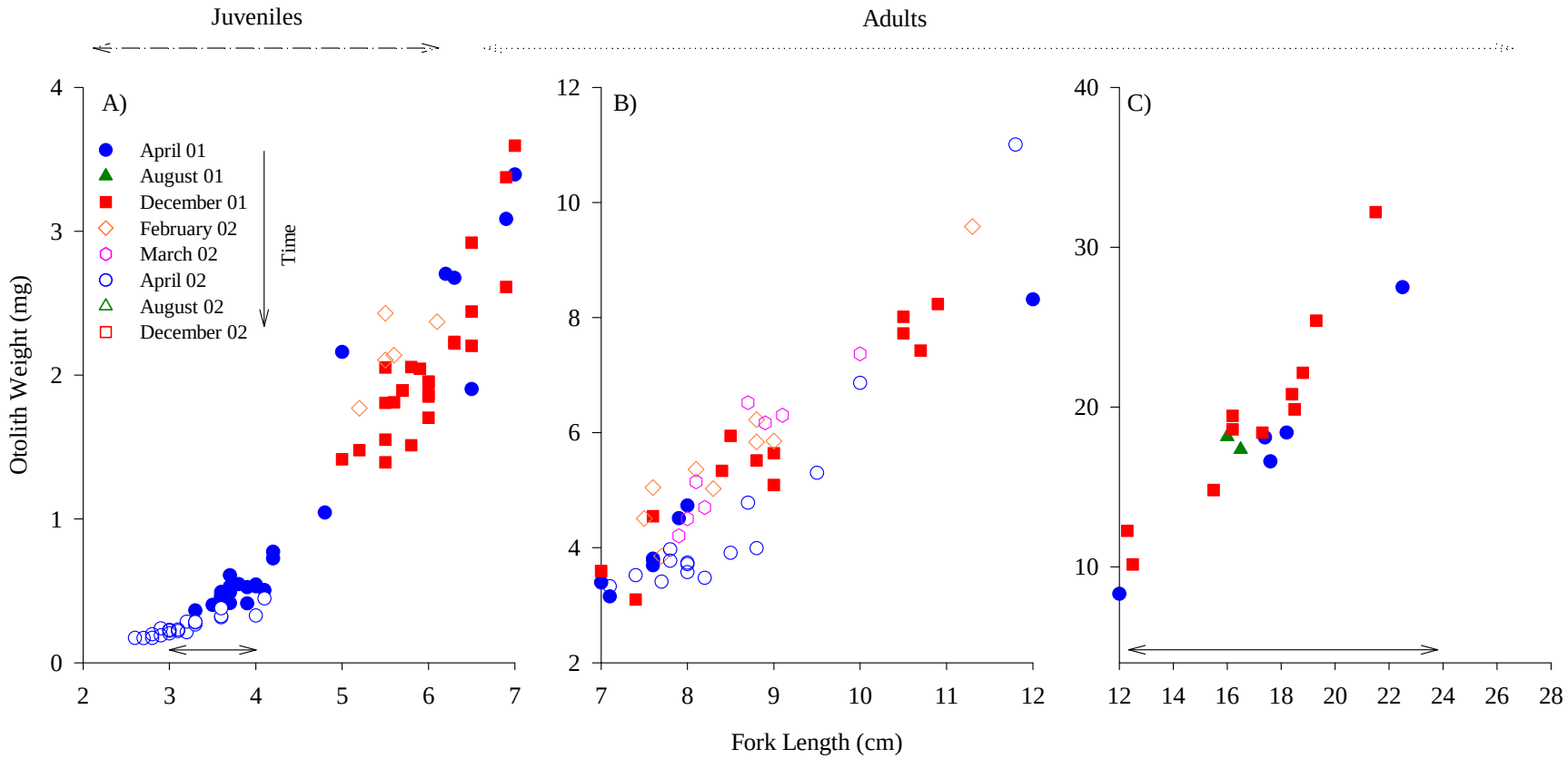


Figure 6.5. Temporal comparisons of otolith weight (mg) versus fork length (cm) for *L. unicolor* at Hooley Pool. Fish size (fork length) has been separated into three graphs to improve visual depiction. Juveniles and adults are shown Sampling times spanned from April 2001 to December 2002. Size classes where times have been compared using ANCOVA have been identified using double-sided arrows.

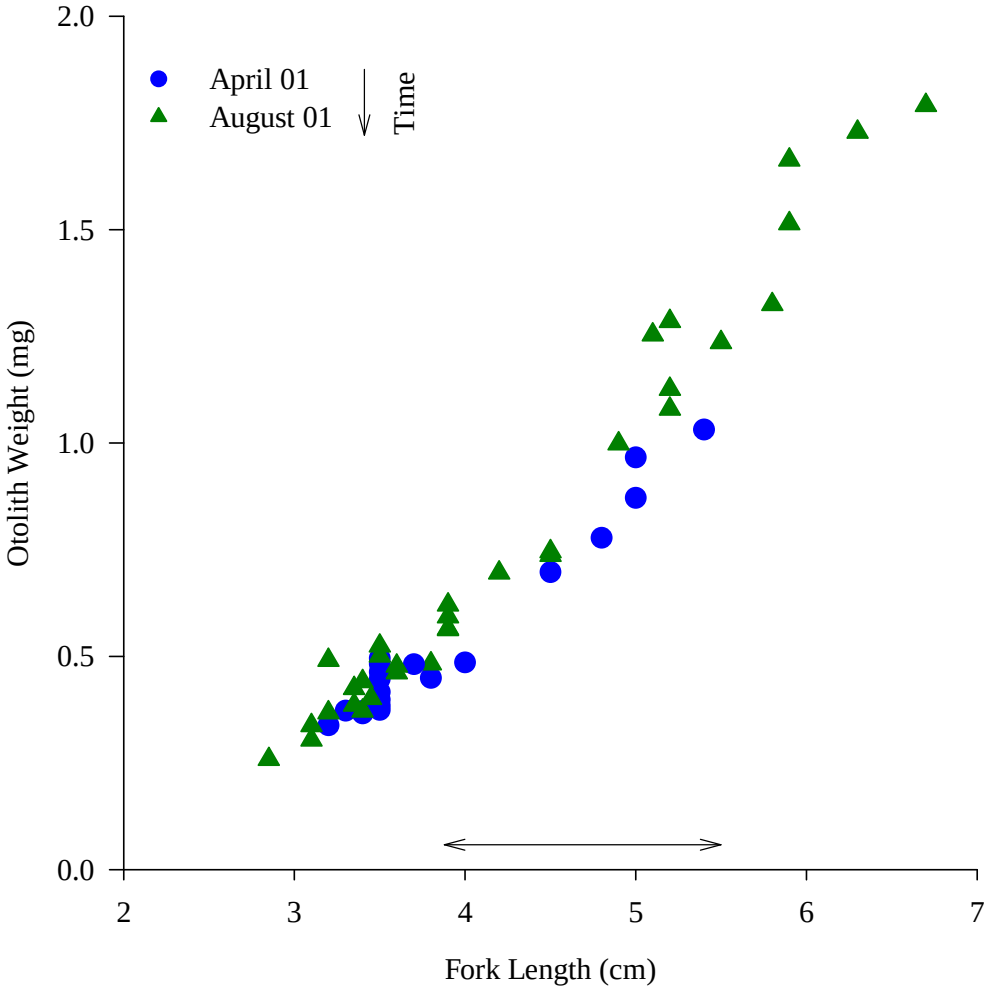


Figure 6.6. Temporal comparisons of otolith weight (mg) versus fork length (cm) for *L. unicolor* at Railbridge Pool. Juveniles only are shown as few large fish were collected. This pool was only sampled twice, in April and August 2001. The size class compared using ANCOVA has been identified using a double-sided arrow.

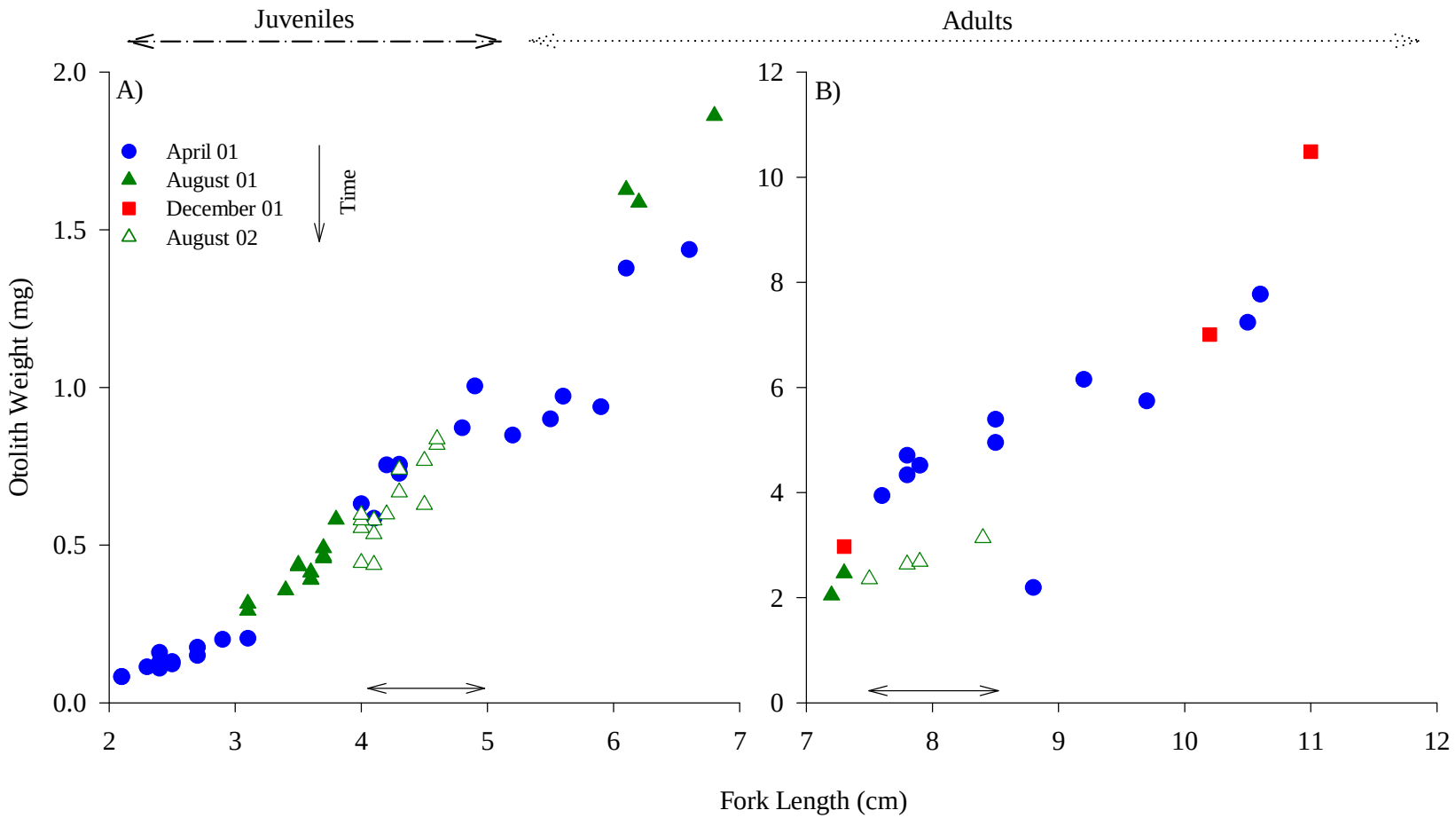


Figure 6.7. Temporal comparisons of otolith weight (mg) versus fork length (cm) for *L. unicolor* at Portland Pool. Fish size (fork length) has been separated into two graphs to improve visual depiction. Juveniles and adults are shown. Large size classes were in low abundance and have been omitted from the graphs. Sampling times spanned from April 2001 to August 2002. Size classes where times have been compared using ANCOVA have been identified using double-sided arrows.

Table 6.2. General linear model ANCOVA for *L. unicolor* at Mallina Pool, comparing otolith weight (mg) among times, with fish size (fork length) as a covariate. The size class compared was 5.0 to 6.8 cm. Data were 1/y transformed prior to the analysis. LS means are presented in their back transformed state, along with their original SEs * indicates significance at the alpha 0.05 level. Letters indicate the order of significant differences among sites.

Source	df	MS	F	p	Date	LS mean	SE
ANOVA					April 2001	2.681[c]	0.064
Model	7	0.093	43.5	<0.0001*	August 2001	2.727[c]	0.114
Error	53	0.002			December 2001		
					April 2002		
Effects Test					August 2002	2.374[b]	0.080
Date	3	0.106	33.08	<0.0001*	December 2002	1.899[a]	0.093
Fish size	1	0.370	173.67	<0.0001*			
Date*fish size	3	0.005	161	0.20			

Table 6.3. General linear model ANCOVA for *L. unicolor* at Mallina Pool, comparing otolith weight (mg) among times, with fish size (fork length) as a covariate. The size class compared was 14.0 to 27.0 cm. * indicates significance at the alpha 0.05 level.

Source	df	MS	F	p	Date	LS mean	SE
ANOVA					April 2001	23.267	0.710
Model	3	751.41	150.44	<0.0001*	August 2001	Not included	
Error	19	4.99			December 2001	Not included	
					April 2002	Not included	
Effects Test					August 2002	Not included	
Date	1	195.99	39.24	<0.0001*	December 2002	29.178	0.621
Fish size	1	1639.78	328.61	<0.0001*			
Date*fish size	1	21.73	4.35	0.051			

Table 6.4. General linear model ANCOVA for *L. unicolor* at Hooley Pool, comparing otolith weight (mg) among times, with fish size (fork length) as a covariate. The size class compared was 3.2 to 4.1 cm. Data were 1/y transformed prior to the analysis. LS means are presented in their back transformed state, along with their original SEs * indicates significance at the alpha 0.05 level.

Source	df	MS	F	p	Date	LS mean	SE
ANOVA					April 2001	0.468	0.012
Model	3	4.233	44.43	<0.0001*	August 2001	Not included	
Error	25	0.095			December 2001	Not included	
					April 2002	0.321	0.016
Effects Test					August 2002	Not included	
Date	1	5.041	52.89	<0.0001*	December 2002	Not included	
Fish size	1	2.477	25.99	<0.0001*			
Date*fish size	1	0.255	2.68	0.11			

Table 6.5. General linear model ANCOVA for *L. unicolor* at Hooley Pool, comparing otolith weight (mg) among times, with fish size (fork length) as a covariate. The size class compared was 12.0 to 24.0 cm. Data were 1/y transformed prior to the analysis. LS means are presented in their back transformed state, along with their original SEs. * indicates significance at the alpha 0.05 level.

Source	df	MS	F	p	Date	LS mean	SE
ANOVA					April 2001	14.583	0.842
Model	3	0.002	36.52	<0.0001*	August 2001	Not included	
Error	12	0.000			December 2001	18.087	0.565
					April 2002	Not included	
Effects Test					August 2002	Not included	
Date	1	0.001	8.99	0.011*	December 2002	Not included	
Fish size	1	0.007	105.16	<0.0001*			
Date*fish size	1	0.000	1.32	0.27			

Table 6.6. General linear model ANCOVA for *L. unicolor* at Railbridge Pool, comparing otolith weight (mg) among times, with fish size (fork length) as a covariate. The size class compared was 3.8 to 5.5 cm. Data were 1/y transformed prior to the analysis. LS means are presented in their back transformed state, along with their original SEs. * indicates significance at the alpha 0.05 level.

Source	df	MS	F	p	Date	LS mean	SE
ANOVA					April 2001	0.665	0.026
Model	3	1.284	97.52	<0.0001*	August 2001	0.779	0.018
Error	17	0.013			December 2001	Not included	
					April 2002	Not included	
Effects Test					August 2002	Not included	
Date	1	0.226	17.15	0.0007*	December 2002	Not included	
Fish size	1	3.333	253.07	<0.0001*			
Date*fish size	1	0.038	2.88	0.10			

Table 6.7. General linear model ANCOVA for *L. unicolor* at Portland Pool, comparing otolith weight (mg) among times, with fish size (fork length) as a covariate. The size class compared was 4.0 to 5.0 cm. * indicates significance at the alpha 0.05 level.

Source	df	MS	F	p	Date	LS mean	SE
ANOVA					April 2001	0.742	0.019
Model	3	0.078	26.56	<0.0001*	August 2001	Not included	
Error	15	0.003			December 2001	Not included	
					April 2002	Not included	
Effects Test					August 2002	0.677	0.016
Date	1	0.018	6.20	0.025*	December 2002	Not included	
Fish size	1	0.190	64.83	<0.0001*			
Date*fish size	1	0.000	0.00	0.99			

Table 6.8. General linear model ANCOVA for *L. unicolor* at Portland Pool, comparing otolith weight (mg) among times, with fish size (fork length) as a covariate. The size class compared was 7.5 to 8.5 cm. Data were 1/y transformed prior to the analysis. LS are presented in their back transformed state, along with their original SEs. * indicates significance at the alpha 0.05 level.

Source	df	MS	F	p	Date	LS mean	SE
ANOVA					April 2001	4.415	0.090
Model	3	0.038	92.19	<0.0001*	August 2001	Not included	
Error	8	0.000			December 2001	Not included	
					April 2002	Not included	
Effects Test					August 2002	2.641	0.088
Date	1	0.058	141.22	<0.0001*	December 2002	Not included	
Fish size	1	0.012	30.37	0.0006*			
Date*fish size	1	0.002	4.20	0.07			

Nematalosa erebi

Temporal variation in growth rate was not as apparent for *N. erebi* as it was for *L. unicolor*. While this species was abundant at five of the six study pools, variation in otolith weight was only observed at only two pools; Mallina and Bilanoo showed variation (Figure 6.8, 6.9), whereas Palm (Figure 6.10), Hooley (Figure 6.11, Table 6.9), and Portland Pools (Figure 6.12) showed none.

Temporal comparisons of growth rate in juvenile fish (in pools that displayed variation, Mallina and Bilanoo) were complicated by the tri-annual breeding of this species. Breeding several times during the year made it difficult to assess if variation in growth rate (otolith weight-at-size) was due to recent changes in pool condition, or if it reflected variation in conditions at the time of spawning. For example, a fish spawned during the warmer temperatures of early summer should grow faster than one spawned during winter (all other things being equal). Changes in growth rate associated with changes in pool condition could only be assessed with confidence for fish collected during the same months (to hold spawning date fairly constant), that is, inter-annual comparisons. Unfortunately, such comparisons were few due to limited sample sizes. Intra-annual comparisons still provided information on variation in growth rate, although whether the cause was recent or past was more difficult to determine.

Like *L. unicolor*, temporal changes in the growth rate of *N. erebi* differed among pools and among size classes within a pool. At Mallina Pool, the growth rate of small juvenile size classes (3.1 to 4.5 cm) increased as the pool shrunk (Figure 6.8.A, Table 6.10) (August 01 versus August 02, data interpolated from Figure 6.8.A). The growth rate of adults (16 to 24 cm) decreased as the pool shrunk (April and August 01 versus April and August 02) (Figure 6.8.C, Table 6.12). The growth rate of intermediate size classes (6.3 to 7.8 cm) did not change (August 01 versus August 02) (Figure 6.8.B, Table 6.11). The increased growth of intermediate sized fish collected in mid-drying conditions (April 02) compared to fish collected during early and late drying (August 01 and 02) (Figure 6.8.B, Table 6.11), supported the assertion that spawning time affected growth rate.

At Bilanoo Pool, large juvenile size classes (9.0 to 12.0 cm) appeared to slow in growth over time. This result could not be stated with certainty as too few fish were collected in April 02 to enable a statistical comparison with April 01 data (Figure 6.9.A). However, fish collected in February 02 had grown significantly slower than those collected in April 01 (Figure 6.9.A, Table 6.13). Interestingly, adult size classes within this pool showed no variation in growth over time (Figure 6.9.B). There were too few small juveniles collected to examine temporal changes in this size class.

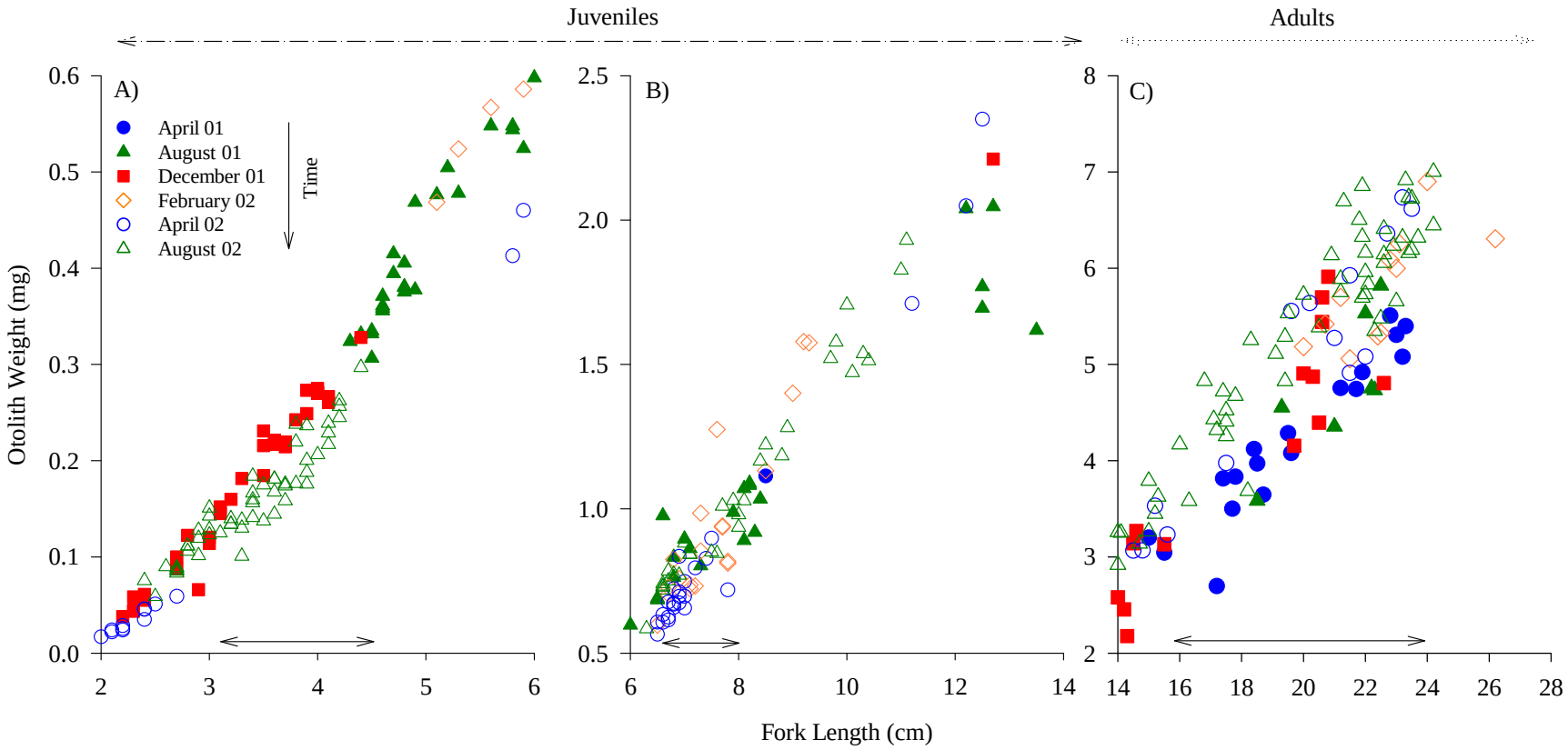


Figure 6.8. Temporal changes in otolith weight (mg) versus fork length (cm) for *N. erebi* at Mallina Pool. Fish size (fork length) has been separated into three graphs to improve visual depiction. Juveniles and adults are shown. Sampling times span from April 2001 to August 2002. Size classes where times have been compared using ANCOVA have been identified using double-sided arrows.

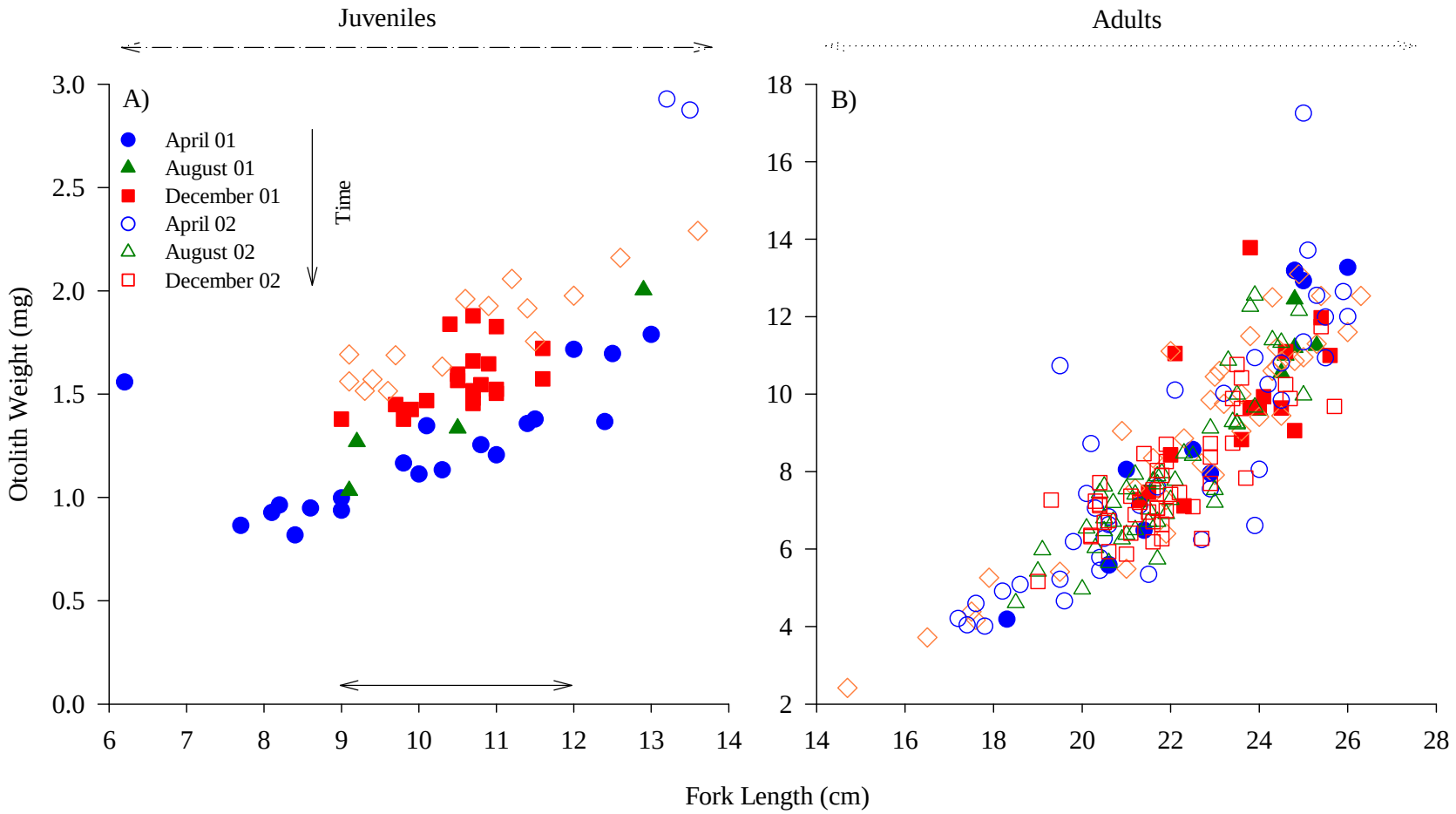


Figure 6.9. Temporal changes in otolith weight (mg) versus fork length (cm) for *N. erebi* at Bilanoo Pool. Fish size (fork length) has been separated into two graphs, adults and juveniles, to improve visual depiction. Sampling times span from April 2001 to December 2002. Size classes where times have been compared using ANCOVA have been identified using double-sided arrows.

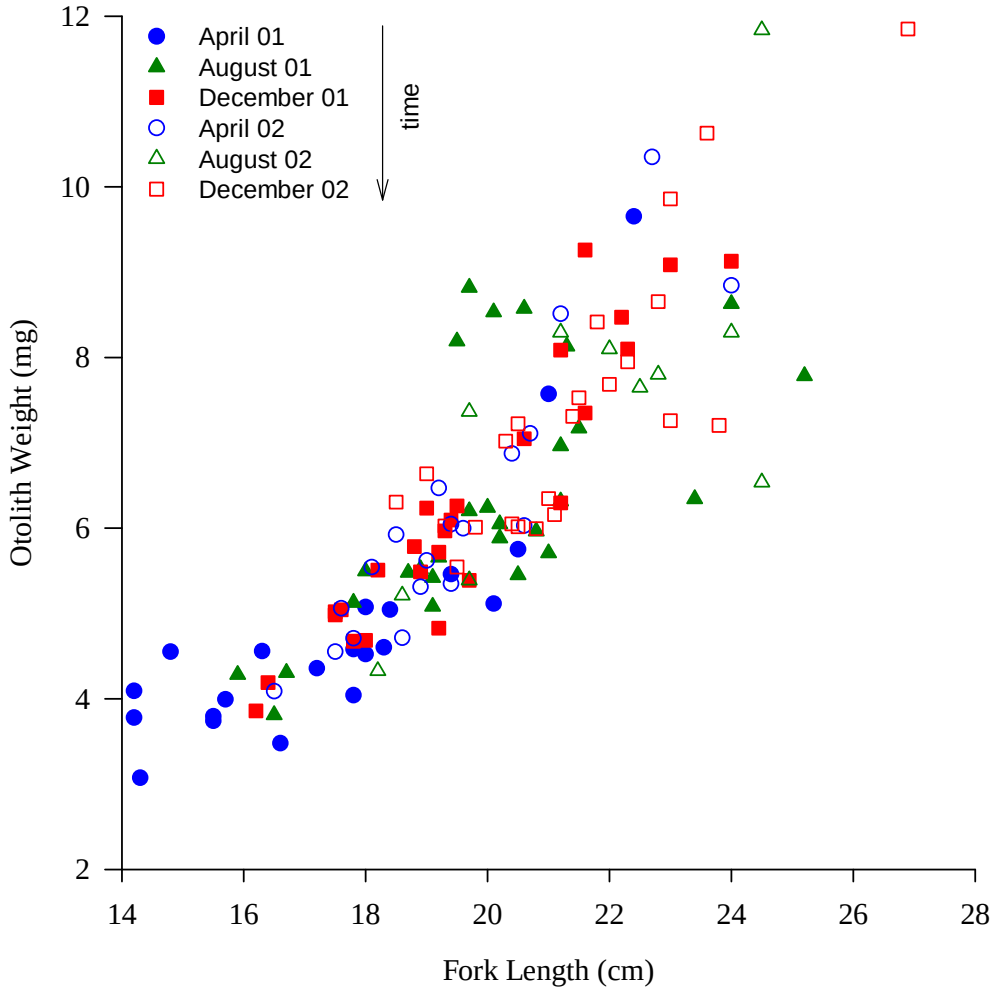


Figure 6.10. Temporal changes in otolith weight (mg) versus fork length (cm) for *N. erebi* at Palm Pool. Only adults are shown because few juveniles were collected. Sampling times span from April 2001 to December 2002.

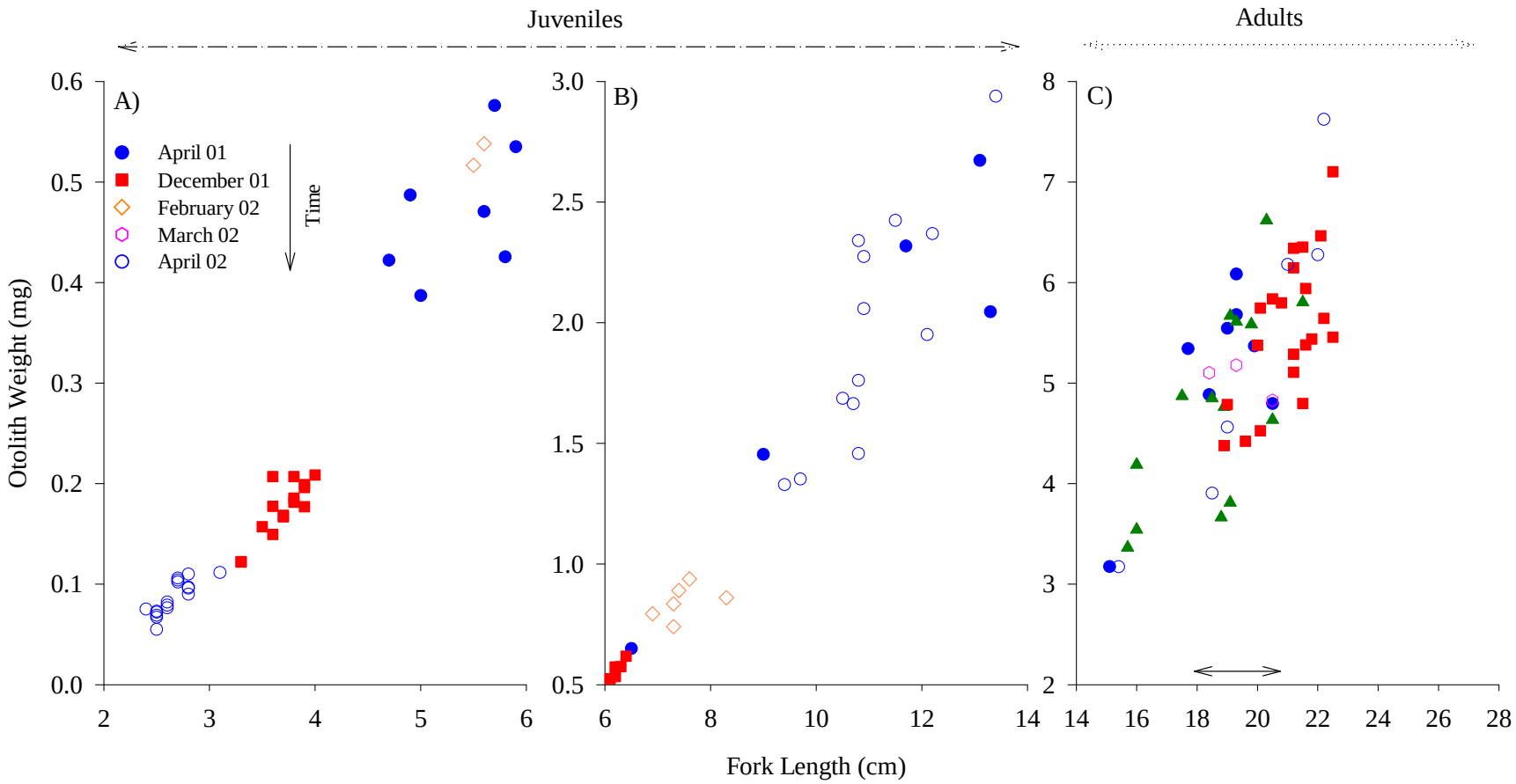


Figure 6.11. Temporal changes in otolith weight (mg) versus fork length (cm) for *N. erebi* at Hooley Pool. At each site, fish size (fork length) has been separated into three graphs to improve visual depiction. Juveniles and adults are shown. Sampling times span from April 2001 to April 2002. Size classes where times have been compared using ANCOVA have been identified using double-sided arrows.

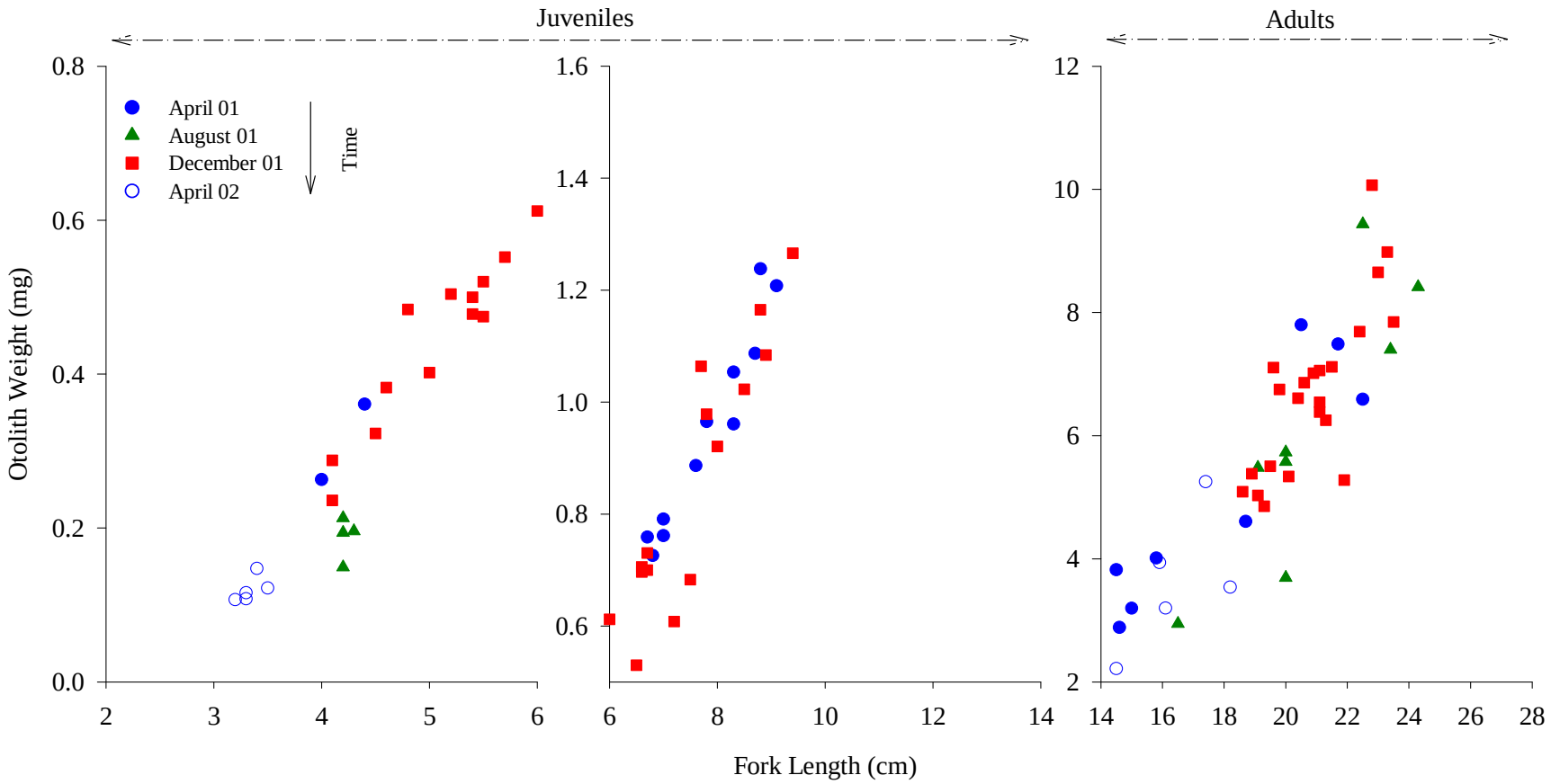


Figure 6.12. Temporal changes in otolith weight (mg) versus fork length (cm) for *N. erebi* at Portland Pool. Fish size (fork length) has been separated into three graphs to improve visual depiction. Juveniles and adults are shown. Sampling times span from April 2001 to April 2002. Size classes where times have been compared using ANCOVA have been identified using double-sided arrows.

Table 6.9. General linear model ANCOVA for *N. erebi* at Hooley Pool, comparing otolith weight (mg) among times, with fish size (fork length) as a covariate. The size class compared was 18.0 to 21.0 cm.

Source	df	MS	F	p	Date	LS mean	SE
ANOVA					April 2001	5.374	0.287
Model	5	0.768	1.63	0.20	August 2001	5.142	0.238
Error	17	0.470			December 2001	4.870	0.272
					April 2002	Not included	
Effects Test					August 2002	Not included	
Date	2	0.383	0.81	0.46	December 2002	Not included	
Fish size	1	1.660	3.53	0.08			
Date*fish size	2	0.630	1.34	0.29			

Table 6.10. General linear model ANCOVA for *N. erebi* at Mallina Pool, comparing otolith weight (mg) between times, with fish size (fork length) as a covariate. The size class compared was 3.1 to 4.5 cm. * indicates significance at the alpha 0.05 level.

Source	df	MS	F	p	Date	LS mean	SE
ANOVA					April 2001	Not included	
Model	3	0.048	167.94	<0.0001*	August 2001	Not included	
Error	57	0.000			December 2001	0.227	0.003
					April 2002	Not included	
Effects Test					August 2002	0.185	0.003
Date	1	0.027	93.52	<0.0001*	December 2002	Not included	
Fish size	1	0.111	389.58	<0.0001*			
Date*fish size	1	0.000	0.30	0.58			

Table 6.11. General linear model ANCOVA for *N. erebi* at Mallina Pool, comparing otolith weight (mg) among times, with fish size (fork length) as a covariate. The size class compared was 6.3 to 7.8 cm. * indicates significance at the alpha 0.05 level. Letters indicate the order of significant differences among sites.

Source	df	MS	F	p	Date	LS mean	SE
ANOVA					April 2001	Not included	
Model	5	0.101	26.14	<0.0001*	August 2001	0.839[b]	0.021
Error	43	0.004			December 2001	Not included	
					April 2002	0.710[a]	0.014
Effects Test					August 2002	0.801[b]	0.015
Date	2	0.067	17.31	<0.0001*	December 2002	Not included	
Fish size	1	0.217	56.12	<0.0001*			
Date*fish size	2	0.001	0.35	0.70			

Table 6.12. General linear model ANCOVA for *N. erebi* at Mallina Pool, comparing otolith weight (mg) among times, with fish size (fork length) as a covariate. The size class compared was 16 to 24 cm. * indicates significance at the alpha 0.05 level. Letters indicate the order of significant differences among sites.

Source	df	MS	F	p	Date	LS mean	SE
ANOVA					April 2001	4.529[a]	0.106
Model	7	8.671	82.59	<0.0001*	August 2001	4.595[a]	0.163
Error	69	0.170			December 2001	Not included	
					April 2002	5.372[b]	0.139
Effects Test					August 2002	5.572[b]	0.062
Date	3	5.094	29.89	<0.0001*	December 2002	Not included	
Fish size	1	16.898	99.16	<0.0001*			
Date*fish size	3	0.035	0.20	0.89			

Table 6.13. General linear model ANCOVA for *N. erebi* at Bilanoo Pool, comparing otolith weight (mg) among times, with fish size (fork length) as a covariate. The size class compared was 9.0 to 12.0 cm. * indicates significance at the alpha 0.05 level. Letters indicate the order of significant differences among sites.

Source	df	MS	F	p	Date	LS mean	SE
ANOVA					April 2001	1.279[a]	0.033
Model	5	0.661	44.91	<0.0001*	August 2001	Not included	
Error	43	0.015			December 2001	1.589[b]	0.028
					February 2002	1.817[c]	0.031
Effects Test					April 2002	Not included	
Date	2	1.035	17.31	<0.0001*	August 2002	Not included	
Fish size	1	1.001	56.12	<0.0001*	December 2002	Not included	
Date*fish size	2	0.011	0.35	0.48			

Changes in Growth Rate among Pools

Comparisons among pools were complicated because growth rates varied through time, at least for some size classes in certain pools (see: Changes in growth rate through time). This meant that when possible, comparisons among pools were carried out at one particular time. The time chosen for these comparisons was that which permitted the greatest number of pools to be included. In certain cases sample sizes were too small to allow a comparison and similar, rather than identical, sampling dates were used, or several sampling times were pooled. Times were pooled only when there was no significant difference in growth rate between the times. There was one occasion when two times with divergent growth rates were included in an analysis. This was for adult *N. erebi*, where growth rate at Mallina Pool varied through time, yet both times allowed the same number of sites to be compared. Including both times allowed an assessment of the magnitude of temporal relative to among-pool variations in growth rate.

Leiopotherapon unicolor

Small juveniles (3.4 to 4.4 cm) collected in April 2001 displayed little difference in growth rate (otolith weight) among pools (Figure 6.13.A). Large juvenile and small adult *L. unicolor* (4.8 to 7.3 cm) collected in April 2001 showed the greatest amount of variation in growth rate (Figure 6.13.A). For the three pools compared, growth rate mirrored pool stability. The fastest growing fish (i.e. lightest otoliths at a given size) were collected at Railbrige Pool, the most unstable pool, the slowest growing fish were collected at Mallina Pool, the most stable of the pools examined for this size class, and fish with intermediate growth were collected from Hooley Pool, which was of intermediary stability (Table 6.14). At this time, the stability of these pools was inversely related to fish density and fish biomass/m^2 (Figure 6.1.A, B); fish with the highest growth rate occurred within pools with the lowest fish density and biomass per-unit-area. Water temperatures (morning and afternoon) during April 2001 were also greatest within the pool where *L. unicolor* had grown fastest (Railbridge Pool). However, the water at Hooley Pool was only marginally warmer than that at Mallina

Pool inferring that water temperature was not a primary factor determining growth rate (Figure 6.2.A, B).

Medium sized adult *L. unicolor* (11 to 15 cm) collected in August and December of 2002 displayed some variation in growth rate but it was not related to pool stability. Fish from the most unstable of the three pools analysed, Mallina Pool, had grown slower than fish from Bilanoo Pool, but fish from Palm Pool, the most stable pool, grew at a similar rate to fish from both of these pools (Figure 6.13.B, Table 6.15).

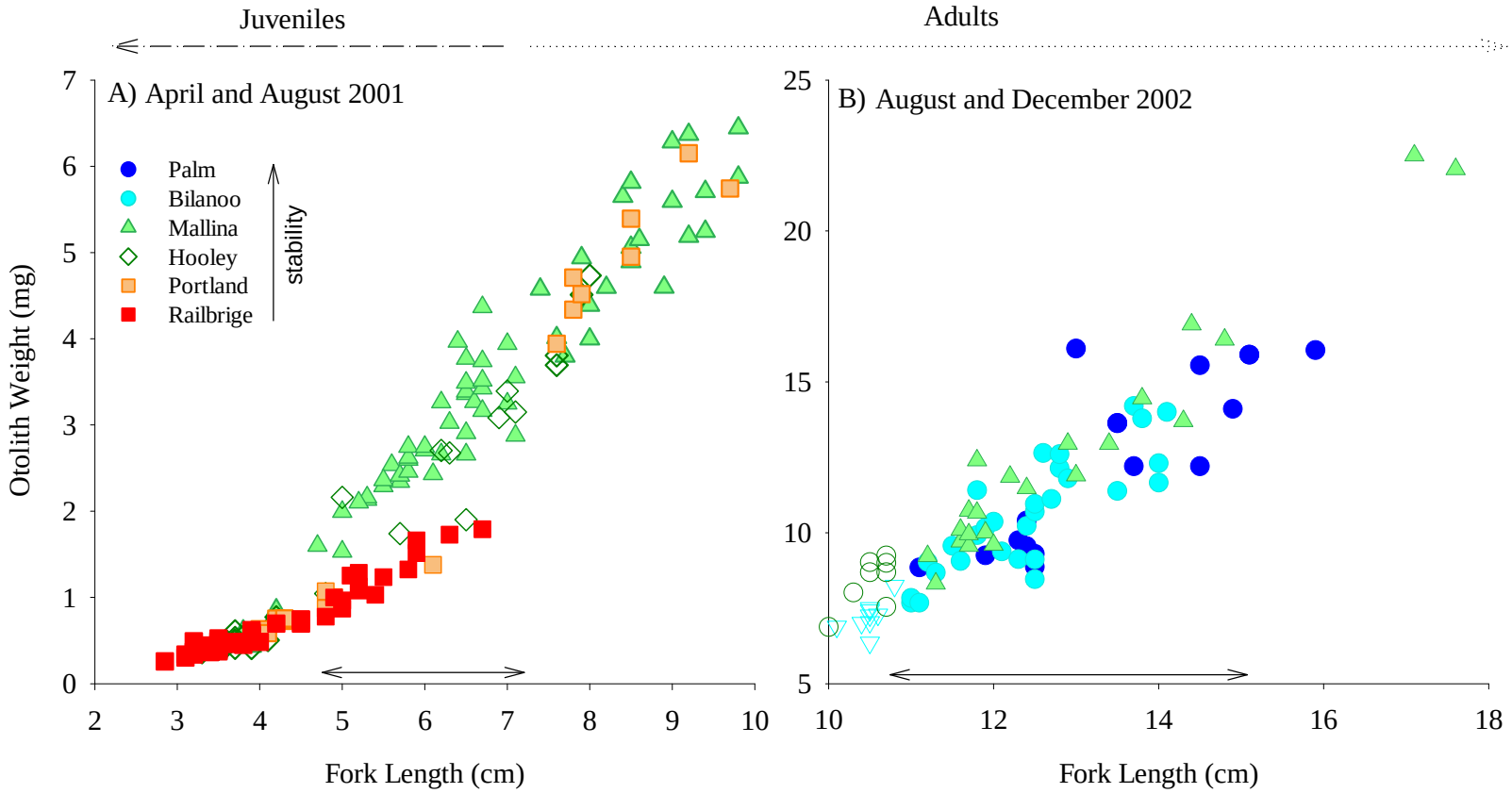


Figure 6.13. Among-pool comparisons of otolith weight (mg) versus fork length (cm) for *L. unicolor*. Graph A shows juveniles and small adults, graph B shows large adults. As temporal variation in otolith weight occurred in juveniles, comparisons among pools were restricted to similar time periods. The dates used are shown on the graphs. Size classes compared using ANCOVA are identified using double-sided arrows.

Table 6.14. General linear model ANCOVA for *L. unicolor*, comparing otolith weight (mg) among sites, with fish size (fork length) as a covariate. The size class compared was 4.8 to 7.3 cm, and the fish were collected in April and August of 2001 Data were $\log_e$ transformed prior to the analysis. * indicates significance at the alpha 0.05 level. Letters indicate the order of significant differences among sites.

Source	df	MS	F	p	Site	LS mean	SE
ANOVA					Palm	Not included	
Model	5	1.168	87.21	<0.0001*	Bilanoo	Not included	
Error	46	0.013			Mallina	2.761^{c}	0.054
					Hooley	2.348^{b}	0.125
Effects Test					Portland	Not included	
Site	2	0.985	73.58	<0.0001*	Railbridge	1.535^{a}	0.122
Fish size	1	0.987	73.59	<0.0001*			
Site*fish size	2	0.021	1.59	0.21			

Table 6.15. General linear model ANCOVA for *L. unicolor*, comparing otolith weight (mg) among sites, with fish size (fork length) as a covariate. The size class compared was 11.0 to 15.0 cm. Fish from Mallina and Palm Pools were collected in December 2002, fish from Bilanoo were collected in August 2002. * indicates significance at the alpha 0.05 level. Letters indicate the order of significant differences among sites.

Source	df	MS	F	p	Site	LS mean	SE
ANOVA					Palm	$10.903^{a,b}$	0.341
Model	5	49.735	35.80	<0.0001*	Bilanoo	10.923^{a}	0.224
Error	58	1.389			Mallina	11.914^{b}	0.265
					Hooley	Not included	
Effects Test					Portland	Not included	
Site	2	6.543	4.710	0.013	Railbridge	Not included	
Fish size	1	222.732	160.326	<0.0001*			
Site*fish size	2	0.537	0.387	0.68			

Nematalosa erebi

Juvenile *N. erebi* displayed variation in growth rate among pools, but differences were relatively minor in comparison to adult *N. erebi*. Variation in growth rate between juveniles was not associated with pool stability. While small juveniles (3.1 to 4.0 cm) had grown faster at Hooley Pool (Dec01), which was more unstable, than those at Mallina Pool (Figure 6.14.A, Table 6.16), visual extrapolation of data (Figure 6.14.A) suggested that fish growth at Palm and Portland Pools was similar to that at Mallina Pool, even though these pools had quite different stability. Additionally, during April 2001, large juvenile fish (8.1 to 9.1 cm) had grown faster at Bilanoo Pool, a relatively stable pool, than at Portland Pool, a relatively unstable one (Figure 6.14.B, Table 6.17). The small number of pools available for these analyses made it unwise to draw conclusions about the relationships between growth rate and fish density and

biomass/m^2. Water temperatures in the littoral zones at the times of analysis were not positively associated with growth rates.

Adult *N. erebi* displayed obvious variation in growth rate among pools, and this increased with fish size (Figure 6.15.A, B). Differences in growth rate were not associated with pool stability and are most simply interpreted by examining the smaller adult fish (14 to 20 cm), as they minimise complications associated with older fish (refer to the following paragraph). Fish at the most stable pool, Palm, had grown slowest, fish from relatively unstable pools, Hooley and Portland, had grown at an intermediate rate, and fish from Mallina Pool, a pool of intermediate stability, had grown fastest (Figure 6.15.A, Table 6.18). Fish from Bilanoo Pool, the second most stable pool, had grown at the same rate to fish within the two unstable pools (Table 6.18).

The larger adult fish (20 to 22 cm) showed a similar pattern, except that now the fish from Bilanoo Pool had grown at a similar rate to those from Palm Pool (Figure 6.15.B, Table 6.19). The alignment of the two most stable pools may be an artefact of the slowing growth rate of adult fish and the increased longevity of fish within these pools. For example, old fish that had stopped (greatly slowed) growing, hence had heavy otoliths for their size, were much more likely to be present in the most stable pools than in the unstable pools (see Chapter 5). While the effects of aging probably contributed to the increased separation of pools in the large adult size classes, this result could have arisen if the factor responsible for the variation in growth rate among pools occurred in the past, for example, the large flood.

It was difficult to determine if the variation in growth rate among pools were associated with fish density and fish biomass/m^2 because otolith weight provides a description of average growth conditions (i.e. over a life time) and because differences in fish density/biomass were not consistent through time (Figure 6.1.A, B). If growth differences were due to past conditions, differences in fish density and fish biomass/m^2 that were most obvious in the early stages of the study, did not

explain them. For example, density and biomass were lowest at Bilanoo Pool and highest at Palm Pool during April and August 2001, yet adult *N. erebi* in these pools had the lowest growth rates.

Table 6.16. General linear model ANCOVA for *N. erebi*, comparing otolith weight (mg) between sites, with fish size (fork length) as a covariate. The size class compared was 3.1 to 4.0 cm. Fish compared were collected during December 2001. * indicates significance at the alpha 0.05 level.

Source	df	MS	F	p	Site	LS mean	SE
ANOVA					Palm	Not included	
Model	3	0.019	102.99	<0.0001*	Bilanoo	Not included	
Error	31	0.000			Mallina	0.222	0.003
					Hooley	0.168	0.003
Effects Test					Portland	Not included	
Site	1	0.023	130.31	<0.0001*	Railbridge	Not included	
Fish size	1	0.028	157.02	<0.0001*			
Site*fish size	1	0.000	1.82	0.14			

Table 6.17. General linear model ANCOVA for *N. erebi*, comparing otolith weight (mg) between sites, with fish size (fork length) as a covariate. The size class compared was 8.1 to 9.1 cm. Fish compared were collected during April 2001. * indicates significance at the alpha 0.05 level.

Source	df	MS	F	p	Site	LS mean	SE
ANOVA					Palm	Not included	
Model	3	0.042	9.74	<0.007*	Bilanoo	0.934	0.027
Error	7	0.004			Mallina	Not included	
					Hooley	Not included	
Effects Test					Portland	1.095	0.030
Site	1	0.069	16.10	<0.005*	Railbridge	Not included	
Fish size	1	0.033	7.73	<0.027*			
Site*fish size	1	0.015	3.53	0.10			

Table 6.18. General linear model ANCOVA for *N. erebi*, comparing otolith weight (mg) among sites, with fish size (fork length) as a covariate. The size class compared was 14.0 to 20.0 cm. Data were pooled for all times of collection for all sites except for Mallina Pool. This pool displayed temporal variation and data is provided for 2001 and 2002.* indicates significance at the alpha 0.05 level. Letters indicate the order of significant differences among sites.

Source	df	MS	F	p	Site	LS mean	SE
ANOVA					Palm	5.079^{c}	0.072
Model	11	14.869	41.30	<0.0001*	Bilanoo	4.523^{b}	0.137
Error	181	0.360			Mallina $_{2001}$	3.724^{a}	0.140
					Mallina $_{2002}$	4.549^{b}	0.119
Effects Test					Hooley	4.481^{b}	0.123
Site	5	5.925	16.46	<0.0001*	Portland	4.566^{b}	0.128
Fish size	1	87.193	242.17	<0.0001*	Railbridge	Not included	
Site*fish size	5	0.762	2.12	0.06			

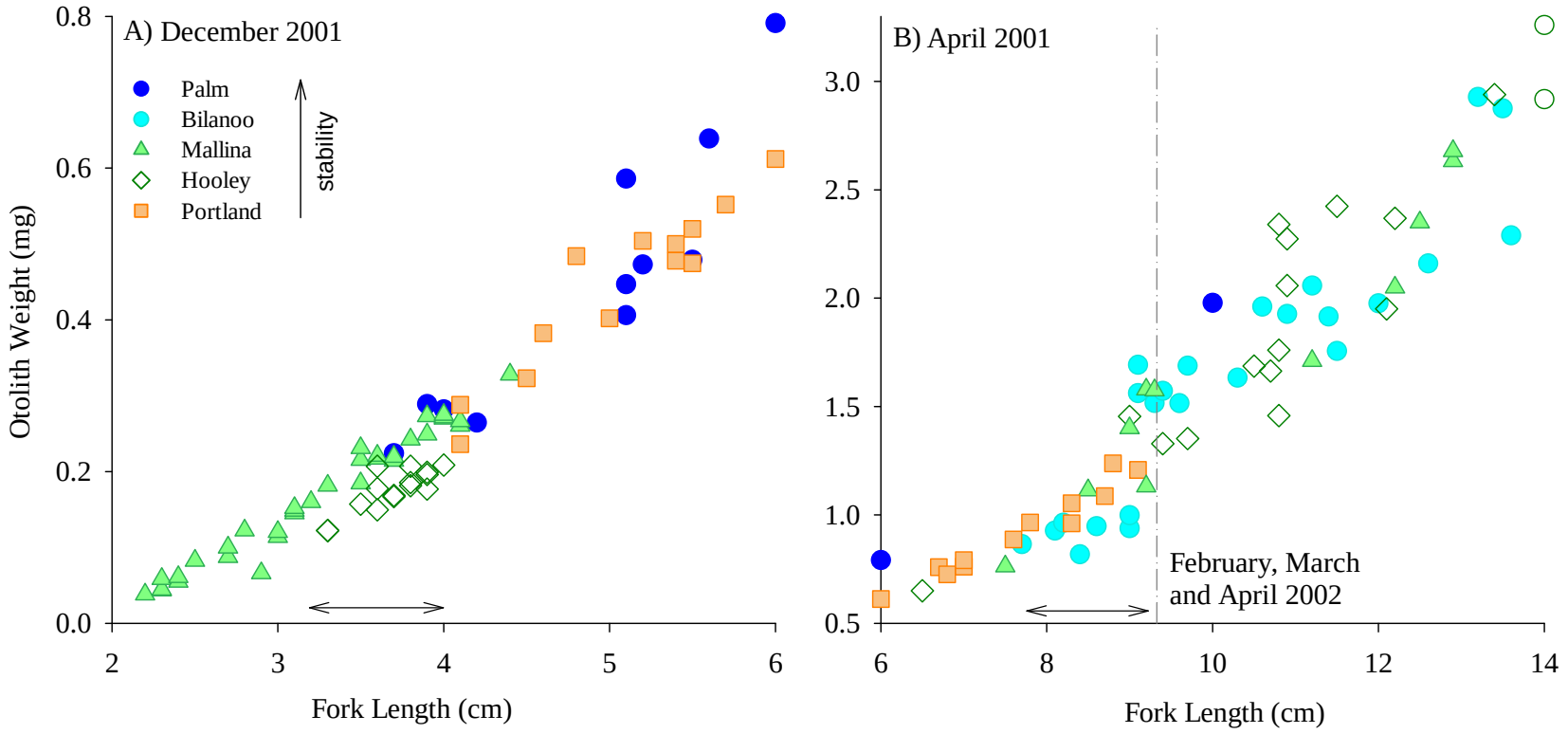


Figure 6.14. Among-pool comparisons of otolith weight (mg) versus fork length (cm) for juvenile *N. erebi*. Graph A shows small size classes, graph B shows large size classes. As temporal variation in otolith weight occurred in juveniles, comparisons among pools were restricted to either one time period, or similar times. The date used is shown on the graphs. Size classes compared using ANCOVA are identified using double -sided arrows.

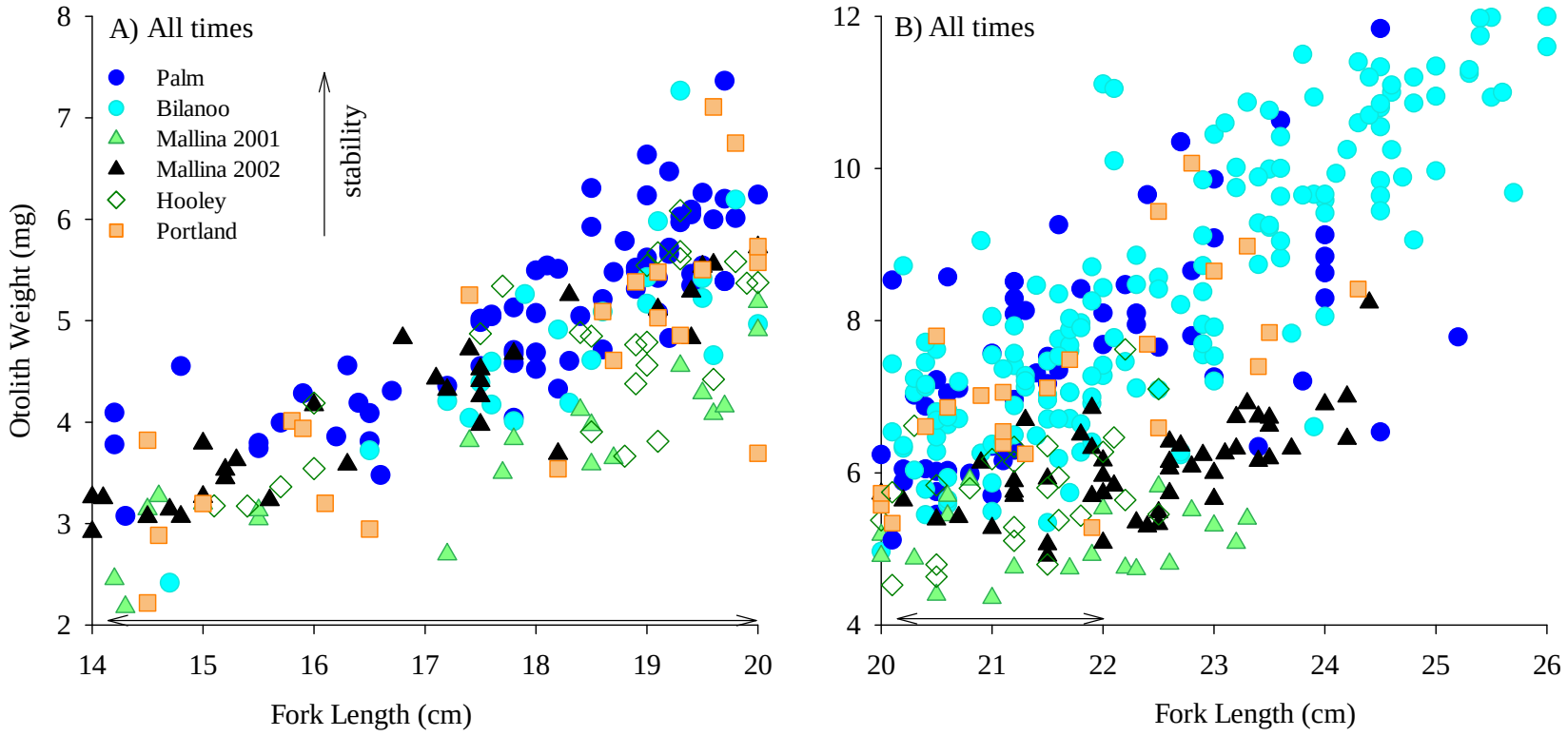


Figure 6.15. Spatial comparisons of otolith weight (mg) versus fork length (cm) for adult *N. erebi*. Graph A shows small; size classes, and graph B shows large size classes. As no temporal variation in otolith weight was found (except Mallina Pool), were pooled across all sampling times. For Mallina Pool, the two most divergent sampling times were included. Size classes compared using ANCOVA are identified using double-sided arrows.

Table 6.19. General linear model ANCOVA for *N. erebi*, comparing otolith weight (mg) between sites, with fish size (fork length) as a covariate. The size class compared was 20.0 to 22.0 cm. Data were pooled for all times of collection for all sites except for Mallina Pool. This pool displayed temporal variation and data is provided for 2001 and 2002. * indicates significance at the alpha 0.05 level. Letters indicate the order of significant differences among sites.

Source	df	MS	F	p	Site	LS mean	SE
ANOVA					Palm	7.107[c]	0.134
Model	11	9.193	14.68	<0.0001*	Bilanoo	6.951[c]	0.090
Error	173	0.626			Mallina $_{2001}$	5.050[a]	0.240
					Mallina $_{2002}$	5.711[b]	0.180
Effects Test					Hooley	5.600[a]	0.174
Site	5	16.037	25.61	<0.0001*	Portland	6.476[b,c]	0.218
Fish size	1	9.874	15.77	0.0001*	Railbridge	Not included	
Site*fish size	5	0.966	1.54	0.18			

Discussion

All of the findings discussed below were based on the premise that otolith weight (at-a-certain-size) is a correlate of growth rate. This was validated for *L. unicolor* (see Appendix VII), but not validated for *N. erebi*. Consequently, all discussion regarding *N. erebi* is based on the assumption that it displays the same association between growth rate and otolith weight (at-size) as *L. unicolor*.

Fish density was not related to pool stability. This result was unexpected, as theorists predict that organism density increases with environmental stability (Pianka 1970). However, Schlosser (1987a) proposed that a non-linear relationship exists between pool stability and fish density. His study of the warm-water streams of Illinois (U.S.A) revealed that fish density was greatest in pools with intermediate stability, being low in very stable pools and highly unstable pools. A reduction in density in the most stable environments is not compatible with general models (Pianka 1970), but may be driven by the increased predation of small fish by the large fish that congregate within deep, stable pools (Schlosser 1987a). The results of this study provided no support for either theory, as there was no clear relationship between fish density and pool stability.

Fish biomass per-unit-area was also not related to pool stability. This was surprising because populations of *L. unicolor* and *N. erebi* both showed an increasing proportion

of large (adult) fish with increasing pool stability (see Chapter 5). Temporal changes in fish biomass were considerable in unstable pools as expected but were also large within Bilanoo Pool, the second most stable pool. Increasing fish density in this pool was not only linked to the concentrating effects of pool shrinkage, but to the increased accessibility of deep-water sections that were too deep to be previously sampled. Great numbers of *N. erebi*, a schooling herbivore, were collected as this pool shrank. While this result highlighted a difficulty associated with sampling fish communities that inhabit deep water, this problem was not encountered at any other site.

The absence of a relationship between pool stability and fish density/fish biomass per-unit-area meant that it was not surprising that no obvious relationship was found between pool stability and growth rate. However, it was surprising that there was little evidence supporting a link between fish density/biomass per-unit-area and growth rate, as many other studies have reported an association (Goto 1998, Schlosser 1998, Post *et al.* 1999, Holmgren and Appelberg 2001, Oliva-Paterna *et al.* 2003). In this study growth rate was correlated with fish density and biomass on only one occasion. Large juvenile *L. unicolor* collected at the commencement of the study (April 2001) had grown faster (growth averaged across the fish's life) in pools where fish density/biomass per-unit-area were, at that time, lower. While this result hinted that density and/or biomass might affect growth rate, the lack of corroboration with other results, suggests that these factors are not of great importance. Indeed, the great number of analyses carried out meant that this result could have arisen by chance.

The majority of studies that report a relationship between fish density and/or fish biomass per-unit-area and growth rate have occurred in relatively stable environments, such as lakes or continuously flowing streams (Goto 1998, Schlosser 1998, Post *et al.* 1999, Holmgren and Appelberg 2001). The absence of a relationship in the Fortescue River may be related to its variable hydrology. Large temporal changes in system productivity are known to be associated with flooding (Stanley *et al.* 1997) and this may overshadow differences in fish density and fish biomass. For example, Bayley (1988) studied the growth rate of young tropical floodplain fishes in the floodplain rivers of the Amazon and found little relationship between biomass per-unit-area and growth rate. He found a significant relationship between growth rate and season and attributed this to variance in productivity. Large-scale shifts in

productivity probably have an important effect on fish growth in the Fortescue River but were not addressed in this study.

Water temperature affects fish growth by affecting metabolism (Weatherley and Gill 1987, Gehrke 1991), and comparative studies in nature have often attributed variance in fish growth to it (Fowler and Short 1996, Spranza and Stanley 2000). However, water temperature did not account for the differences in growth rate of *L. unicolor* and *N. erebi* in the pools of the Fortescue River. Like fish density/biomass, water temperature did not differ among pools in a consistent manner. Greater diurnal fluctuation in smaller pools (see Appendix VIII) may have eroded the association between sites and temperature differences.

While the primary factor(s) affecting growth rate was not apparent, the fact that the two study species showed different trends in growth rate among pools implied that the factor(s) differed between the species. This result differed from Spranza and Stanley 's (2000) study, where all three species of their study showed elevated condition factors within the unstable sections of an Oklahoman prairie stream, even though the species occupied different trophic positions. However, a similar result was observed in the prairie streams of Kansas (USA) by Quist and Guy (2001). The growth of three species (creek chubs, red shiners and green sunfish) was related to the amount of woody debris, but not so for the central stoneroller. Quist and Guy (2001) suggested that an unmeasured physical factor was most important for the growth of the central stoneroller. Unmeasured physical factors could have been responsible for the patterns observed in this study. Alternately, differences in species in biology, such as trophic position and/or physiological tolerances, may have been responsible.

Additional factors complicating the investigation into growth rate include migration between pools, and the use of otolith weight (at size) as a measure of growth rate. For example, individuals migrating between pools will erode the association between pool conditions and growth rate because otolith weight is an average of growth rate over the lifetime of the fish. A fast growth rate also reduces the capacity of otolith weight to reflect variance in growth rate (Jenkins *et al.* 1993). *N. erebi* grows at a faster rate than *L. unicolor*, attaining approximately 14 cm in its first year, whereas *L. unicolor* attains approximately 6-8 cms in its first year (Bishop *et al.* 2001). This may explain

why site related differences in *N. erebi*'s growth rate became more obvious in the larger fish.

Further evidence that growth rate in the Fortescue River is very complex was the fact that patterns of growth rate varied between juvenile and adult fish. For example, within-pool comparisons over time revealed (for two of the three pools that shrank) that the growth rate of juvenile *L. unicolor* increased as pools shrunk, but it slowed in adults. Ontogenetic shifts in diet and size-selective pressures may have caused this result.

Small fish, particularly larvae, are limited by their small gape size to certain foods (Wilbur 1980). When they grow, their increased gape size allows them to diversify their diet (Grossman *et al.* 1982, Rahel *et al.* 1984, Yant *et al.* 1984, Grossman *et al.* 1985), and this may alter their growth rate and survival (Hjelm *et al.* 2000, Holmgren and Appelberg 2001). While ontogenetic shifts in diet no doubt take place in the fish of the Fortescue River, increasing growth of juveniles as a pool shrinks seems unlikely, and is suggestive of size-selective survivorship. For example, if mortality in juveniles is related to size, the death of slow-growing individuals from the population over time will cause a seeming increase in growth rate, although in actuality it does not (Sinclair *et al.* 2002). This supposition is supported by studies that report that small fish are more vulnerable to starvation and predation than larger fish (Jobling 1995, Hutchings 1997, Post *et al.* 1999). Variation in the types (and strength) of competitive interactions (including predation) with size has been reported elsewhere. Post *et al.* (1999) conducted whole lake experiments on the rainbow trout, *Onchorynchus mykiss*, and found that while the growth of large trout was driven by competition for food (exploitative competition), that the growth of the smallest size classes was controlled not only by competition for food, but by interference competition (including predation) by larger size classes.

It was of particular interest that fish density differed considerably among pools at the start of the study but converged toward the density of fish in the most stable pool (Palm) as the study progressed. This result is thought worthy of speculation. It is suggested that the large flood, which preceded the study, introduced variability into the system by spatially altering recruitment success. The prolonged drought, during

which most of this study took place, reduced this variability by increasing the strength of deterministic processes (mainly biological interactions) on the fish communities. For example, as conditions deteriorated recruitment may have declined and become more similar to that in the most stable pool. Additionally, fish communities inhabiting shrinking pools should have become resource limited and started to approach equilibrium conditions. The strength of stochastic and deterministic processes in stream fish communities has been vigorously debated (see Grossman *et al.* 1982, Rahel *et al.* 1984, Yant *et al.* 1984, Grossman *et al.* 1985, Ross *et al.* 1985, Matthews *et al.* 1988, Grossman *et al.* 1990); this result provides support for biologically driven determinism.

Summary

In the Fortescue River the growth rate of *L. unicolor* and *N. erebi* was not related to pool stability. Pool stability was not related to fish density, fish biomass per-unit-area, or water temperature. Fish growth rate was not related to fish density, fish biomass per-unit-area, or water temperature. The factors affecting fish growth rate were species specific and often varied with fish size. Fish growth rate in the Fortescue River is very complex.

Chapter 7

Life History Characteristics and Environmental Stability

Introduction

The stability of the environment is thought to play an important role in shaping the life history characteristics of organisms (MacArthur and Wilson 1967, Pianka 1970, Southwood *et al.* 1974, Stearns 1976). One of the major ways it does so is by affecting the ways in which individuals die (Dobzhansky 1950, Pianka 1970). Mortality in stable (constant or predictable) environments is generally related to organism density (and competitive interactions), because population size is close to the environment's carrying capacity (Pianka 1970). As competitive strength is commonly a function of size, and the size of offspring is positively related to adult size and inversely related to fecundity, organisms in stable environments mature late (at a larger size) and produce a small number of large 'fit' offspring (termed K-selection, Pianka 1970). Organisms in stable environments often guard their offspring (Pianka 1970, Hutchings 1997). In contrast, mortality in unstable (unpredictable) environments is typically catastrophic, being a function of environmental conditions and not an individual's size (Pianka 1970). As long-term survival is uncertain, organisms mature rapidly and invest a large proportion of their energy into reproduction (Jobling 1995). The small size of adults, and the irrelevance of size to offspring survival, means that adults in unstable environments maximise their reproductive success by producing a large number of small offspring (termed r-selection, Pianka 1970).

Early models linking environmental stability and life history characteristics operated along a two-endpoint continuum (the r-K continuum). However, subsequent studies have indicated that three endpoints (a triangular continuum) may be more appropriate (Kawasaki 1979, Baltz 1984, Winemiller 1992, Winemiller and Rose 1992). Three endpoints allow a greater separation of environmental types than was possible under the r-K continuum. For example, the r-K continuum makes no delineation between a constant environment and a predictable environment, yet a predictable environment can refer to one that undergoes cyclical changes through time (i.e. periodic) or one that is relatively unaltered through time (i.e. stable).

Winemiller (1992) put forward a triangular model which distinguishes between environments that are relatively stable (constant), seasonal (cyclic), and temporally

stochastic (referred to from now on as unstable). The model is based on trade-offs along three demographic axes (age at maturity, fecundity, and juvenile survivorship) (see Figure 7.1). Organisms with late maturation, high juvenile survivorship, and low fecundity represent the 'equilibrium' life history endpoint and should prevail within stable environments. Organisms with relatively late maturation (coinciding with their reproductive season), low juvenile survivorship, and high fecundity represent the 'periodic' life history endpoint and should prevail within seasonal environments. Organisms with early maturation, low juvenile survivorship, and relatively low fecundity (limited by body size) represent the 'opportunistic' life history endpoint and should prevail within unstable (temporally stochastic) environments. 'Opportunistic' species are also expected to be quite responsive (plastic) in their reproductive output in order to make the most of optimal conditions (Lewontin 1965, Baird *et al.* 1987, Stearns 1989, Hutchings 1997).

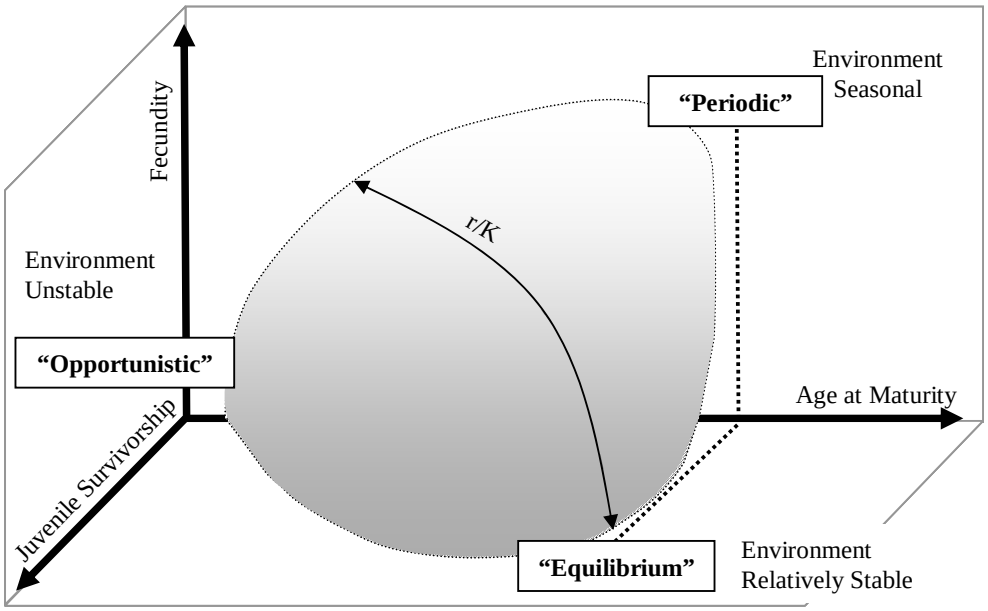


Figure 7.1. Winemiller's triangular model of life history strategies, adapted from Winemiller (1992). The three life history endpoints (equilibrium, periodic, and opportunistic) are shown in relation to three demographic traits (age at maturity, fecundity and juvenile survivorship). Life history endpoints are correlated with environmental types (stable, seasonal, or unstable). The shaded region represents all possible life history combinations between these endpoints and represents a continuum. The position of the r-K continuum along the adaptive surface is shown.

While studies conducted *within* a species (intra-specific) have generated support for the association between life history traits and environmental stability (Reznick and

Endler 1982, Brown 1985, Fernandez-Delgado and Herrera 1995, Baker and Foster 2002), studies involving *many* species (inter-specific) have not been as convincing. Many researchers (Kramer 1978, Beumer 1979, Puckridge and Drewien 1988, Spranza and Stanley 2000), including Winemiller (1989), have noted that species with different endpoint strategies occur within the same environmental type. For example, only 69% of the fish species inhabiting the seasonal environments of Venezuela displayed 'periodic' strategies (Winemiller 1989). Although scientists argue that extraneous factors, such as: phylogenetic grouping (Stearns 1976, Gottelli and Pyron 1991, Winemiller and Rose 1992), size (Winemiller 1989), exposure to predation (Stearns 1976, Reznick and Endler 1982, Reznick *et al.* 1990, Gottelli and Pyron 1991, Winemiller and Rose 1992, Rodd and Reznick 1997), and diet (Winemiller 1989, Winemiller and Rose 1992) are responsible for the departure of a species' life history traits from expectation, these factors have the potential to undermine the broad relevance of the model.

This chapter examines the applicability of Winemiller's (1992) triangular model to the fish of the Fortescue River, that is, the extent to which the stability of the environment in which these species live is correlated with their life history traits. The Fortescue River provides a good opportunity to assess the model for three reasons: (1) the river is far removed from Venezuela, where the initial insights for model were gained, and as such, contains phylogenetically distinct species; (2) the environment within which the river is situated, while seasonal, has a large degree of instability (stochasticity) compared to the environs of Venezuela; and (3) the Fortescue contains regions that vary considerably in their stability (and their fish community, see Chapter 4), providing an opportunity to examine the applicability of the model at a finer scale (i.e. within the river).

If Winemiller 's (1992) triangular model has widespread generality, then ~70% of the species within the Fortescue River should display life history traits which fall midway between the 'periodic' and 'opportunistic' endpoints of the model. However, as variation in environmental stability existed within the Fortescue River, it was predicted that species would group together according to their fine scale environmental preference, that is, they would orient themselves along an axis approximating the r-K continuum. Species restricted to stable environs (persistent

pools) would have strategies which tended towards the equilibrium ('K') end of the continuum (i.e. *Anguilla bicolor, Arius graeffei, Hypseleotris compressa*); whereas species which inhabited the more unstable sections of the catchment (the ephemeral pools) would group towards the 'r' end of the continuum (i.e. *Amniataba percoides, Glossogobius giurus, Leiopotherapon aheneus, Nematalosa erebi, Neosilurus hyrtlii*), with the species which occurred within the most temporary or unstable pools (*Leiopotherapon unicolor, Melanotaenia australis*) being at the extremity.

It was also predicted that species that inhabited the seasonal environment with inherent instability (the ephemeral pools) would show plasticity in their reproductive traits. That is, exhibit variation in the timing of their maturation and/or spawning and the nature of their reproductive investment (size and number of eggs). Plasticity was investigated by comparing reproductive traits between pools that differed in their physical attributes.

While the primary goal of this chapter was to examine the applicability of Winemiller's (1992) model to the fish of the Fortescue River, this chapter also describes the reproductive biology of the resident species, as the fish from this region have received virtually no attention. Reproductive information is collated with data from previous chapters in the thesis to generate a table of life history traits. This table also presents information from studies conducted elsewhere in Australia, and provides an opportunity to assess the relationship between environmental stability and life history traits at a geographic level.

Methods

Reproductive Biology and Plasticity

Study Sites

Fish were collected from the six focal pools (Palm, Bilanoo, Mallina, Hooley, Portland, and Railbridge). These pools varied considerably in their stability and their physical conditions (Table 7.1); a detailed description is provided in Chapter 2.

Each pool was sampled on eight occasions: April, August, and December 2001 and February, March, April, August, and December 2002. Monthly sampling in this remote region was not possible, due to logistical and financial restraints. However, sampling was intensified during the summer-wet season, as reproductive activity was expected to be greatest at this time. Low rainfall during the 2001/2001 summer wet season caused Railbridge, Hooley and Portland Pools to dry during the 18-month study period, reducing the spatial diversity of samples.

Table 7.1. Physico-chemical parameters and stability (variability in maximum depth) of the six focal pools. Values describe pool conditions at the start of sampling (April 2001). The surface area of large pools is underestimated as lengths greater than 500 m were not measured. Details of the method used to determine variability in pool depth is provided in Chapter 2.

Pool	Surface Area (m^2)	Length (m)	Width (m)	Maximum Depth (m)	Turbidity (ntu)	Variability in depth	
Palm	>15000	>500	30	3.2	3	6	stable
Bilanoo	>40000	>500	80	4.0	1	17	↓
Mallina	5220	290	18	2.0	2	30	
Hooley	7200	300	24	1.5	3	47	
Portland	3000	150	20	1.5	7	61	
Railbridge	1200	80	15	3.3	7	96	unstable

Focal Species

Although all species were of interest, three (*A. percoides*, *L. unicolor*, and *N. erebi*) were studied in greater detail. Detail was most important for the assessment of reproductive plasticity, which was expected to occur within the aforementioned species, as they occurred within the ephemeral reaches of the river, where environmental instability was greatest. Another species, *M. australis*, also occurred within this unstable environment, but its extremely small size and associated logistical difficulties, meant that it was studied opportunistically. *L. aheneus* was also studied in some detail, primarily because it is endemic to the region and nothing is known of its life history. Information on all other species (*A. graeffei*, *A. bicolor*, *G. giurus*, *N. hyrtlii*, *H. compressa*) was collected where and when possible.

Collection of Samples

At each sampling date, fish were collected using the drop-net, panel gill nets, and a beach seine, as described in Chapter 3 and 4. The drop-net provided a good description of the fish community (see Chapter 3), and collected the majority of

individuals used in the study. The gill nets were known to favour larger fish and were used to collect the largest size classes, whose low abundance meant they could be missed by the drop-net (see Chapter 3).

At each sampling occasion, a sub-sample of fish, which included representatives from across the size range available, were sacrificed. Each fish's weight (0.1 g), fork length (cm) and sexual status were recorded. Female gonads were preserved. If the ovary was large and eggs were visible (i.e. ripe), then one lobe was stored in a solution of FAACC (4% formaldehyde, 5% acetic acid, 1.3% calcium chloride), and the other was stored in 10% formalin. If the ovary was not ripe, then it was stored in FAACC.

Laboratory Analysis of Preserved Samples

In the laboratory, all ovaries were blotted dry and weighed (0.001 g). The majority were then sectioned using histological procedures to enable a cytological evaluation of their development.

Histological Procedures

A 2-4 mm transverse section was cut from a randomly chosen lobe of the ovary and dehydrated in 70%, 90% and 100% ethanol, followed by 100% chloroform and then embedded in paraffin wax. A 6 µm transverse section was cut and stained with Gill's Hematoxylin, followed by an Eosin counterstain. To ensure that gonad development did not differ along the length or between lobes of the ovary, a section of the anterior, central and posterior portion of one lobe were compared with each other and with the central portion of the remaining lobe. This was carried out for three individuals of *L. unicolor*, *A. percoides*, *N. erebi*, and *L. aheneus*. The fish used spanned the size range of mature females and were collected at different times during the spawning season, and from various sites. As development did not differ along the length of an ovary, or between its lobes, all subsequent sections were taken from the central section of a randomly chosen lobe.

Each section was classified according to its most developed oocyte stage, following the description outlined for *Scomberomorus commerson* (Mackie and Lewis 2001) (Table 7.2). Oocyte stages were based on those summarised by West (1990) and included the chromatin nucleolus stage (CNS), perinucleolus stage (PNS), cortical alveoli stage (CAS), yolk globule stage (YGS), migratory nucleus stage (MNS). The

presence of post-ovulatory follicles (POFs), atretic oocytes, and yellow-brown bodies was also noted.

Table 7.2. Microscopic maturity staging system used to determine the reproductive status of females of Fortescue River study species. The staging system is based on that of Mackie and Lewis (2001). Oocyte stages are quoted in abbreviated form: chromatin nucleolus stage (CN), perinucleolus stage (PN), cortical alveoli stage (CA), yolk globule stage (YG), migratory nucleus stage (MN), and post-ovulatory follicles (POF).

Maturity Stage	Microscopic description
J (juvenile)	Tissue comprises undifferentiated gonia.
1 (immature)	Contains little ovarian tissue. In early stages only CN oocytes are present. In later stages CN and PN oocytes increase in number. Yellow brown bodies are uncommon.
1a (immature developing)	Has the same features as an immature ovary but contain CA oocytes.
2 (mature resting)	Dominated by early stage previtellogenic oocytes (CN, PN). If spawning has recently finished then CA and yellow brown bodies may be present.
3 (developing)	Described by the appearance of CA oocytes and ends with the appearance of early YG oocytes.
4 (developed)	Commences with the appearance of YG oocytes. This stage represents the onset of the reproductive season. As the season progresses the number and size of the YG increases, and then once spawning has commenced the number YG typically decreases.
5a (pre-spawn)	Defined by the appearance of MN oocytes and ends when they are released into the lumen.
5b (spawning)	Defined by the presence of hydrated oocytes in the lumen and new POFs in the gonad.
5c (post-spawn)	Defined by the presence of new or old POFs.
6 (spent)	Marks the end of the reproductive season, and is the precursor for the resting stage. The criterion was that >50% of the YGS oocytes are atretic. Toward the end of this stage ovaries are dominated by previtellogenic oocytes, however the remnants of YG oocytes are still present. Once the atretic YG oocytes are gone the ovary is classified as resting (F2). The ovary is disorganised and yellow brown bodies are common.

Spawning Season

Spawning season is typically assessed in two ways, by comparing the relative frequency of resting, developing, ripe, and spawning females (mature) within a population over time, or by comparing the change in the ratio of ovary to body weight over time (West 1990). While microscopic evaluation of development is the most accurate method, the use of ovary to body weight, or the gonadosomatic index (GSI, see Equation 1), is often preferred as it does not require histological sectioning, and thereby increases the sample size, hence power to investigate trends over time, or between sites (West 1990). To ensure that GSI trends were not skewed by immature

fish, fish close to the size at maturity were included only if histological sectioning revealed they were mature.

(1) GSI = [wet weight of gonad/(wet weight of fish-wet weight of gonad)]*100

In this study both methods were used. The GSI provided a clear visual trend of the reproductive season, whereas the histological staging allowed a precise indication of the presence of spawning. Detailed information about the spawning behaviour of fishes was also more useful for spatial comparisons investigating plasticity in reproduction than trends in GSI. This is because GSI can be legitimately compared only if all fish are at exactly the same stage of development (West 1990), and if the relationship of gonad weight to fish size increases at a linear rate (Hunter and Macewicz 1985, West 1990).

Age and Size at Maturity

Age at maturity could not be estimated because fish were difficult to age (see Appendix III). To obtain an accurate estimate of size at maturity, developmental status was determined using histology (Murua *et al.* 2003). To reduce confusion in distinguishing between stage 1 and 2 ovaries, only fish collected during the spawning season were used in the analysis. Females were considered to be mature if they were at stage 2 or above. Length at 50% maturity was determined using a logistic general linear model designed by John McKinlay from the Department of Fisheries Western Australia.

Oocyte Development and Maximum Size

Oocyte size frequency distributions provide an insight into the mode of spawning of a species. In ripe fish, if all of the oocytes within the ovary are of a similar size it suggests that all the oocytes will be released together (synchronous development). However, if oocytes are present in two or more size classes, it suggests that the species undergoes multiple spawning periods, and only the largest size class will be released during the spawning season (group synchronous). Alternately, if oocytes of all sizes are present it suggests that mature oocytes are being continuously recruited (asynchronous development).

Oocyte size frequency distributions were constructed using data from histological sections of ovaries classified as ripe or spawning (stages F4 and F5). If the ovary contained a great number of oocytes, then a representative sub-section of the ovary was examined. Within this section, oocytes sectioned through the nucleus were numbered, and 30 were randomly chosen for measurement. Oocyte surface area was measured using image analysis software, Image Pro Plus (Media Cybernetics), and converted to oocyte diameter, assuming that oocytes were spherical (Gillanders *et al.* 1999, Nichols and Acuna 2001). The ovaries of 10 to 15 fish were examined for each of the focal species. Fewer individuals were used for non-focal species, and sample size depended on availability.

Maximum oocyte size provided an estimate of egg size, and was determined by examining oocytes under a dissecting microscope. This was used in preference to histological sections, as this procedure is known to affect egg size (West 1990). Histological sections were used to identify fish that were in spawning (F5a/b) conditions. A sub-sample of the mid portion of the ovary (stored in 10% formalin) was placed into glycerol. When hydrated oocytes were present they were identified by their large size and translucent appearance. Photographs of the oocytes were taken and their surface area determined using image analysis software, Image Pro Plus (Media Cybernetics). Maximum size was estimated assuming that oocytes were spherical. Several of the largest oocytes were measured from each fish; and three to five fish were examined for each species, unless fewer were available.

Fecundity

Estimates of total (annual) and batch fecundity were desirable, as the former was helpful in geographic comparisons, and the latter was required for Winemiller's (1992) model. However, it is difficult to estimate total fecundity for species which have continuous oocyte recruitment, and oocyte reabsorption (atresia) (Hunter *et al.* 1992, Murua and Saborido-Rey 2003). These limitations do not affect Winemiller 's (1992) model because it uses batch fecundity. Unfortunately, batch fecundity was also not easy to determine, because very few fish were collected at the appropriate stage (i.e. hydrated oocytes present, prior to spawning (Murua *et al.* 2003). That said, Winemiller (1989) did not validate the reproductive status of his fish "fecundity was recorded as the average number of the largest oocyte size class based on three fully-gravid females". As Winemiller (1989) logged estimates of fecundity (so too did this

study), it was assumed that an approximation would suffice. Ripe fish at as late a stage as possible, but prior to spawning, were used. While Winemiller (1989) only counted the largest size class of oocytes, this study counted the large and medium size classes, due to their continuous distribution. Estimates from this method should not be quoted as precise values for batch or total fecundity, hence have been omitted from the life history table. Note, that when species were synchronous spawners, it was simple to distinguish oocytes that were to be spawned, and if species spawn their oocytes in one batch, then batch fecundity equals seasonal and total fecundity (Hunter *et al.* 1992).

Like Winemiller (1989), this study used the gravimetric method to determine fecundity. This involved weighing the ovary and taking three to five sub-samples (weighed to the nearest 0.001 g). Sub-samples were placed into glycerol and the medium to large oocytes were counted. The appropriate number of sub-samples to examine was deemed to be reached when the coefficient of variation for the number of oocytes per unit weight was <5% (Murua *et al.* 2003). Fecundity was estimated by the product of gonad weight and oocyte density (Murua *et al.* 2003).

Life History Comparison

The table described 14 life history traits: maximum length, size at maturity, age at maturity, longevity, spawning season, number of spawning bouts per year, fecundity, oocyte size, type of oocyte development, oocyte type, fertilisation type, level of parental care, time to hatching, and size of larvae at hatching.

The table was constructed using information gathered from the reproductive biology section of this chapter, previous chapters and appendices of this thesis, and published literature from other studies carried out in Australia. Information on freshwater eels was also taken from studies conducted in New Zealand. Supplementary data were gained largely from individual journal articles; however, Pusey *et al.* 's (2004) book “Freshwater Fishes of North-Eastern Australia” contained a summary of the life history characteristics of most species.

To examine whether the life histories traits of the fish of the Fortescue supported Winemiller’s (1992) model, species’ traits were plotted onto a template of the model.

The template was as similar as possible to the original model, including axes of age at maturity, and fecundity (log fecundity), but its third axis was investment per progeny rather than juvenile survivorship. This substitution occurred because information on juvenile survivorship was not available, and because these measures are highly correlated (Winemiller and Rose 1992). Investment per progeny was calculated following Winemiller and Rose (1992) as ln[(egg diameter+1)(parental care+1)], and parental care was scored following Winemiller (1989) as the summation of A, B, C and D, where "A = special placement of zygotes (1) or zygotes and larvae (2), B = brief period of nutritional contribution to larvae (2), or long period of contribution to larvae or embryos (4), C = brief period of parental protection by one sex (1), or both (2), or long period of parental protection by one sex (2), or both (4), and D = extremely long period of gestation (4)". Egg diameter (mm) was calculated when possible from hydrated oocytes; otherwise yolk globule oocytes were used. Using yolk globule oocytes underestimates the egg size of a particular species; however the error associated with this was negligible compared to the differences in egg size between species. The estimate of fecundity used in the model was, following Winemiller's lead (see Winemiller 1989, Winemiller and Rose 1992), batch fecundity. Estimates of fecundity were $\log_{10}$ transformed because it reduced the variation in fecundity between species allowing them to be easily compared on the graph, and because it minimised the impact of inconsistencies in the measurement of fecundity (note Winemiller typically logged fecundity, see Winemiller 1989). The template of the model included three freshwater species that epitomised the endpoint strategies. This enabled the fish of the Fortescue River to be examined in a larger perspective. Endpoint species were taken from Winemiller (1989) and included: *Rachovia maculipinnis* ('opportunistic'), *Brycon whitei* ('periodic'), and *Potamotrygon orbignyi* ('equilibrium').

Estimates of fecundity, age at maturity, and level of investment per progeny for the species inhabiting the Fortescue River, were taken whenever possible from information gained during this study. However, if data were not available then information from the closest population (generally the Northern Territory populations studied by Bishop *et al.* 2001) were used. If this information was presented as a range rather than a mean, the mid-point of the range was used as a surrogate mean value.

Results

Reproductive Biology and Plasticity

A total of 1677 female fish were collected during the study. Of these, 1320 were weighed for gonadosomatic analyses and 1180 had their ovaries sectioned to provide detailed information on spawning patterns.

Age and Size at Maturity

Age at maturity is an important life history trait and one of the three parameters used in Winemiller's (1992) triangular model. However, estimating age proved to be difficult (see Appendix III). The average size at maturity (greater than 50%) for females was 6.2 cm for *L. unicolor*, 4.0 cm for *A. percoides*, 2.7 cm for *L. aheneus*, and 10.4 cm for *N. erebi* (Figure 7.2). Values for *A. percoides* and *L. aheneus* should be interpreted with caution, as few immature fish were collected. Data for *L. unicolor*, *A. percoides* and *L. aheneus* suggested quite rapid and invariable attainment of sexual maturity among individuals of these species. In contrast, there appears to be much more variability in size at which individuals of *N. erebi* reach maturity.

Seasonality of Spawning

Spawning pattern was not correlated with a species' environmental type. The two species that inhabited the relatively 'unstable' environment (*L. unicolor* and *M. australis*) displayed different patterns. *L. unicolor* spawned seasonally, linking its reproductive effort with the potential summer wet season (Figure 7.3), whereas ripe female *M. australis* were collected throughout the year. Similarly, *A. percoides*, *N. erebi*, and *L. aheneus*, all of which inhabited the relatively 'intermediary' environment, displayed different patterns. *A. percoides* bred during the summer wet, *L. aheneus* bred throughout the year with a peak during the mid-dry season (August), and *N. erebi* bred several times during the year (Figure 7.3). It should be noted that species with seasonal spawning patterns (i.e. *L. unicolor* and *A. percoides*) remained in a ripe state for a protracted period (Figure 7.4).

Plasticity in Ovarian Maturation

Plasticity (variation) in ovarian maturation was observed in all species that were examined in detail (i.e. *A. percoides, L. aheneus, L. unicolor*, and *N. erebi*). At any particular sampling date, females at one site would be more or less advanced than those at another site (Figure 7.4, 7.5). Plasticity was observed for species that

occurred within the most 'unstable' environment (*L. unicolor*), and those inhabiting the environment with an 'intermediate' level of stability (*A. percoides, L. aheneus* and *N. erebi*). Variation was most apparent in the species that did not breed seasonally (*L. aheneus* and *N. erebi*).

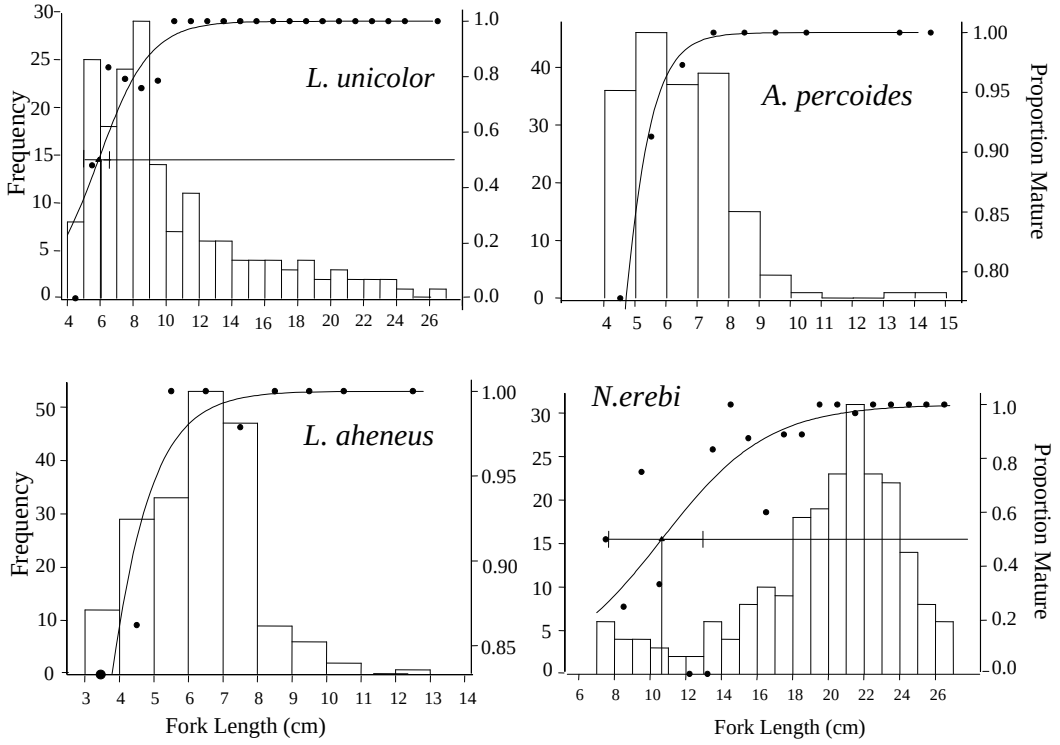


Figure 7.2. Size frequency histograms showing the proportion of mature female fish, for *L. unicolor*, *A. percoides*, *L. aheneus*, *N. erebi*. Estimates of the 50% maturity ogive are shown for *L. unicolor* and *N. erebi*. Estimates of 50% maturity for *L. aheneus* and *A. percoides* were smaller than the females collected, hence the size at maturity is not shown on their graphs.

Mode of Spawning and Fecundity

Ovaries from ripe and spawning *L. unicolor*, *A. percoides*, *L. aheneus*, *N. erebi* and *M. australis* were asynchronous. That is, they contained a continuous distribution of oocyte size classes (Figure 7.6 and 7.7; Plate 7.1.A, B, C; Plate 7.2.A, C), implying that mature (yolk globule) oocytes were being continuously recruited from the dominant reserve stock of chromatin nucleolar and perinucleolar oocytes. The presence of atretic oocytes in mature *L. unicolor* and *A. percoides* indicated that these protracted spawners were able to absorb their oocytes if they were not ready to spawn. The co-occurrence of hydrated oocytes and post-ovulatory follicles in the ovaries of

M. australis and *L. aheneus* indicated that they spawn many times (batch spawners) in quick succession. These traits mean that they are capable of making the most of favourable conditions.

Ovaries from ripe (stage 4) *A. graeffei*, *H. compressa*, *N. hyrtlii* and *G. giurus* were group synchronous. That is, they contained two discrete groups of oocytes, the mature (yolk globule) oocytes and the immature (chromatin nucleolar, perinucleolar, and cortical alveolar) oocytes (Figure 7.7; Plate 7.2.D, E, F). Group-synchronous ovaries imply that species do not have the opportunity to increase their reproductive output beyond what is initially determined, and hence cannot be as responsive (in terms of fecundity) as asynchronous species.

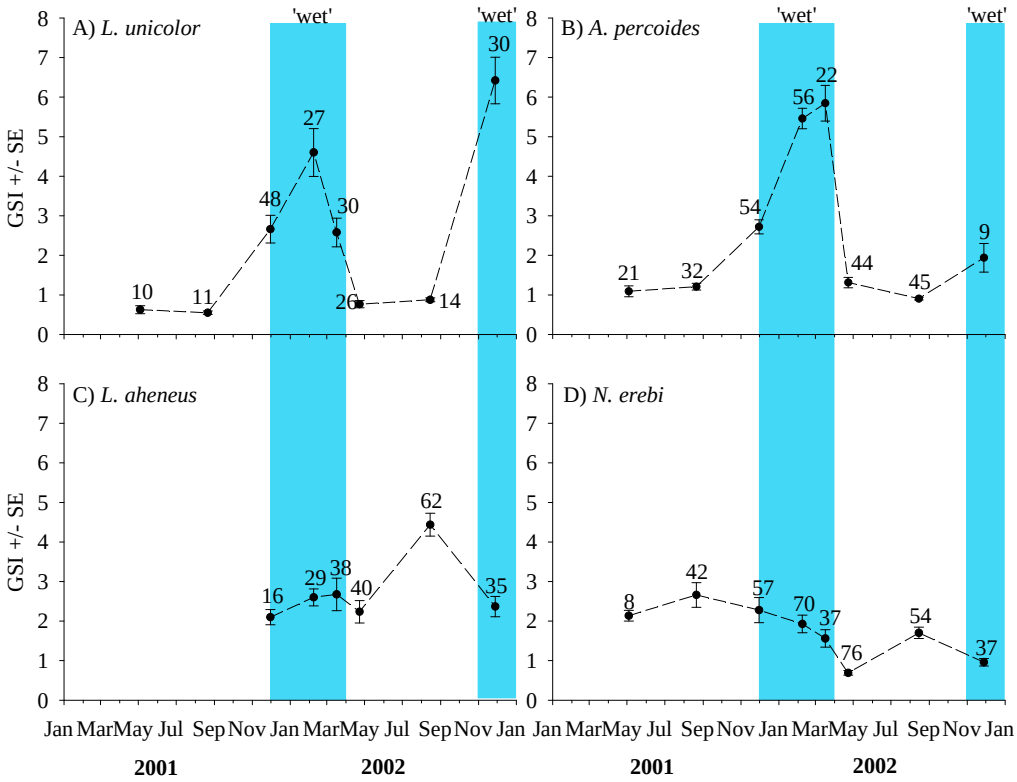


Figure 7.3. Seasonal reproductive trends in the female gonadosomatic (GSI) index for: A) *L. unicolor*, B) *A. percoides*, C) *L. aheneus*, and D) *N. erebi* during 2001 and 2002. Only mature fish were used, and fish were pooled across sites, for each sampling date. The graph shows the average GSI and its associated standard error, sample size (n) is also provided. The timing of the 'wet season' is shown in blue.

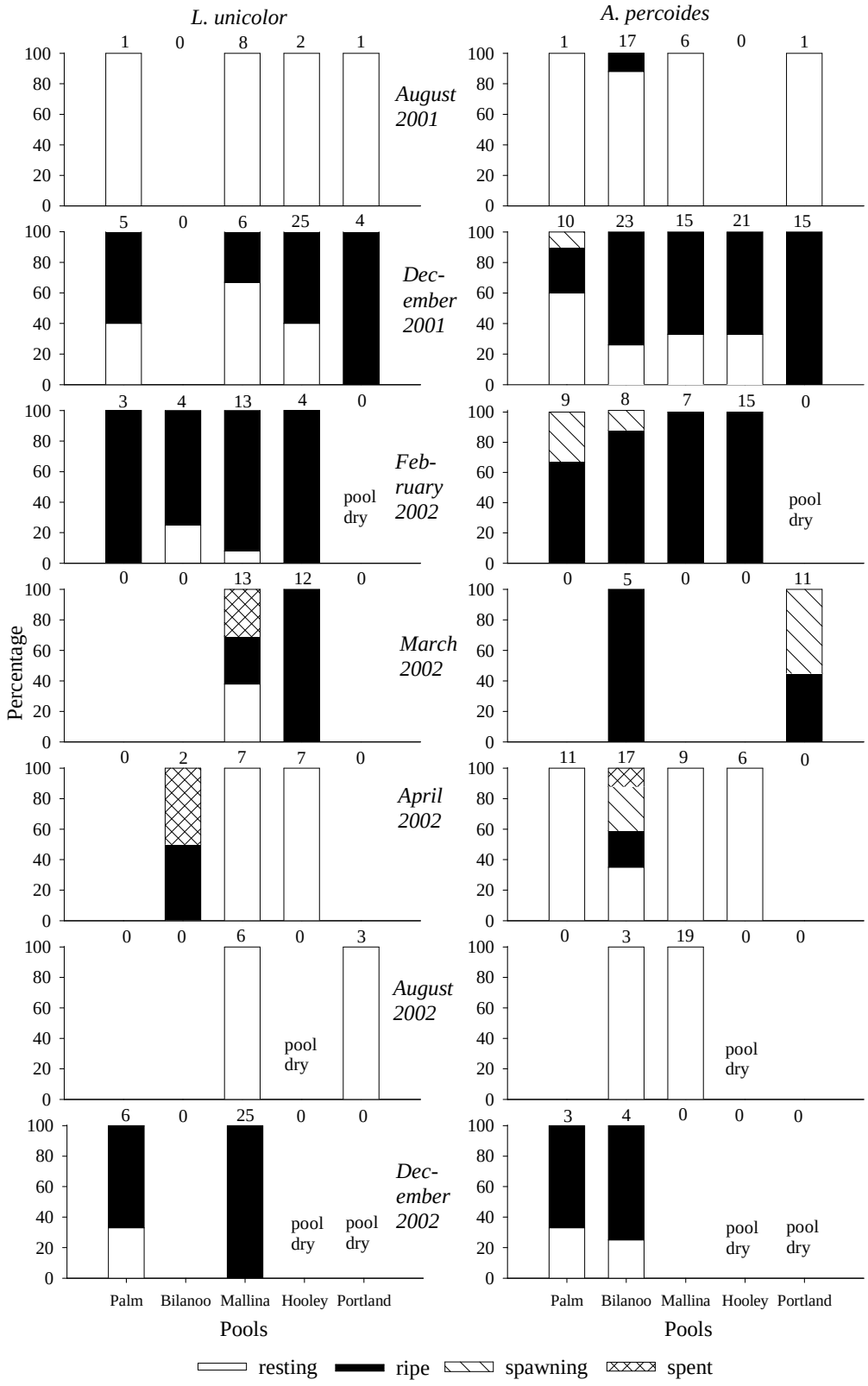


Figure 7.4. Spatial variation in percentage maturity for female *L. unicolor* and *A. percoides* collected during August and December 2001, and February, March, April, August and December 2002. The sample size is provided above each pool. Site/time combinations where no females were collected are shown as a blank, when this was because the pool had dried it is indicated on the graph.

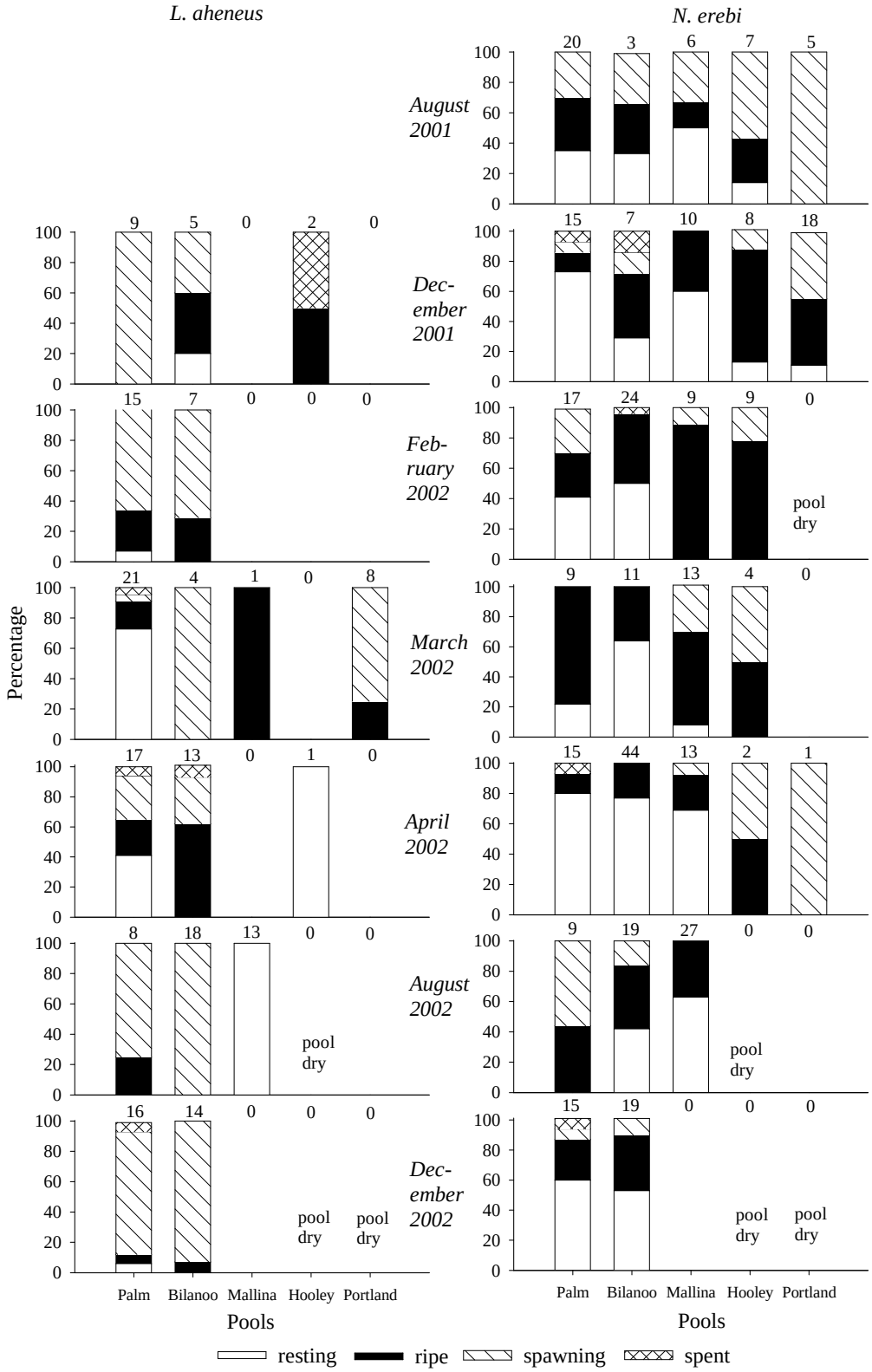


Figure 7.5. Spatial variation in percentage maturity for female *L. aheneus* and *N.erebi* collected during August and December 2001, and February, March, April, August and December 2002. The sample size is provided above each pool. Site/time combinations where no females were collected are shown as a blank, when this was because the pool had dried it is indicated on the graph.

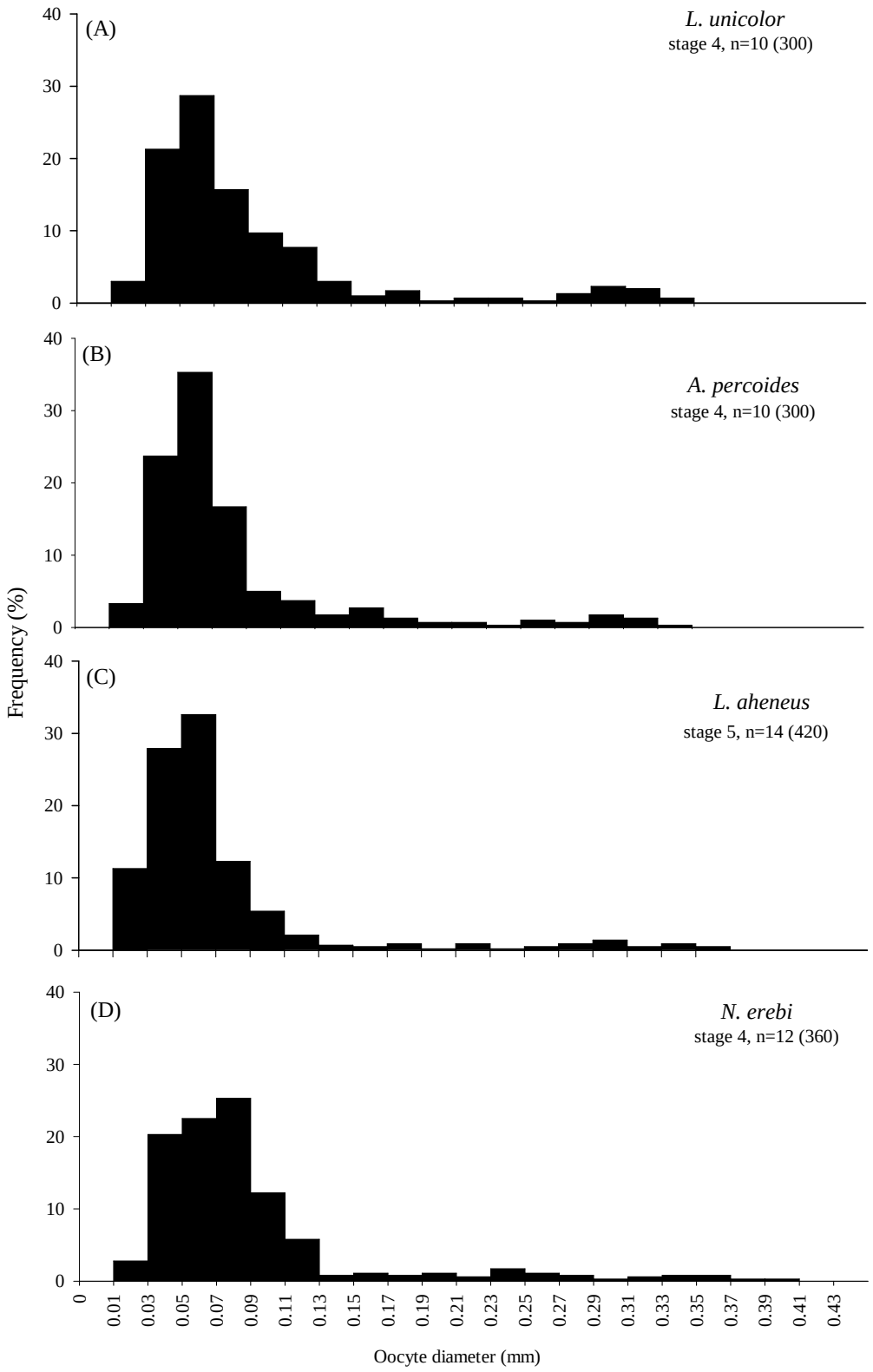


Figure 7.6. Oocyte size frequency distributions for ripe (stage 4) or spawning (stage 5a) fish. A) *L. unicolor*, B) *A. percoides*, C) *L. aheneus*, and D) *N. erebi*. The number of fish examined (n) is provided, as is the number of oocytes measured, which are shown in parentheses.

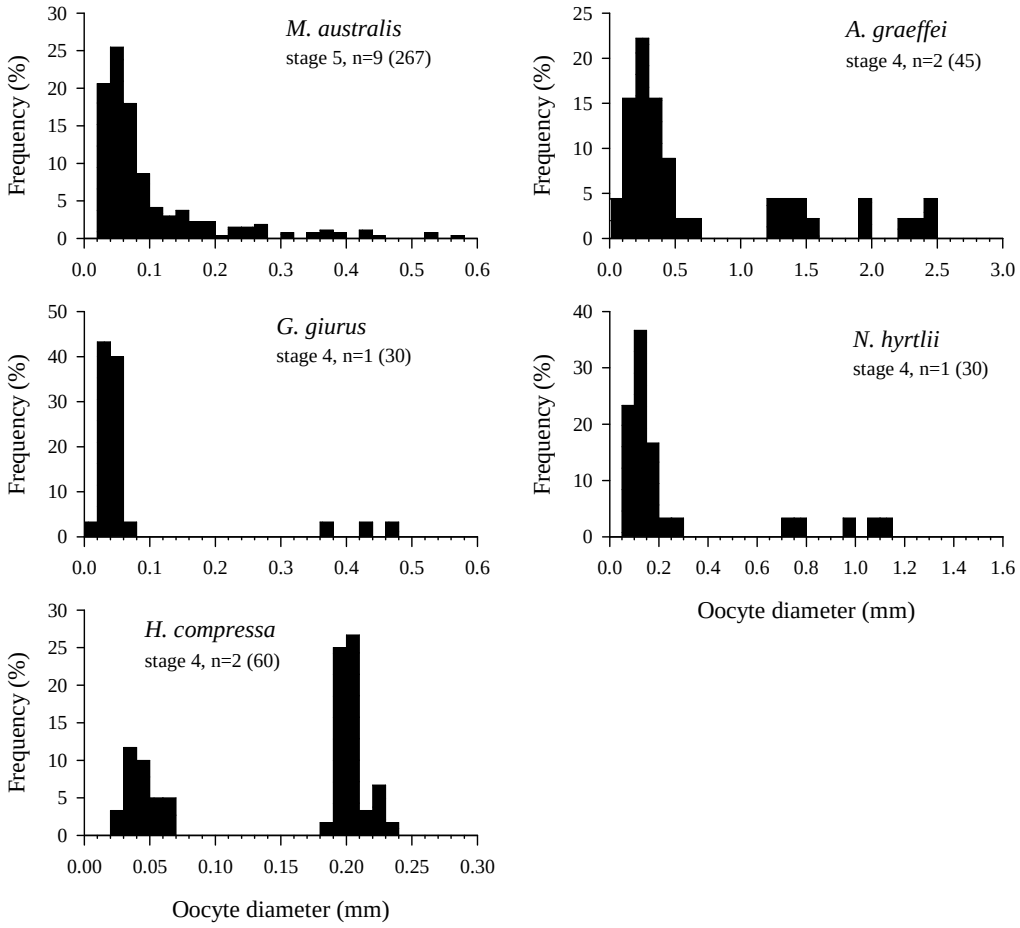


Figure 7.7. Frequency distributions of oocyte diameters in ripe (stage 4) or spawning (stage 5) ovaries for the non-focal species: *H. compressa*, *A. graeffei*, *N. hyrtlii* and *G. giurus*. n=the number of fish and the number of oocytes measured is provided in parentheses. Estimates for *G. giurus* only reflect the width of the oocytes as they are pyriform in shape.

Winemiller's (1989) method of determining fecundity (see methods) allowed a comparison between species, revealing that *M. australis* had the lowest fecundity, followed by *A. graeffei* and *N. hyrtlii* (Table 7.3). Species with the highest fecundity included *L. unicolor*, *N. erebi* and *H. compressa* (Table 7.3). There was massive variation in fecundity, with the most fecund species (*L. unicolor*) producing on average approximately five thousand times more eggs than the least fecund species (*M. australis*).

Table 7.3. Fecundity estimates for the fish of the Fortescue River. Estimates were taken on ripe (stage 4) fish, and represent the number of oocytes within the medium to large size class.* indicates that a species had group synchronous ovaries, and that the data provides an estimate of seasonal fecundity. The numbers of fish examined for each species (n) are provided, as is the size range (fork length, FL).

Species	Fecundity	n	Range of FL (cm)
A. graeffei	140±3.5*	2	39.0-50.0
A. percoides	18496±4482	7	4.7-14.0
G. giurus	1938*	1	6.7
L. unicolor	121829±68928	5	6.8-24.6
L. aheneus	9184±2538	4	6.6-9.5
M. australis	23±4.8	6	4.4-6.4
N. erebi	48260±10180	3	18.5-22.3
N. hyrtlii	375*	1	13.8
H. compressa	39823±266.5*	2	6.5-6.5

Oocyte Size

L. unicolor, *A. percoides* and *H. compressa* produced relatively small oocytes (Table 7.4). *N. erebi*, *L. aheneus* and *G. giurus* produced oocytes approximately twice as large as those produced by *A. percoides*. *M. australis* produced oocytes that were even larger still, but were relatively small compared to *N. hyrtlii* and *A. graeffei*, which produced oocytes approximately 5 and 10 fold larger than *A. percoides*. Except for species where hydrated oocytes were collected (i.e. *L. aheneus* and *M. australis*) oocyte size (yolk globule) is an underestimate of their final size.

Table 7.4. Maximum oocyte diameter for the study species. The status of the oocyte is presented. Yolk globule oocytes have not yet undergone hydration and provide an underestimate of the size of spawned oocytes. * = average size of pyriform oocytes, as maximum length and width were inversely related.

Species	Maximum Diameter (mm)	Oocyte type
A. graeffei	4.10	Yolk globule or possibly hydrated
A. percoides	0.43	Yolk globule (late migratory nucleus or very early hydrated)
G. giurus	0.77 x 0.28*	Yolk globule
H. compressa	0.32	Yolk globule
L. aheneus	0.80	Hydrated
L. unicolor	0.43	Yolk globule
M. australis	1.00	Hydrated
N. erebi	0.60	Yolk globule
N. hyrtlii	2.70	Yolk globule

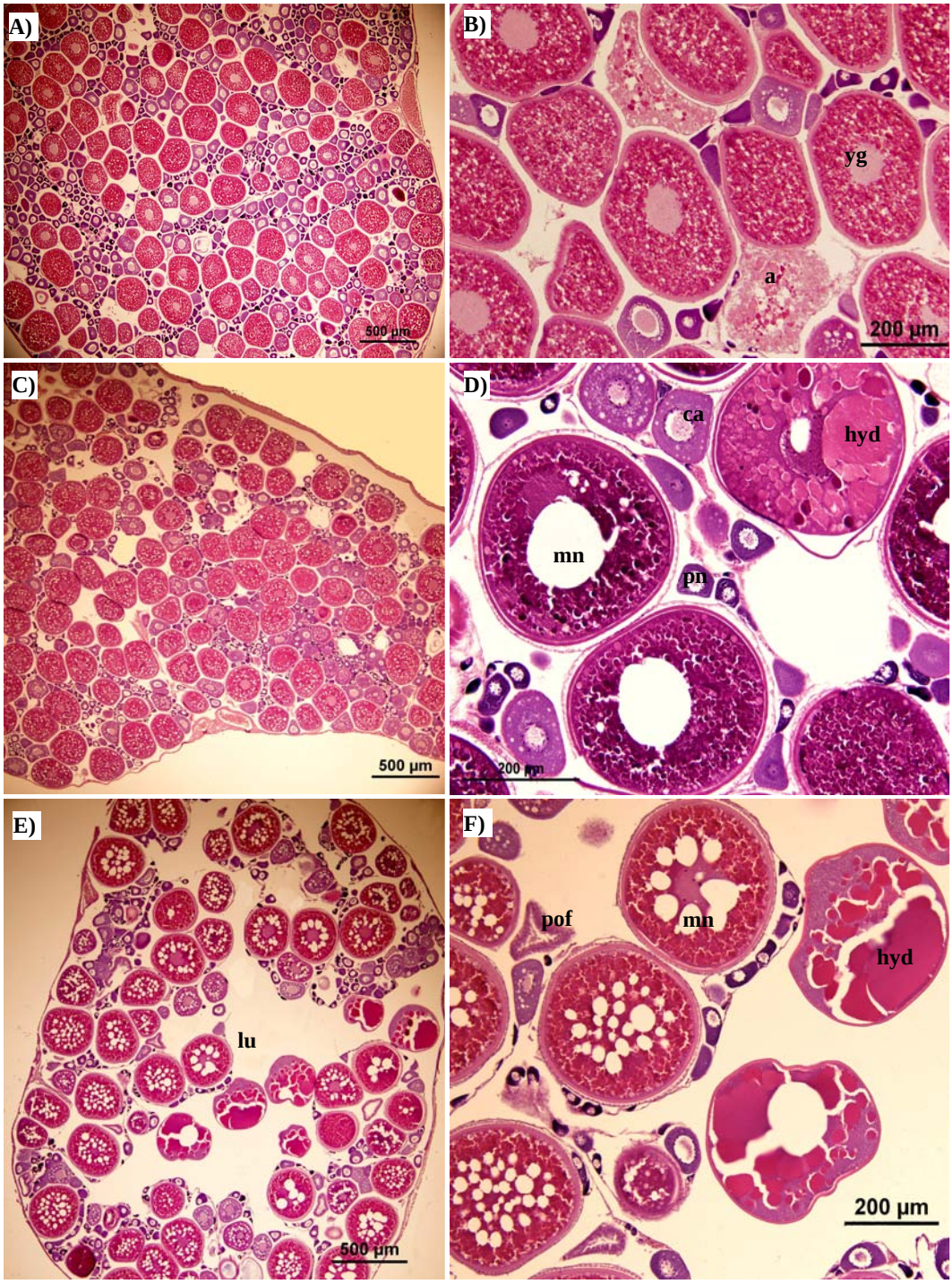


Plate 7.1. Transverse histological sections of ovaries: (A) – general structure of a ripe (F4 stage) ovary of *L. unicolour*; (B) – sub-section of *L. unicolor* (F4); (C) - general structure of a ripe (F4) ovary of *A. percoides*; (D) – sub-section of *A. percoides* (F5a) ovary, showing oil drop coalescence within the migratory nucleus oocytes; (E) – general structure of a spawning (F5a/b/c) ovary of *L. aheneus*, and; (F) – sub-section of a *L. aheneus* (F5) ovary. Oocyte stages are indicated alphabetically and include; perinucleolar (pn), cortical alveoli (ca), yolk globule (yg), atretic yolk globule (a) migratory nucleus (mn), and hydrated (hyd). Post-ovulatory follicles (pof) and the lumen of the ovary (lu) are also indicated. Scale bars are provided.

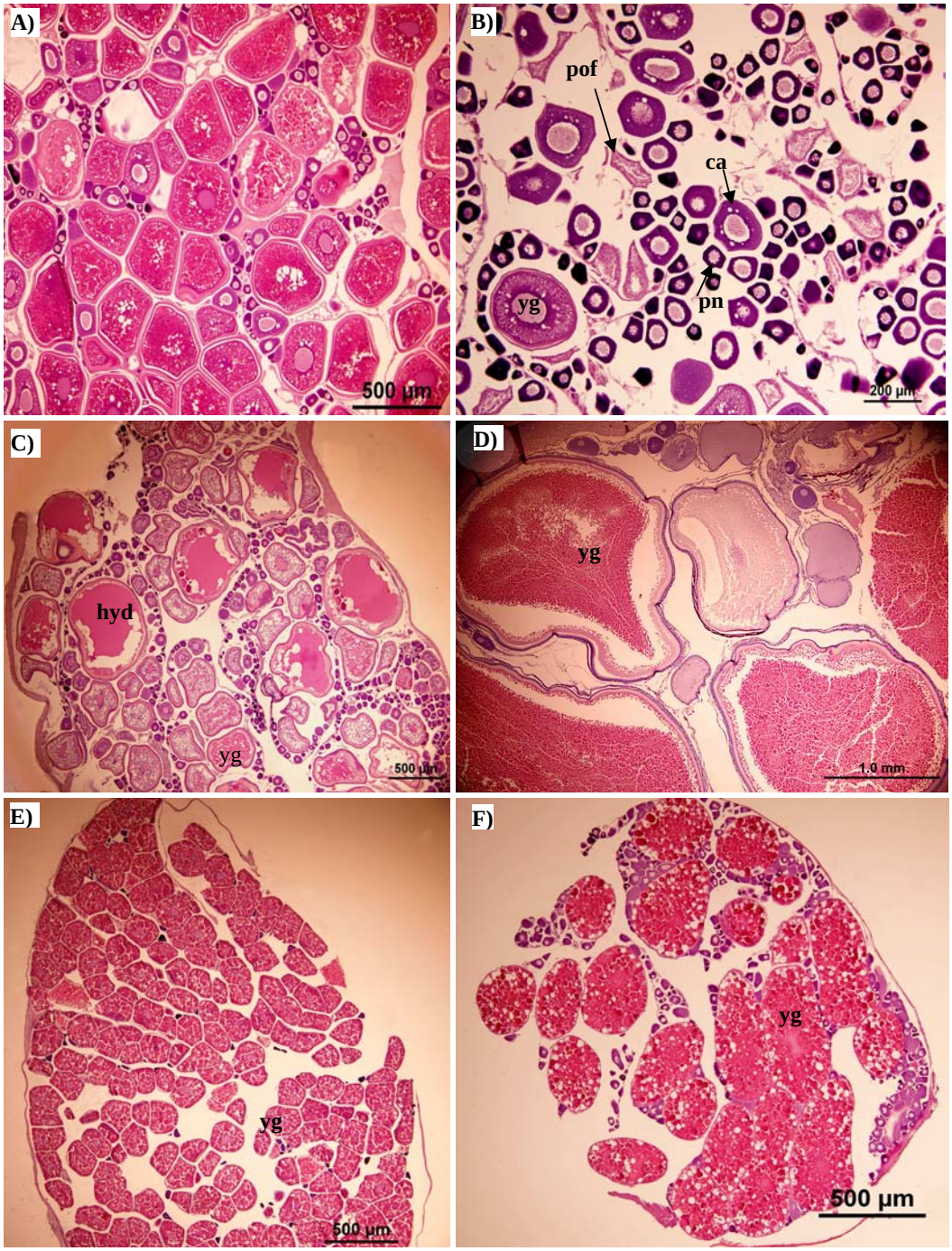


Plate 7.2. Transverse histological sections of ovaries: (A) – general structure of a ripe (F4 stage) ovary of *N. erebi*; (B) – sub-section of a spent *N. erebi* (F6); (C) - general structure of a ripe (F4) ovary of *M. australis*; (D) – general structure of a ripe (F4) ovary of *A. graeffei*; (E) – general structure of a ripe (F4) ovary of *H. compressa*, and; (F) – general structure of a ripe (F4) *G. giurus* ovary. Oocyte stages are indicated alphabetically and include; perinucleolar (pn), cortical alveoli (ca), yolk globule (yg), migratory nucleus (mn) and hydrated (hyd). Post-ovulatory follicles (pof) are also indicated. Scale bars are provided.

Life Histories and the Environment

Species' life history strategies reflected the stability of the river at large. That is, most species (7 of 10) had life history traits that lay between 'opportunistic' and 'periodic' endpoints (Figure 7.8), reflecting the seasonal yet unpredictable nature of rainfall in this desert region. Those species that did not conform to this expectation had either extremely 'opportunistic' or 'periodic' life history traits (*M. australis* and *A. bicolor*), or mildly 'equilibrium' traits (*A. graeffei*) (Figure 7.8).

Life history strategies did not separate according to the stability of the pools occupied within the river. This was most easily observed by examining species within the 3-dimensional life history space of Winemiller's (1992) model (see Figure 7.8). For example, *M. australis* and *L. unicolor,* both inhabited the relatively 'unstable' environment, but displayed 'opportunistic' versus relatively 'periodic' strategies respectively. In addition, *A. bicolor*, *A. graeffei* and *H. compressa* all inhabited the relatively 'stable' environment but displayed extremely 'periodic', mildly 'equilibrium' and 'opportunistic-periodic' strategies respectively. Another departure from expectation was *N. hyrtlii,* which resided within the relatively 'intermediary' environment, but had a considerably lower fecundity and larger oocyte size than most of its neighbours. However, this result was based on only one individual and should be considered with caution.

The Model in General

All species lay within the three dimensional space of predicted life history combinations (note that *A. bicolor'*s traits were extreme but agreed with the model). However, the absence of an axis that incorporated the number of spawning bouts per year meant that the model did not clearly distinguish a species' seasonality of spawning. For example, the protracted seasonal spawners (*L. unicolor*, *A. percoides*, Figure 7.4) were proximate to the multiple (*N. erebi*) and relatively continuous spawning species (*L. aheneus*) (Figure 7.5, Figure 7.8).

Table 7.5. The life history traits of the fish of the Fortescue River used to test Winemiller's (1992) model, and the stability of the environment in which they occurred. Investment per progeny was used as a correlate of juvenile survivorship. Fecundity referred to batch fecundity where possible. If hydrated oocytes were not obvious then fecundity refers to the number of large and medium sized oocytes. Fecundity estimates were logged to the base 10 prior to graphing.

Environmental Stability	Species	Fecundity	Age at Maturity (yrs)	Investment / Progeny
Stable	*A. bicolor*	225000000	17.5	0.20
Stable	*A. graeffei*	140	~2	2.73
Stable	*H. compressa*	39823	1	1.38
Intermediate	*N. erebi*	48260	0.75	0.47
Intermediate	*L. aheneus*	9184	~0.75	0.59
Intermediate	*A. percoides*	18496	1	0.35
Intermediate	*G. giurus*	1938	1	0.42
Intermediate	*N. hyrtlii*	375	1	1.31
Unstable	*L. unicolor*	121829	1	0.36
Unstable	*M. australis*	19	0.25	0.74

Geographic Comparisons

Some of the species found within the Fortescue River (*L. unicolor, A. percoides, H. compressa, G. giurus)* displayed similar life history characteristics to conspecifics found elsewhere in Australia (Table 7.6). However, several species showed differences. For example, *N. erebi* in the Fortescue River were smaller and matured at a smaller size than individuals collected in South Australia and the Northern Territory (Table 7.6). Similarly, *N. hyrtlii* collected in the Fortescue River were considerably smaller (less than half as long) as individuals collected in the Northern Territory and Queensland (Table 7.6). There was also preliminary evidence (only one reproductive sample was collected) that they have considerably lower fecundity (Table 7.6). While reduced fecundity could merely be an artefact of reduced size, the fact that this population produces larger eggs (Table 7.6) suggests that it has a different life history strategy. Furthermore, the ripe *N. hyrtlii* collected in the Fortescue was ripe in April (late wet season), whereas they are reported to spawn in the early wet November-December in the Northern Territory and Queensland (Table 7.6). Another species that showed geographic variance in life history traits was *A. graeffei*. Individuals collected in the Fortescue River were ripe in August (mid dry season), whereas fish in New South Wales are ripe in November-December (Table 7.6).

This study generated some contention about the mode of spawning of several species. *L. unicolor* and *N. erebi* were previously classified as uni-modal (or group-

synchronous), whereas histological examination conducted during this study revealed that they have asynchronous oocyte development (Table 7.6).

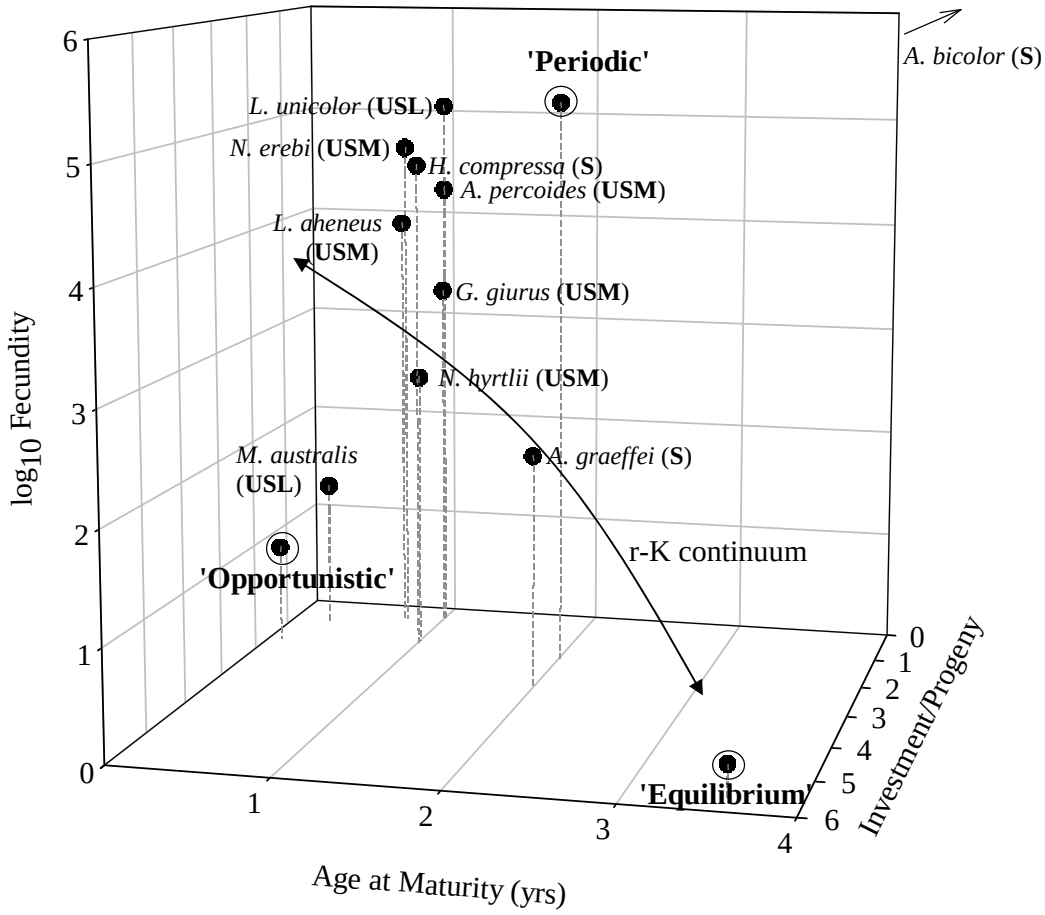


Figure 7.8. The life history strategies of the freshwater fish species of the Fortescue River according to Winemiller's (1992) model. Investment per progeny was used in place of the level of juvenile survivorship as it was easier to obtain and has been found to be a strong correlate, and was determined as ln[(egg diameter+1)(parental investment+1)]. To orient species in relation to Winemiller's model, three species, which represented the three life history endpoints, were taken from Winemiller's (1989) study and included in the graph. These species have been circled, and include *Rachovia maculipinnis* (opportunistic), *Brycon whitei* (periodic) and *Potamotrygon orbignyi* (equilibrium). An abbreviated form of the environmental type with which the species from the Fortescue occurred within is provided in parenthesis along side each species name. This includes; S = stable pools, USM = the unstable section of the catchment with a moderate (intermediate) level of persistence, USL = the unstable section of the catchment with low persistence. The r-K continuum is shown on the model with a double-ended arrow.

Table 7.6. The life history characteristics of the freshwater fish species of the Fortescue River. Data is presented for various geographic regions of Australia, including: this study (Pilbara), the Northern Territory (NT), Queensland (QLD), New South Wales (NSW), South Australia (SA), Papua New Guinea (PNG), and elsewhere (ELS). Fish lengths are quoted as distance from the snout to the tip of the caudal fin (total length, TL), distance from the snout to the caudal peduncle (standard length, SL), or distance from the snout to the caudal fork (fork length, FL).

Family **Species**	**Anguillidae** ***Anguilla bicolor***	**Clupeidae** ***Nematalosa erebi***	**Ariidae** ***Arius graeffei***	**Plotosidae** ***Neosilurus hyrtlii***	**Melanotaeniidae** ***Melanotaenia australis***
Maximum Length (mm)	600 TL (Allen *et al.* 2002). Pilbara: Uncalibrated observations suggest that its size may be > 600.	NT: 340 FL (Bishop *et al.* 2001). NSW: 470 TL (Briggs 1980). Pilbara: 269 FL	NT: 395 FL (Bishop *et al.* 2001). NSW: ♀494 ♂453 SL (Rimmer 1985b). Pilbara: 500 FL.	NT: 400 TL (Bishop *et al.* 2001). QLD: 454 SL (Pusey *et al.* 2004). Pilbara: 176 TL	*M. splendida* QLD: 105 TL (Beumer 1979). *M. australis* Pilbara: 84 FL
Size at Maturity (mm)		SA: ♀199, ♂159 TL (Puckridge and Walker 1990). NSW: ♀80 (Briggs 1980) NT: ♀140, ♂130 FL (Bishop *et al.* 2001). Pilbara: ♀104 FL	NT: Ripe ♀ collected at 270 FL, small sample size (Bishop *et al.* 2001). NSW: 50%mature 270 -280 (Rimmer 1985a).	NT: 135 TL (Bishop *et al.* 2001) Pilbara: One ripe ♀ collected, 138 TL.	*M. splendida* QLD: ♂'s dominated large size classes (Beumer 1979). *M. australis* Pilbara: ♀'s > 35 FL were mature. Few small females were examined and size at maturity may have been lower.
Age at Maturity (yrs)	10-25yrs (Allen *et al.* 2002).	SA: 2 or 3 yrs, ♀'s began to mature in 2nd yr (Puckridge and Walker 1990). NT: 6 months to 1yr (Bishop *et al.* 2001). Pilbara: Estimated at between 0.5 to 1 yr.	*Arius leptasis* which grows to a similar size to *A. graeffei*, matures at 2 yrs (Bishop *et al*. 2001).	Pilbara: Estimated at 1 yr.	*M. splendida* QLD $_{aquaria}$: 0.25 year (Humphrey *et al.* 2003b).
Longevity (yrs)	ELS: *A. australis* >32 ys (Sloane 1984).	SA: Unvalidated estimate of >10yrs (Puckridge 1992).	Pilbara: Uknown, but cursory examination of unvalidated otoliths suggest it may be >6 yrs.		

Table 7.6. Continued

Species	*Anguilla bicolor*	*Nematalosa erebi*	*Arius graeffei*	*Neosilurus hyrtlii*	*Melanotaenia australis*
Spawning season	Once per life time (Allen *et al.* 2002). ELS: once per life time (Lockman and Young 2000).	SA: Dec-Feb (Puckridge and Walker 1990). NSW: Oct-Dec (Lake 1967, Briggs 1980). NT: Throughout the year, with a peak in the early wet (Bishop *et al.* 2001). PNG: Aseasonal (Roberts 1978). Pilbara: Several times during the year, spawning varies with site conditions	NT: Ripe females collected in the late dry season, assumed spawning occurred in the late dry and wet (Bishop *et al.* 2001). NSW: ~ 1 month in Summer (November to December) (Rimmer 1985a). Pilbara: Ripe fish collected in August.	NT: Start of the wet season (Bishop *et al.* 2001) QLD: Start of the wet, spawning was associated with floods (Orr and Milward 1984). Pilbara: Ripe fish collected in April.	*M. splendida* QLD: Spawn throughout the year (Beumer 1979), spawning concentrated during the dry season (Sept-Oct) (Pusey *et al.* 2001). *M. australis* Pilbara: Throughout the year.
Spawning Bouts				QLD: Several spawning events occurred during the season. Unsure if females took part in one or several spawnings (Orr and Milward 1984).	*M. splendida* QLD: Multiple, number not known (Pusey *et al.* 2001). *M. australis* Pilbara: Multiple, exact number not known.
Fecundity (batch or otherwise)	ELS: *A. australis* 1.5 to 3 million eggs lifetime fecundity and total fecundity (semelparous) (Todd 1981a).	SA: 33000-880000, and increases greatly with size (Puckridge and Walker 1990). NT: 80000-230 000 (Bishop *et al.* 2001). Pilbara: 48260±10180 large and medium oocytes, ovaries stage 5a (n=3, FL range: 185-223mm).	NSW: Range of 40-122, mean of 70.5, linear relationship with size (Rimmer 1985a). Pilbara: 140.5±3.5 oocytes, ovaries at stage 4 or 5a (n=2, FL range: 390–500mm).	NT: One female only was examined, number of intra-ovarian eggs was 3630 (Bishop *et al.* 2001). Qld: 1 600 (186mm fish) to 15 300 (267mm fish) (Orr and Milward 1984). Pilbara: 375 oocytes, ovary at stage 4 (n=1, FL: 138mm).	*M. splendida* QLD $_{\text{aquaria study}}$: average batch size of 31-32 (Beumer 1979). QLD: Batch size increases with body size (Pusey *et al.* 2001, Humphrey *et al.* 2003a). *M. australis* Pilbara: 23±4.8 large and medium oocytes, ovaries at stage 5a (n=6, FL range 44-64mm).

Table 7.6. Continued

Species	*Anguilla bicolor*	*Nematalosa erebi*	*Arius graeffei*	*Neosilurus hyrtlii*	*Melanotaenia australis*
Egg size (mm)	ELS: Intra ovarian eggs of *A. australis* 0.22 diameter (Todd 1981a & 1981b).	SA: Vitellogenic ova >0.25, eggs caught in trawl ~0.83. Egg size does not alter with fish size (Puckridge and Walker 1990). NT: Mean 0.43 (Bishop *et al.* 2001). Pilbara: Migratory nucleus yolk globule maximum size = 0.60.	NSW: Mature oocytes 11.0-13.7 (Rimmer 1985a). Fertilised eggs 12.3-15.2 (Rimmer 1985c). No relationship between egg size and fish length or weight (Rimmer 1985a). Pilbara: Maximum yolk globule or possibly hydrated oocyte = 4.1.	NT: 1.3±0.9 intra-ovarian (Bishop *et al.* 2001) QLD: 2.6 water hardened (Orr and Milward 1984). Pilbara: Maximum yolk globule oocyte = 2.7.	*M. splendida* QLD: Maximum 1.10 (intraovarian). Ovulated but unfertilised eggs 1.12 (Pusey *et al.* 2004). Humphrey *et al.*'s (2003) aquaria study reported 0.93 – 1.20 for ovulated eggs. *M. australis* Pilbara: Maximum yolk globule oocyte = 0.45. Hydrated oocyte = 1.10.
Type of oocyte development	Synchronous	SA: Spawn a single batch of ova (Puckridge and Walker 1990). Pilbara: Asynchronous	NSW: Synchronous (Rimmer 1985a) Pilbara: Group synchronous	Pilbara: Group synchronous.	*M. splendida* QLD: Asynchronous (poly modal) (Beumer 1979). *M. australis* Pilbara: Asynchronous
Egg type	Planktonic (Pusey *et al.* 2004).	SA: Initially demersal, becoming pelagic (Puckridge and Walker 1990).		QLD: Non-adhesive, demersal (Orr and Milward 1984).	*M. splendida* QLD: Demersal with adhesive threads that attach to foliage (Beumer 1979).
Oviparous / viviparous	Oviparous (Pusey *et al.* 2004).	Oviparous	Oviparous	Oviparous	Oviparous
Parental Care	QLD: None known (Pusey *et al.* 2004).	SA: Nil (Puckridge and Walker 1990)	NSW: Males mouth brood for 6-8weeks (Rimmer 1985c).	QLD: None (Orr and Milward 1984).	*M. splendida* None known (Pusey *et al.* 2004). *M. australis* Pilbara: None observed.
Hatch time	ELS: *A. australis* ~45 hrs (Lockman and Young 2000).		NSW: 4-5 weeks (Rimmer 1985c).	QLD: 60 hrs (Orr and Milward 1984).	*M. splendida* QLD: 7-12 days (Beumer 1979).
Size of larvae at hatching (mm)	*A. australis* ~2.5 TL (Lockman and Young 2000).	SA: 2.5-3.5 TL (Puckridge and Walker 1990).	NSW: Released from mouth at up to 59 TL (Rimmer 1985c).	QLD: 5.7 to 6.0 TL and poorly developed (Orr and Milward 1984).	*M. splendida* QLD: 3.92 – 4.62 (Pusey *et al.* 2004).

Table 7.6 Continued.

Family		**Terapontidae**		**Gobiidae**	**Eleotridae**
Species	***Leiopotherapon unicolor***	***Leiopotherapon aheneus***	***Amniataba percoides***	***Glossogobius giurus***	***Hypseleotris compressa***
Maximum Length (mm)	300 (Allen *et al.* 2002) NT: 236 FL (Bishop *et al.* 2001). QLD: 194 TL, ♀'s dominated large size classes (Beumer 1979). Pilbara: 265 FL, ♂'s dominated small size classes and ♀'s the large size classes.	Pilbara: 153 FL	NT: 188 FL (Bishop *et al.* 2001). Pilbara: 145 FL	NT: ~112 TL (Bishop *et al.* 2001). Pilbara: 210 TL.	NT: 69 FL (Bishop *et al.* 2001). NSW: 100 (Auty 1978). Pilbara: 73 FL.
Size at Maturity (mm)	NT: ♀94, ♂74 FL (Bishop *et al.* 2001). QLD: ♀58, ♂66 TL (Beumer 1979). $NSW_{translocated}$: ♀78, ♂58 TL (Llewellyn 1973). Pilbara: ♀62 FL.	Pilbara: Small sample size suggests ♀27 FL.	NT: ♀45, ♂65 but may be smaller (Bishop *et al.* 2001). Pilbara: Limited information suggests ♀40 FL.	NT: ~35 TL (Bishop *et al.* 2001).	NT: ≤ 43 FL (Bishop *et al.* 2001). QLD: 41.3 SL (Pusey *et al.* 2004).
Age at Maturity	$NSW_{translocated}$: Estimated at 1yr (Llewellyn 1973). NT: Estimated at 6 months to 1yr (Bishop *et al.* 2001). QLD: 3-6 months (Pusey *et al.* 2004). Pilbara: Estimated at 1 yr.	Pilbara: Estimated at between 6 months to a year.	NT: Estimated at 1yr (Bishop *et al.* 2001). Pilbara: Estimated at 1 yr.	NT: Estimated at <1yr (Bishop *et al.* 2001). Pilbara: Estimated at 1 yr.	NT: Unsure, but may be 1yr (Bishop *et al.* 2001). Pilbara: Estimated at 1 yr.
Longevity (yrs)	QLD: Estimated at between 2-3 yrs for most, occasionally 4-5yrs (Pusey *et al.* 2004). Pilbara: Unvalidated otoliths suggest 4yrs.		Estimated at between 3-4 yrs, no studies undertaken (Pusey *et al.* 2004).		

Table 7.6 Continued.

Species	*Leiopotherapon unicolor*	*Leiopotherapon aheneus*	*Amniataba percoides*	*Glossogobius giurus*	*Hypseleotris compressa*
Spawning season	NT: Early wet (Bishop *et al.* 2001). $NSW_{translocated}$: Nov to Feb (Llewellyn 1973). QLD: Early wet, Dec/Jan or Jan/Feb (Beumer 1979). Nov – Jan (Pusey *et al.*2004) Pilbara: The summer wet (late Nov to March).	Pilbara: Throughout the year.	NT: Late dry (Sept/Oct) to early wet (Nov/Dec) (Bishop *et al.* 2001). Pilbara: The summer wet (late November to April).	NT: Wet season and possibly during the dry (Bishop *et al.* 2001). Pilbara: Ripe fish and larval gobies (6mm TL) collected in April.	NT: Mid wet season (Jan-Mar) (Bishop *et al.* 2001). QLD: Ripe fish found in January and May/April (Pusey *et al.* 2004). NSW: September to March (Llewellyn 1983). Pilbara: Ripe fish collected in April.
Spawning bouts (#/yr)	Pilbara: Multiple, exact number not known.	Pilbara: Multiple, exact number not known.	Unknown, thought to be a batch spawner (Pusey *et al.* 2004). Pilbara: Multiple, exact number not known.		NSW: Approximately 20 per spawning season (Auty 1978)
Fecundity (batch or otherwise)	NT: Total fecundity 15600-80000 (Bishop *et al.* 2001). QLD: Total fecundity ranged from 3563-94169, and varied annually (Beumer 1979). $NSW_{translocated}$: Total fecundity 24000-113200 (Llewellyn 1973). Fecundity increased with size (Beumer 1979) and weight (Llewellyn 1973). Pilbara: 121829±68929 large and medium oocytes, ovaries at stage 4 (n=5, FL: range 68-246mm).	Pilbara: 5077±2539 large and medium oocytes, ovaries at stage 5a (n=4, FL: range 66-95mm).	NT: Total fecundity 800-400 000 (Bishop *et al.* 2001). Pilbara: 18496±4482 large and medium oocytes, ovaries at stage 4 (n=7, FL: range 47-140mm).	NT: 1000 (35mm TL) – 16 000 (60mm TL) (Bishop *et al.* 2001). Pilbara: 1938 oocytes, ovary at stage 4 (n=1, FL: 67mm).	NSW: Batch fecundity of ~2500 (measured post-spawn). Total fecundity >40 000 (Auty 1978). QLD: seasonal fecundity, mean 32 768±7 197 SE. Total fecundity increases linearly with fish size (Pusey *et al.* 2004). NT: Total fecundity, mean 18 000 ± 4535 SE (Bishop *et al.* 2001). Pilbara: 3982±266 oocytes, ovaries at stage 4 (n=2, FL: 65mm).

Table 7.6 Continued.

Species	*Leiopotherapon unicolor*	*Leiopotherapon aheneus*	*Amniataba percoides*	*Glossogobius giurus*	*Hypseleotris compressa*
Egg size (mm)	NT: 0.24-0.23 (intra-ovarian) (Bishop *et al.* 2001). QLD: Maximum 0.60 (intra-ovarian), 0.55-0.75 (water hardened) (Beumer 1979). $NSW_{translocated}$: 0.67-0.81 (water hardened) (Llewellyn 1973). Pilbara: Maximum size of yolk globule oocyte 0.43.	Pilbara: Maximum hydrated oocyte = 0.80.	NT: Generally between 0.24-0.32, range 0.16 to 0.40 (Bishop *et al.* 2001). Pilbara: Maximum size of late migratory nulcleus or early hydrated oocyte = 0.43.	NT: Eggs are pyriform in shape (intra-ovarian: 0.3 long, 0.1 wide) (Bishop *et al.* 2001). Pilbara: Yolk globule oocyte, on average 0.77 long, 0.28 wide.	NSW: Water hardened eggs are ~0.27x0.31. Slightly pear shaped with many oil globules (Auty 1978). QLD: 0.32±0.01SE (Pusey *et al.* 2004). Pilbara: Maximum yolk globule oocyte = 0.32.
Type of oocyte development	QLD: Synchronous (uni-modal) (Beumer 1979). Pilbara: Asynchronous	Pilbara: Asynchronous	Asynchronous (Pusey *et al.* 2004) Pilbara: Asynchronous	Pilbara: Group synchronous.	Pilbara: Group synchronous.
Egg type	Demersal, non-adhesive (Llewellyn 1973).	Pilbara: Demersal	NT: Demersal, non-adhesive (Bishop *et al.* 2001).	NT: Demersal (Bishop *et al.* 2001).	NSW: Adhesive demersal (Auty 1978).
Oviparous / viviparous	Oviparous	Pilbara: Oviparous	Oviparous	Oviparous	NSW: Oviparous (Auty 1978).
Parental Care	$NSW_{translocated}$: Nil (Llewellyn 1973).	Pilbara: None known	None known (Bishop *et al.* 2001, Pusey *et al.* 2004).	Unknown. Males of this family are known to build nests and guard eggs (Breder and Rosen 1966).	NSW: Male guards eggs in nest (Auty 1978).
Hatch time	$NSW_{translocated}$: 2 days (Llewellyn 1973).			NT: Unknown, estimated as several days (Bishop *et al.* 2001).	NSW: ~12hrs (26-28ºC) (Auty 1978).
Size of larvae at hatching (mm)	QLD: 1.52-2.41 (Beumer 1979). $NSW_{translocated}$: 1.72-2.56, (Llewellyn 1973).				NSW:1 TL and poorly developed (Auty 1978).

Discussion

Life History Strategies and the Environment

The life history traits of the fish of the Fortescue River provided support for Winemiller's (1992) triangular model, relating environmental type and life history strategies at a large scale, but not at a fine scale.

Applicability of the Model at a Large Scale

At a large scale, the life history traits of species reflected the nature of the environment they inhabited. Most of the fish species within the Fortescue River (7 of 10) had life history traits which fell between the 'opportunistic' and 'periodic' endpoints on Winemiller's (1992) model, reflecting the seasonal but inherently variable nature of rainfall in this desert region. Those species that did not conform to this expectation had either 'opportunistic' (*M. australis*), extremely 'periodic' (*A. bicolor*), or mildly 'equilibrium' life history traits (*A. graeffei*). This result was not as successful as Alkins-Koo's (2000) study of six species in a tropical intermittent stream in the West Indies, where 83% of species displayed traits in accordance with the environment type, but was similar to Winemiller's (1989) study of the fish inhabiting seasonal waterbodies in Venezuela, which found that 69% of species had traits in accordance with the model's prediction, and provides support for widespread applicability of the model.

Phylogenetic constraints appear to account for the two species that did not conform to the model's expectations. Almost all melanotaeniids display 'opportunistic' traits (Winemiller 1992), ariids display 'equilibrium' life history strategies, involving oral incubation of the eggs by the males (Winemiller 1992, Allen *et al.* 2002), and anguillids are long lived, maturing late in life, producing a large number of eggs, and breeding only once (semelparous) (Lockman and Young 2000, Allen *et al.* 2002).

While most species fell in roughly the anticipated area on the model's 3D space, they did not align themselves along the r-K continuum of the model as expected. This result appears to be a consequence of the fact that species did not group together in accordance with their fine scale environmental distributions, as discussed below.

Applicability of the Model at a Fine Scale

At a fine scale, species' life history strategies did not group according to the stability of the environment they inhabited. Not only did species from different environment types have similar life histories, but species which inhabited the same environmental type had different life histories. For example, *H. compressa*, which was restricted to the relatively 'stable' environment, had an 'opportunistic-periodic' life history strategy, similar to *A. percoides*, which inhabited environments with relatively 'intermediate' stability. Likewise, *M. australis* and *L. unicolor* both inhabited the relatively 'unstable' environment, yet *M. australis* displayed an 'opportunistic' strategy, whereas *L. unicolor* displayed an 'opportunistic-periodic' strategy.

Phylogenetic constraints aside, potential causes of the dissociation of environmental type and life history traits within the Fortescue River include:

1) The habitation of several environmental types and the flood/drought nature of the Fortescue River. All species, except for those restricted to the stable environments, inhabited more than one habitat type. For example, *L. unicolor* occurred within the river's most unstable pools, but also occurred within the other two more moderate environmental types. Occupation of several environmental types should mean that divergence (evolution) associated with selective pressures within one environmental type will be reduced when populations mix during periods of flood. Genetic studies are needed to quantify how panmictic/divergent the fish meta-populations are.

2) Physiological rather than life history limitations to species' distribution. It is likely that the distribution of a species throughout the catchment was related more to physiological tolerances than the suitability of its life history strategy. For example, the restriction of *H. compressa* to the stable environment appeared to be due to its preference for brackish, macrophyte-rich habitats (Allen *et al.* 2002, Pusey *et al.* 2004), rather than its life history requirements, which appeared to be well suited to the catchment at large. Similarly, the absence of *N. erebi* from the most unstable pools (Chapter 4), was probably caused by the vulnerability of this species to low oxygen levels (Bishop *et al.* 2001, Pusey *et al.* 2004), which commonly occur within small shrinking pools (Trammer 1977, Schlosser 1991, Ostrand and Marks 2000).

3) Difficulties in obtaining estimates of the three parameters used in Winemiller's (1992) model. The model requires estimates of fecundity, juvenile survivorship, and age at maturity, which were difficult to obtain. This study had no information on

juvenile survivorship and, following Wanzenbock and Keresztessy (1995), used an index of parental investment in its place. This was assumed to be of little importance as Winemiller and Rose (1992) note that it is highly correlated with juvenile survivorship. Fecundity was also difficult to determine because most of the fish collected were not at the correct stage of development (see the Methods section). However, the log transformation of the data in conjunction with the broad template in which the results were couched meant that this imprecision was probably of minor relevance.

Trophic status is known to affect life history strategies (Wilbur *et al.* 1974), and has been put forward by Winemiller (1989) as a potential cause for the incongruence between life history strategies and environmental stability. However, it was probably of negligible importance to the fish of the Fortescue River, because most species occupied similar positions on the food web (see Appendix VI). The one exception may be *Neosilurus hyrtlii*, which had a lower fecundity than anticipated by its environmental type. This species has been known to, and appeared to, consume a significant amount of detritus (Pusey *et al.* 2004, Appendix VI), which has been correlated with low fecundity (Winemiller and Rose 1992).

The coexistence of divergent life history strategies may impart benefits to populations inhabiting stable environments (populations approaching equilibrium conditions), because it may reduce competitive interactions or reduce vulnerability to predation (Kramer 1978). However, such benefits are unlikely to be important in the relatively unstable environment of the Fortescue River, as biological interactions should be minimal (Schlosser 1987a, Bayley and Li 1992). Whatever the cause, this study showed that more than one life history strategy can be successful within an environment, adding to the findings of other empirical studies (Kramer 1978, Beumer 1979, Puckridge and Drewien 1988, Winemiller 1989, Spranza and Stanley 2000).

One species that agreed with theoretical predictions was *A. graeffei*. This species was restricted to the stable (permanent) pools, and displayed the most ‘equilibrium’ life history strategy of all of the resident species. The relatively long maturation and low fecundity of this species make it poorly suited to the boom/bust dynamics of the

ephemeral sections of the catchment; hence make it the most likely candidate to suffer extinction within this river.

Limitations of the Model

The model showed relatively little separation between the protracted seasonal spawners, *L. unicolor* and *A. percoides*, and the multiple and continuous spawners, *N. erebi* and *L. aheneus* respectively. The lack of differentiation between *L. unicolor* (or *A. percoides*) and *N. erebi* occurred largely because *N. erebi* matures at a much larger size, which counteracts the reductions in fecundity that typify species that spawn multiple times in a year. The cause of the similarity between *L. aheneus* and *A. percoides* was not so clear, but difficulties associated with the determination of batch fecundity, the axis which contained the greatest amount of variation, and thereby ability to separate species, may have reduced this study's ability to separate species with different spawning seasonality. This caveat aside, it is clear that separation between strategies within the model's 3D space is relative. Using endpoints taken from Winemiller (1989) allows the life history strategies of the fish of the Fortescue to be placed within a larger context, but by doing so may reduce the separation between species' life histories. It is therefore suggested that the model should not be relied upon to indicate a species' seasonality of spawning, especially when species fall mid-way between life history endpoints. More importantly, a species' seasonality of spawning should not be used in isolation as a surrogate of its life history strategy.

The semelparous and catadromous nature of *A. bicolor* presented a special case for the model. *A. bicolor* probably spends between 10 and 25 years maturing in the Fortescue River, before it migrates into the tropical deep sea to spawn (Allen *et al.* 2002). Survival over such a long period within the Fortescue River is no doubt linked to its habitation of the most 'stable' environment within the river. However, the model identifies this species as extremely 'periodic', that is, associated with a strongly seasonal environment. While its life history traits suggest that spawning in this species is linked to some periodicity in nature, its reliance on a stable environment within the Fortescue is undeniable. Winemiller's (1992) model cannot make this link, and appears therefore, to be inappropriate for species that are semelparous, or large-scale migrators.

Another limitation of the model is that it provides only a general description of the environmental types associated with the three life history endpoints. General descriptions are open to interpretation and may introduce error. For example, an environment may seem to be 'highly stochastic' in one person's eyes, yet may be viewed as 'midway between stochastic and periodic' by another. It would be advantageous if the model could incorporate a quantitative description of the environment. Hydrologists have recognised the ecological importance of quantifying variability (frequency and magnitude of departure from central tendency) within river systems, and have taken steps to describe flow type (Poff and Ward 1989, Poff and Allan 1995, Richter *et al.* 1996, Richter *et al.* 1997, Puckridge *et al.* 1998). Puckridge *et al.*'s(1998) method can produce one summary value that could be incorporated into Winemiller's (1992) model. With the environment type objectively described, the expected outcome would be more accurately defined, and it would be easier to identify those species that depart from expectation. In this study, most fish fell between the 'opportunistic' and 'periodic' endpoints as anticipated, but they lay closer to the 'periodic' endpoint than the 'opportunistic' endpoint (endpoints quantified by the life history traits from Winemiller's 1989 study). However, it is impossible to know if the environment was more 'periodic' than initially recognised, or if the fish of the Fortescue are predisposed to have relatively 'periodic' life histories. The latter suggestion seems likely for two reasons: (1) the Fortescue River is amongst the most hydrologically variable rivers in the world (Chapter 2, Appendix I), hence it should be suited as much, if not more, to 'opportunistic' life histories as other freshwater environments; (2) all the species within the Fortescue River have relatively recent marine ancestors (Allen *et al.* 2002), and marine species are most commonly 'periodic' strategists (Winemiller and Rose 1992).

While phylogeny may account for the virtual lack of 'opportunisitic' life history strategies (excepting *M. australis*) within the hydrologically variable Fortescue River, it still leads one to question the importance of environmental stochasticity on the life history strategies of freshwater fish. For example, several groups of freshwater fish which display 'opportunisitic' life history traits, such as dwarf cichlids (Cichlidae) and killifishes (Cyprinodontidae) (Winemiller 1992), reside within relatively stable environments (Lowe-McConnell 1975). Opportunism may arise in these settings more as a function of fish size and vulnerability to predation than environmental stability.

Plasticity in Reproduction

Plasticity in reproduction was expected for species that inhabited the ephemeral section of the catchment, because offspring survival was likely to vary in space and time. As anticipated, variation in reproduction among sites was evident for all species that were monitored. Species that bred several to many times during the year (i.e. *N. erebi* and *L. aheneus*) showed considerable variation in the development of female gonads. Breeding at different times in different pools may be adaptive; however it may simply be a consequence of random variation between relatively isolated populations. Species that bred seasonally (i.e. *L. unicolor* and *A. percoides*) also spawned at different times in different pools. Not surprisingly, these species appeared to link their reproductive output with optimal conditions, that is, rainfall.

The investigation into the variance in the size and number of oocytes was not possible as too few females at an appropriate stage of development were collected. Additionally, comparisons of gonad weight (reproductive investment) in ripe fish were not undertaken, as this method is valid only if fish are at exactly the same stage of development (Bagenal 1974), which gonad development patterns suggested was unlikely. Researchers are cautioned to make careful note of the mode of development, type of fecundity, and variation in the timing of reproduction of study species before making comparisons.

Geographic Variation in Life History Traits

Information on the interrelationship between environmental stability and life history traits was also gained from comparisons of life history traits within a single species across Australia. This analysis removed some of the complication involved with the community investigation as it removes the extraneous effects of phylogeny and biology on a species' life history traits (Stearns 1976). It was predicted that fish populations within the Fortescue River would have more 'opportunistic' traits than populations in less variable river systems. Unexpectedly, many of the resident species (i.e. *L. unicolor*, *A. percoides*, *H. compressa*) showed little variation in life history traits across the country, suggesting either, that the theory is inappropriate, or that these species are strongly constrained by their genetic makeup. These species were omitted from geographic comparisons, removing the possible obfuscatory effect associated with a genetic 'straightjacket'. Comparisons with other species supported theoretical expectations. *N. erebi* occupying the northern, cyclone affected region of

the continent (Fortescue River and Northern Territory), are relative 'colonisists', compared to those inhabiting the temperate regions of Australia (South Australia and New South Wales). For example, females in the tropics mature within a year, breed several times a year, and make a smaller investment (based on gonadosomatic ratio, thought to be a correlate of fecundity, Jobling 1995) for each spawning event (Bishop *et al.* 2001, the results of this study), whereas females in temperate zones take two years to mature, breed only once a year, and make a larger investment for their single spawning (Lake 1978, Briggs 1980, Puckridge and Walker 1990). Variation also exists between the northern populations of *N. erebi*, with individuals in the more variable environment (the Fortescue River) obtaining a smaller maximum size, and maturing at a smaller size than populations in the more predictable environment (the Northern Territory). Similarly, *N. hyrtlii* within the Fortescue River are more 'opportunistic' than populations in tropical Queensland and the Northern Territory. For example, the fish in the Fortescue River are much smaller, and the ripe individual collected suggests that they have lower fecundity and larger oocytes than individuals collected elsewhere in the country (Orr and Milward 1984, Bishop *et al.* 2001).

Summary

The life history traits of the fish of the Fortescue River provide support for Winemiller's (1992) model, which relates environmental type and life history strategies at a large scale (the river system as a whole), but not at a fine-scale (habitats within the river). At a large-scale most species display strategies that fall between the 'opportunistic' and 'periodic' endpoint, reflecting the unpredictably seasonal nature of rainfall in this desert region. The relevance of 'large-scale' environmental stability is reinforced by the fact that species that display variation in life history traits across the country have more 'opportunistic' traits within the variable (unstable) Fortescue River than those in less variable (more stable) river systems. At a fine-scale, there is little correlation between species' life history traits and the stability of the pools they inhabit. This is thought to be a consequence of phylogenic constraints, the indiscrete occupation of environmental types, the intermixing of populations during flooding, and physiological rather than life history limitations on species' distributions across the catchment. Winemiller's (1992) model has certain limitations and future tests should more explicitly quantify environmental stability in relation to species' generation times.

Appendices

Appendix I ***Flow Variability of the Fortescue River***

Flow variability was assessed at one site within the western catchment of the Fortescue River, Gregory's Gorge. Gregory's Gorge is located on the main channel of the river, 18.5 km downstream of Millstream National Park, and has a catchment of 14629 km^2. Total monthly flow data (GL) were obtained from the Department of the Environment (formerly, the Water and Rivers Commission), see Table AI.1. Flow records were analysed according to Puckridge *et al.*'s (1998) methodology, which are summarised below.

1) The earliest 20 years of continuous data were used.
2) As the records contained zero flows, one was added to all monthly data, as per Puckridge *et al.* (1998). This prevented median values from being zero, allowing variability measures to be calculated, see Table A.2.
3) Twenty three measures of hydrological variability were examined for each data set. A brief description of the measures has been quoted from Puckridge *et al.*'s (1989) paper and is provided in Table A.2.
4) Hydrologic variables were incorporated with Puckridge *et al.*'s (1998) data for 52 rivers world wide (the raw data were kindly provided by J. Puckridge).
5) Data were range standardised, that is, each variable was divided by the maximum value obtained, for that variable, for all rivers. A summary median was constructed from the range standardised values for all 23 variables.

The summary median for Gregory's Gorge was 0.58, higher than Cooper's Creek (0.47) and the Diamantina (0.39) (Figure AI.1). The hydrologic descriptors in which Gregory's Gorge scored the highest value included: ANTF, FALA, RSAM, RSRT, FLRT, and PEAK. Apart from ANTF, all of these measures were related to the variance in the rising and falling limbs of the hydrograph. Flow at Gregory's Gorge went up and down more times than at Cooper's Creek, and there was greater variance in the amplitude of the peaks and troughs. This is probably caused by the greater number of sources of rainfall for this river, and their variance in magnitude.

Table I.1. Total monthly discharge (GL) and annual discharge for Gregory's Gorge from 1969 to 1988. Data are courtesy of the Department of the Environment.

Yr.	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Annual
1969	0.000	1.111	0.045	0.000	0.078	0.438	0.516	0.380	0.208	0.030	0.000	0.000	2.806
1970	0.000	12.552	0.793	0.071	30.952	22.172	0.423	0.340	0.260	0.051	0.000	0.000	67.615
1971	26.679	336.417	4.936	1.280	0.326	115.878	0.925	0.844	0.367	0.103	0.000	0.000	487.755
1972	0.757	4.904	0.726	0.000	0.000	0.000	0.405	0.467	0.092	0.000	0.000	0.000	7.351
1973	120.14	1.613	219.665	1.055	0.503	0.925	0.615	0.592	0.176	0.002	0.000	1.193	346.479
1974	102.185	12.458	0.424	0.308	0.493	0.561	0.638	0.716	0.841	0.029	0.000	4.292	122.945
1975	0.098	0.046	0.061	0.069	0.000	0.000	0.000	0.117	0.014	0.000	0.000	1180.932	1181.337
1976	20.400	6.783	66.956	0.576	0.349	0.379	0.431	0.362	0.165	0.059	0.002	0.188	96.480
1977	0.184	0.664	0.042	0.000	0.000	0.000	0.620	4.886	0.253	0.000	0.000	0.289	6.938
1978	2.682	0.594	0.811	0.440	0.054	0.138	0.269	4.518	0.217	0.012	0.000	0.000	9.736
1979	0.040	1.647	11.651	0.022	0.063	0.002	0.000	0.000	0.000	0.000	0.000	0.516	13.938
1980	33.609	8.107	1.111	0.371	0.017	1.364	2.798	0.141	0.002	0.000	0.000	0.259	47.780
1981	51.932	103.972	3.425	0.388	1.229	0.279	0.180	0.058	0.001	0.000	0.000	2.587	164.051
1982	0.001	0.245	0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.247
1983	3.841	7.063	572.316	0.568	3.305	0.466	0.557	0.398	0.104	0.006	0.000	0.048	588.672
1984	6.026	192.003	1.327	0.364	0.240	0.110	0.156	0.086	0.003	0.000	0.000	0.000	200.315
1985	0.000	1.848	0.034	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.882
1986	2.345	21.761	1.290	4.295	3.093	0.390	0.306	0.221	0.033	0.000	0.000	1.248	34.982
1987	0.688	1.874	1.352	7.364	0.304	39.886	0.493	0.340	0.180	0.009	0.000	0.000	52.490
1988	0.000	0.479	0.437	0.004	0.000	0.000	0.264	0.309	0.050	0.001	0.000	0.000	1.544

Table I.2. Measures of hydrological variability, from Puckridge *et al.* (1998), and values obtained from analysis of 20 years of flow data from two sites of the Fortescue River, Gregory's Gorge. Variability is calculated as (range/median)*100. I have included additional descriptions to aid understanding; these are provided after NB headings. *=measures which were greater than those recorded for all rivers as measured by Puckridge *et al.* (1998).

Code	Flow variability measure	Greg.
ASKEW	((Mean – median)/median) of all annual flows	2.43
ANTF	Variability between years of each year's variability between months	4644.0*
ATOT	Variability of all annual flows	1900.8
FALA	Variability of amplitude of all falling limbs	41656.4*
FIVE	Variability of sums of every five year's total annual flows NB. The sums are continuous over time, that is, the first five years for a data set starting from 1970 would be; 1970+71+72+73+74, the second would be 1971+72+73+74+75. Also include the sum of the last 4 years. This seemingly erroneous addition was replicated to ensure compatibility with Puckridge *et al.*'s data	212.6
FLDR	Variability of the duration of all falling limbs (for zero flows, duration calculated to end of continuous zero flows). NB. The results from FALA were divided by the number of months that the flow was falling.	166.6
PSFR	Variability of number of pulses (peak to peak or trough to trough) in each year	100
FLRT	Variability of discharge fall per month for all falling limbs NB. For each falling limb, discharge fall per month was determined by dividing the amplitude of the falling limb by the number of months that flow was falling (zero flows ignored). For example, if the monthly values were 562, 302, 133, 11, 375, then the amplitude of the fall 551 was divided by 4 to give an average monthly fall for that limb of 137.75. Variability was determined by comparing all falling limbs.	33495.4*
LSEA	Inverse of variability between months of number of pulse troughs in each month	0.0042
MDAN	Median between years of each year's variability between months	2468.3
MDMF	Median between months of each month's variability between years NB. Determine the variability of each month (i.e. Jan, Feb..etc) across years, and then determine the median of these values.	1610.8
MSKEW	((Mean – median)/median) of all monthly flows NB. Examine all data values at once.	77.6
MNTF	Variability between months of each month's variability between years NB. The same as MDMF except determine the variability rather than the median.	7262.9
MTOT	Variability of all monthly flows NB. Sum all values for each month. Determine the variability of these values.	2426.9
PEAK	Variability of all peak discharges NB. There was some controversy surrounding the determination of peak and trough flows. Richter *et al.* (1996) describes high pulses as "those periods during which water levels rise above the 75th percentile" and low pulses as "drops in water levels below the 25th percentile". However, Puckridge *et al.* (1989) did not provide a definition, and examination of their raw data suggested that any local maximum or minimum of water flow was used as a peak or trough.	38698*
PSEA	Inverse of variability between months of number of pulse peaks in each month NB. The number of pulse peaks in January, Feb…etc were tallied and their variability assessed.	0.0029
RSAM	Variability of amplitude of all rising limbs NB. A rising limb was defined as an increase in flow over time.	42804.4*
RSDR	Variability of duration of all rising limbs	200

Code	Flow variability measure	Greg.
	NB. See FLRT.	
RSRT	Variability of discharge rise per month of all rising limbs	49011.9*
	NB. See FLRT.	
SEVN	Variability of sums of every seven year's total annual flows	174.9
	NB. Follow guidelines as per FIVE, however include the sum of the last six years. This seemingly erroneous addition was replicated to ensure compatibility with Puckridge *et al.*'s data.	
THRE	Variability of sums of every three year's total annual flows	316.0
	NB. Follow guidelines as per FIVE, however include the sum of the last two years plus the total annual flow of all years (i.e. 20). This seemingly erroneous addition was replicated to ensure compatibility with Puckridge *et al.*'s data.	
TRGH	Variability of all minimum discharges	678.3
ZEROF	% of all months in record with zero flow	28.7

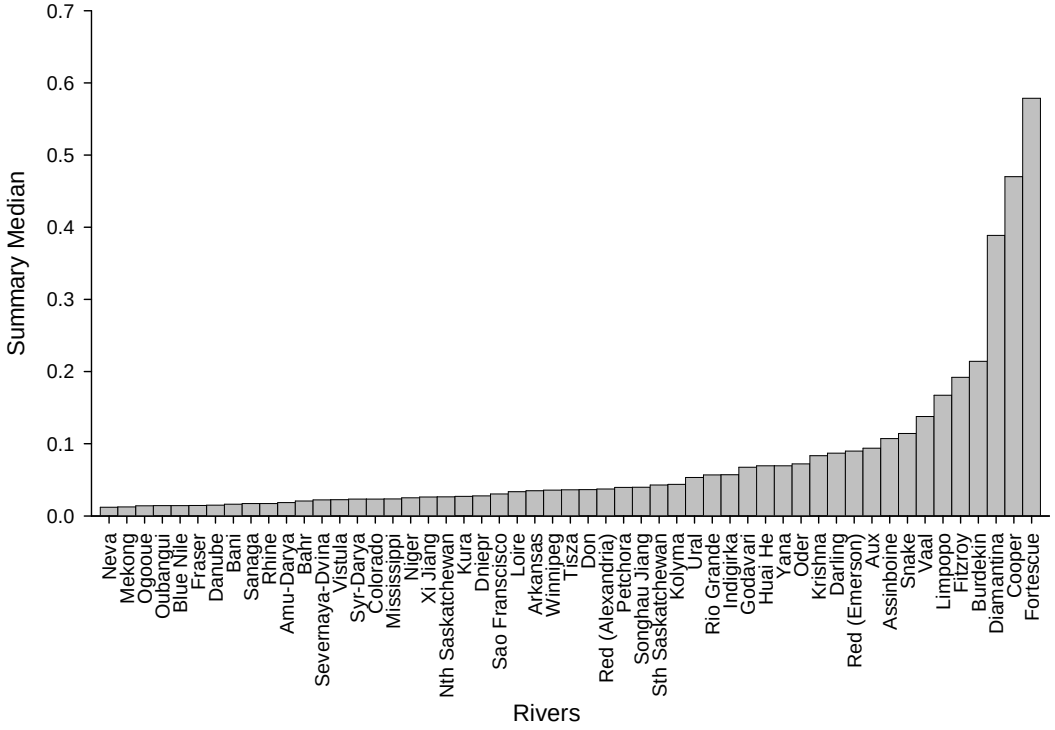


Figure I.1. Summary medians for each river of range standardised hydrological measures. All data used in this figure, except for data on the Fortescue River, are from Puckridge *et al.* (1998).

References

Puckridge, J.T., Sheldon, F., Walker, K.F. and Boulton, A.J. (1998) Flow variability and the ecology of large rivers. *Marine and Freshwater Research* **49**: 55-72.

Appendix II **Fish Collected with the Drop-net**

Table II.1. The number (abundance) of individuals of each species collected during each deployment of the drop-net from each of the focal pools at each of the sampling dates (April 2001 to August 2002). All size classes are included, estuarine species have been omitted.

Site	Date	Drop #	*A. graeffei*	*A. percoides*	*G. giurus*	*H. compressa*	*L. ahenaeus*	*L. unicolor*	*M. australis*	*N. erebi*	*N. hyrtlii*
Palm	Apr 01	1	0	0	0	0	0	0	2	15	0
		2	0	2	4	0	0	0	10	12	0
		3	0	0	5	0	9	0	7	7	0
		4	0	0	0	0	0	0	3	9	0
	Aug 01	1	0	0	9	0	0	0	6	0	0
		2	0	1	7	0	7	0	1	24	0
		3	0	1	4	0	1	0	1	15	0
		4	0	0	1	0	0	0	0	11	0
		5	0	8	7	0	12	1	2	4	0
		6	0	0	0	0	1	0	0	6	0
	Dec 01	1	0	4	37	0	12	0	62	1	0
		2	0	2	52	0	59	1	57	1	0
		3	0	2	31	0	22	0	2	6	0
		4	0	5	22	0	3	0	58	6	0
		5	0	7	3	0	3	0	97	27	0
	Apr 02	1	0	14	54	0	36	1	2	4	0
		2	0	9	47	0	32	0	27	2	3
		3	0	3	38	0	5	0	14	38	0
		4	0	1	7	0	20	0	73	6	0
		5	0	1	3	0	6	0	44	16	0
		6	0	0	7	0	9	0	75	16	0
	Aug 02	1	0	2	22	0	13	0	16	0	0
		2	0	0	33	0	4	0	11	2	0
		3	0	0	43	0	15	0	2	0	0
		4	0	0	16	0	2	0	0	0	0
		5	0	1	8	0	3	0	4	0	0
Bilanoo	Apr 01	1	0	0	0	0	0	0	0	22	0
		2	0	1	0	0	2	0	0	2	0
		3	0	5	4	11	11	0	1	1	1
		4	0	5	0	0	1	0	0	0	0
		5	0	0	0	0	0	0	0	7	1
		6	0	1	1	1	11	0	1	0	1
	Aug 01	1	0	0	1	0	0	0	0	0	0
		2	0	1	0	0	0	0	0	0	0
		3	0	1	0	0	0	0	0	0	0
		4	0	6	0	0	2	0	0	1	0
		5	0	5	0	0	9	0	2	0	0
		6	0	16	5	8	3	0	1	4	0
		7	0	0	0	0	0	0	0	0	0
		8	0	0	1	0	0	0	0	1	0
		9	0	4	0	0	2	0	0	6	0
	Dec 01	1	0	1	4	0	2	0	1	3	0
		2	0	2	12	0	4	0	0	0	0
		3	0	4	2	0	1	0	0	0	0
		4	0	1	3	8	2	0	0	16	0
		5	0	26	11	0	0	1	21	0	0
		6	0	3	6	13	3	0	5	0	0
		7	0	2	7	0	5	0	0	2	0
Bilanoo	Dec 01	8	0	4	8	0	2	0	31	0	0

Site	Date	Drop #	*A. graeffei*	*A. percoides*	*G. giurus*	*H. compressa*	*L. aheneus*	*L. unicolor*	*M. australis*	*N. erebi*	*N. hyrtlii*
cont.	Cont.										
	Apr 02	1	1	14	12	0	19	0	11	86	0
		2	1	0	12	0	0	0	0	6	0
		3	1	0	1	0	0	0	0	20	0
		4	0	8	6	2	8	1	17	0	0
		5	5	1	3	0	0	0	0	164	0
		6	1	0	0	0	0	0	0	0	0
		7	0	8	14	3	1	2	14	1	0
		8	0	9	10	0	10	2	5	0	0
	Aug 02	1	0	0	11	0	2	0	0	0	0
		2	0	0	3	0	0	0	0	13	0
		3	0	2	23	0	1	0	1	0	0
		4	0	0	11	65	18	0	32	0	0
		5	0	1	10	27	2	1	4	0	4
		6	3	0	0	0	0	0	0	24	0
		7	0	2	7	8	2	0	0	0	0
		8	0	0	7	1	2	0	0	0	0
		9	0	1	3	18	14	1	4	0	0
Mallina	Apr 01	1	0	3	0	0	0	8	312	9	1
		2	0	13	0	0	0	14	59	42	0
		3	0	16	0	0	0	47	74	23	0
		4	0	8	0	0	0	7	201	2	0
	Aug 01	1	0	1	0	0	0	0	1	0	0
		2	0	7	0	0	0	0	0	1	0
		3	0	6	0	0	0	8	113	1	0
		4	0	1	0	0	0	0	10	0	0
		5	0	9	0	0	0	5	25	0	0
		6	0	15	0	0	0	4	27	3	2
		7	0	18	0	0	0	5	403	95	0
		8	0	5	0	0	0	3	6	0	0
	Dec 01	1	0	9	0	0	0	6	10	1	0
		2	0	9	0	0	0	4	6	2606	0
		3	0	21	0	0	2	4	12	2	0
		4	0	8	0	0	0	16	39	108	0
		5	0	8	0	0	0	8	21	39	1
	Apr 02	1	0	12	0	0	0	10	1	19	1
		2	0	21	1	0	0	3	3	14	0
		3	0	13	0	0	0	7	28	7	1
		4	0	16	1	0	0	4	36	82	0
		5	0	13	1	0	0	11	29	29	1
		6	0	15	18	0	0	10	21	210	4
		7	0	7	2	0	0	6	4	44	7
	Aug 02	1	0	4	0	0	0	3	0	3	1
		2	0	36	0	0	0	5	0	67	2
		3	0	7	1	0	0	4	1	3	2
		4	0	17	1	0	0	7	9	4	1
		5	0	13	0	0	0	4	12	0	10
Hooley	Apr 01	1	0	9	5	0	0	37	12	6	3
		2	0	5	1	0	0	6	7	1	0
		3	0	11	3	0	0	25	7	6	2
		4	0	1	0	0	0	7	8	1	0
	Aug 01	1	0	0	0	0	0	0	0	0	0
		2	0	0	0	0	0	0	0	0	0
		3	0	0	0	0	0	0	0	0	0
		4	0	0	0	0	0	0	0	0	0
Hooley	Dec 01	1	0	23	6	0	1	37	23	4	0

Site	Date	Drop #	*A. graeffei*	*A. percoides*	*G. giurus*	*H. compressa*	*L. aheneus*	*L. unicolor*	*M. australis*	*N. erebi*	*N. hyrtlii*
Cont.											
		2	0	22	3	0	3	48	33	11	0
		3	0	19	7	0	4	40	8	0	0
		4	0	11	0	0	10	31	37	2	7
	Apr 02	1	0	1	1	0	0	9	36	185	0
		2	0	0	2	0	0	15	44	8	0
		3	0	6	2	0	2	17	23	45	0
		4	0	0	3	0	0	6	5	0	1
		5	0	0	6	0	1	12	15	44	1
		6	0	1	4	0	1	8	24	45	0
Portland	Apr 01	1	0	9	0	0	0	1	20	2	0
		2	0	1	2	0	0	0	27	0	0
		3	0	5	6	0	0	12	11	9	0
		4	0	3	1	0	0	2	10	5	0
	Aug 01	1	0	1	6	0	1	0	7	1	0
		2	0	0	1	0	0	0	0	0	0
		3	0	4	2	0	1	0	0	0	0
		4	0	1	3	0	0	1	16	0	0
		5	0	2	1	0	1	1	3	1	0
		6	0	6	7	0	0	0	0	0	6
	Dec 01	1	0	30	36	0	0	3	329	155	0
		2	0	5	17	0	1	2	117	98	0
	Apr 02	1	0	0	0	0	0	3	6	0	0
		2	0	2	0	0	0	52	1	0	0
		3	0	1	0	0	0	56	9	0	0
		4	0	4	0	0	0	41	0	0	0
		5	0	0	2	0	0	27	3	0	0
		6	0	18	0	0	0	103	8	0	0
		7	0	3	0	0	0	69	13	0	0
		8	0	0	0	0	0	23	0	0	0
	Aug 02	1	0	31	1	0	7	54	17	2	0
		2	0	44	5	0	1	37	0	0	0
		3	0	3	1	0	0	7	2	2	0
		4	0	0	13	0	0	2	1	3	0
		5	0	19	4	0	0	35	9	0	0
		6	0	0	3	0	0	5	0	0	0
		7	0	18	0	0	5	20	20	0	0
		8	0	17	0	0	1	23	0	0	0
Rail-bridge	Apr 01	1	0	0	0	0	0	9	1	0	0
		2	0	0	0	0	0	10	7	0	1
		3	0	0	0	0	0	8	0	0	1
	Aug 01	1	0	0	0	0	0	123	9	0	
		2	0	0	0	0	0	94	7	0	0
		3	0	0	0	0	0	19	110	0	0
		4	0	0	0	0	0	67	32	0	1

Appendix III **Age Estimation of Fishes**

Introduction

Size is a poor indicator of age in fish, especially in adult fish (Pawson 1990). Most researchers use periodic markings within the bones of fish to age them. For example, fish that inhabit temperate environs undergo periods of high (summer) and low (winter) growth each year, creating annual marks (band) in their bones. The inner-ear bones of fish, the otoliths, are preferentially used in age studies because they grow daily and are not reabsorbed during periods of stress or low growth (Jones 1992). Banding patterns (e.g. annual bands) must be validated because it is possible that fish lay down more than one band each year, for example if their growth slows during reproduction. Validation is commonly achieved by staining fishes' otoliths *in vivo* with a fluorescent dye, and recapturing the marked individuals one year later (Geffen 1992). The presence of one annual band during this period provides positive support for the method.

This study made two attempts to validate annual-banding in the fishes of the Fortescue River. The first method involved marking otoliths in the field and attempting to re-catch the fish one year later. The second method involved marking the otoliths of fish held in aquaria. This method was established in recognition of the potential difficulties involved with the mark and recapture of field animals.

Methods

Otoliths were marked *in vivo* using the fluorescent dye, tetracycline hydrochloride. Two techniques of assimilation were used depending on the size of the fish. For large fish (>5 cm), the dye was dissolved in a solution of saline and injected into the coelom of fish at a concentration of 0.05 mg/g. Small fish (2-3 cm) were immersed in a solution of tetracycline hydrochloride (280 mg/L) for 24 hrs (Brooks *et al.* 1994). The holding container was shaded from sunlight as the dye is known to be light-sensitive (Geffen 1992). Large fish were also marked externally so that they could be recognised. This involved injecting a small amount of fluorescent elastomer (VIE tags, North West Marine Technology) under the dermis. Laboratory trials revealed that all of these procedures had minimal impact on fish survival, adversely affecting <5% of experimental animals. Prior to all injections, the fish were anaesthetised in a solution of clove oil (40 ppm).

Field validation took place at three sites (Railbridge Pool in August 2001, Hooley Pool in December 2001 and Portland Pool in April 2002). Relatively small pools were chosen for the validation experiment to maximise the chance of recapture. Species tagged included: *Leiopotherapon unicolor* (n= 644) and *Amniataba percoides* (n= 265). *Nematalosa erebi* and *Melanotaenia australis* were not tagged as these species were sensitive to removal from water, and experimental procedures would have generated unacceptable mortality. Tagged fish were placed into cages and held within the pool for 24 h to allow them to recover and to gauge mortality. The field study reported low mortality (<5%), in agreement with preliminary laboratory trials. One fish was sacrificed and its otolith retained to confirm that the procedure had been effective. All other fish were released into the pool.

The laboratory validation experiment was conducted using 20 *L. unicolor*. These fish had been translocated from the Murchison River, Western Australia, to The

University of Western Australia's grounds (Perth, Western Australia) several years earlier. Fish ranged in size from 5.7 to 16.0 cm, and were marked according the procedure outlined above. Fish were given a unique tag and were distributed amongst four aquaria. Temperature within the aquaria was altered through the year to mimic the conditions of the pools of the Fortescue River. Fish were fed *ad libitum*, once a day, six days a week. The experiment commenced in late July 2002 and ran until October 2003.

Recaptured fish, and laboratory individuals at the end of the study, were anaesthetised, sacrificed, and their sacculus otoliths removed. Otoliths were dried, placed into eppendorfs and kept in a dark, air-conditioned space.

Otoliths were attached to the end of microscope slide using crystal bond heat sensitive glue. They were ground down towards the nucleus using wet emery paper. The slide was heated and the otolith was rotated 90º and glued nucleus side down on the centre of the slide and polished again. Once the section was a thin slither it was polished using lapping film, and examined under dissecting and compound microscopes for band (age) determination.

During the reading of bands, the distance between the opaque band (as opposed to the translucent) and the edge of the otolith was noted. As it was predicted that bands were formed seasonally, the distance between the band (i.e. winter) and the edge of the otolith was used as another source of affirmation. This technique, termed marginal increment analysis is often used to validate annual bands when marking is not possible.

Results and Discussion

Field Validation

The field mark-recapture experiment failed to validate annual-band formation. This was because no fish were captured a year after they had been tagged with tetracycline. The failure to recapture fish was due to the small amount of rain that fell during the summer of 2001/02, which meant that the small pools used to conduct the validation in mostly dried before the year was up. For example, Railbridge and Hooley pool dried completely before any marked fish could be collected. Several tagged fish were collected from Hooley Pool in March of 2002 (3.5 months after tagging). At Portland Pool the late date of tagging (i.e. April 2002) meant that no fish from this pool were collected one year later as the study had ceased (note the pool dried over the summer of 2002/03, anyway).

Examination of the few fish collected from Hooley Pool after three months supported the idea that bands of low growth were laid down during the winter months (see Plate lll.1). That is, the band of low growth was deposited before the tetracycline injection (in December) and growth remained high until the fish was collected in March (i.e. high growth over the summer).

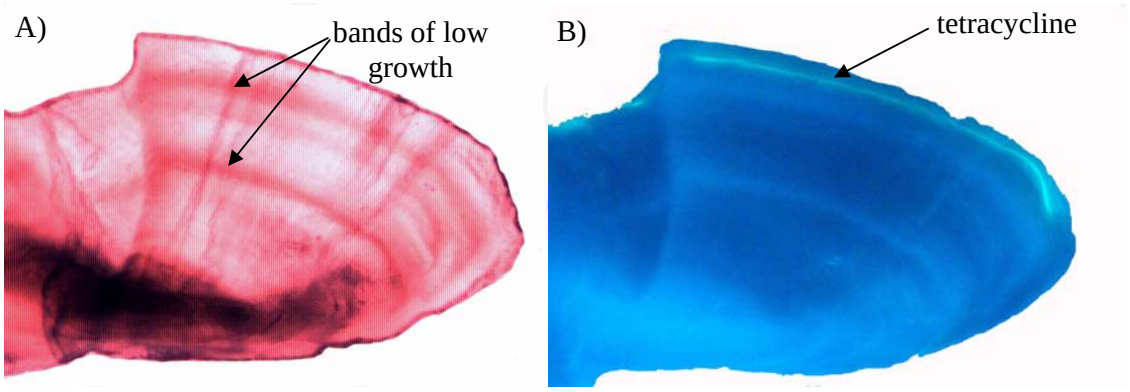


Plate III.1. Cross section of the otolith of *A. percoides* from Hooley Pool that was injected with tetracycline in December 2001 and re-captured in March 2002 (3.5 months later). (A) the otolith viewed under normal light showing bands of low growth, (B) the otolith viewed under ultra-violet light, showing the location of the band of tetracycline.

Laboratory Validation

The laboratory experiment did not validate annual-band formation. For while bands were clear in the fish kept in the ponds in Perth (see Plate III.2.A), there was no sign of a band being laid down during the year they were kept in aquaria (see Plate III.2.B). The *ad libitum* diet which would have been unlikely in the ponds may have kept growth rate high the year round removing the annual band.

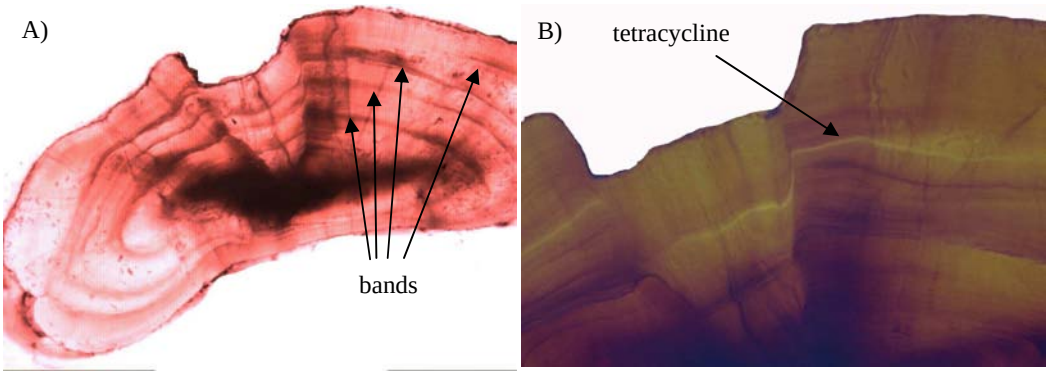


Plate III.2. Laboratory validation experiment. (A) A *L. unicolor* from Shenton Park showing clear banding patterns. (B) A *L. unicolor* from Shenton Park which was injected with tetracycline and held in an aquaria for 13 months. Note that there is no band between the tetracycline mark and the edge of the otolith indicating that changes in temperature alone (in the aquaria) were not able to produce a band in *L. unicolor*.

Banding of otoliths in field fishes

Although the validation of annual-banding was not successful the otoliths of fish collected in the field ($n \approx 300$) were examined. Banding appeared to be associated with seasonal patterns in temperature, as fish collected in December had a smaller margin to the band of slow growth than those collected in April. This result supported the findings of the one A. *percoides* collected 3.5 months after injection with

tetracycline. Sectioning a great number of fish revealed that while distinct bands occurred in some fish (see Plate III.3.A,B) banding patterns were not as clear in others (see Plate III.3.C,D). So, while bands appear to be caused by seasonal changes in water temperature, other factors may cause banding. Researchers are reminded that environmental conditions, which affect growth rate, can vary considerably among pools and may disrupt the relationship between time and number of bands. Further work needs to be done to resolve the matter.

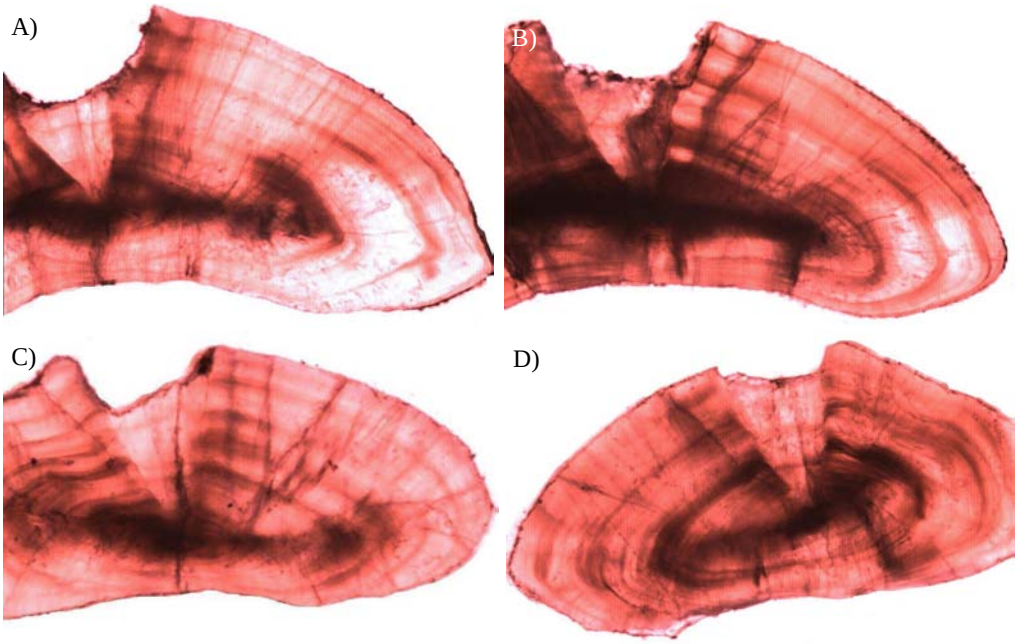


Plate III.3. Cross sectioned otoliths of *L. unicolor* viewed under a light microscope. (A) Fish from Mallina Pool fork length 22.9cm collected in August 2002, (B) Fish from Mallina Pool fork lenth 19.8 cm collected in August 2002, (C) Fish from Hooley Pool fork length 8.0 cm collected in April 2001, (D) Fish from Railbridge Pool fork length 13.6 cm collected in April 2001. Photos are not to scale.

References

Brooks, R.C., Heidinger, R.C. and Kohler, C.C. (1994) Mass-marking otoliths of larval and juvenile walleyes by immersion in oxytetracycline, calcein, or calcein blue. *North American Journal of Fisheries Management* **14**: 143-150.

Geffen, A.J. (1992) Validation of otolith increment deposition rate. *Canadian Journal of Fisheries and Aquatic Sciences* **117**: 101-113.

Jones, C.M. (1992) Development and application of the otolith increment technique. *Canadian Journal of Fisheries and Aquatic Sciences* **117**: 1-11.

Pawson, M.G. (1990) Using otolith weight to age fish. *Journal of Fish Biology* **36**: 521-531.

Appendix IV *Size Frequency Distributions*

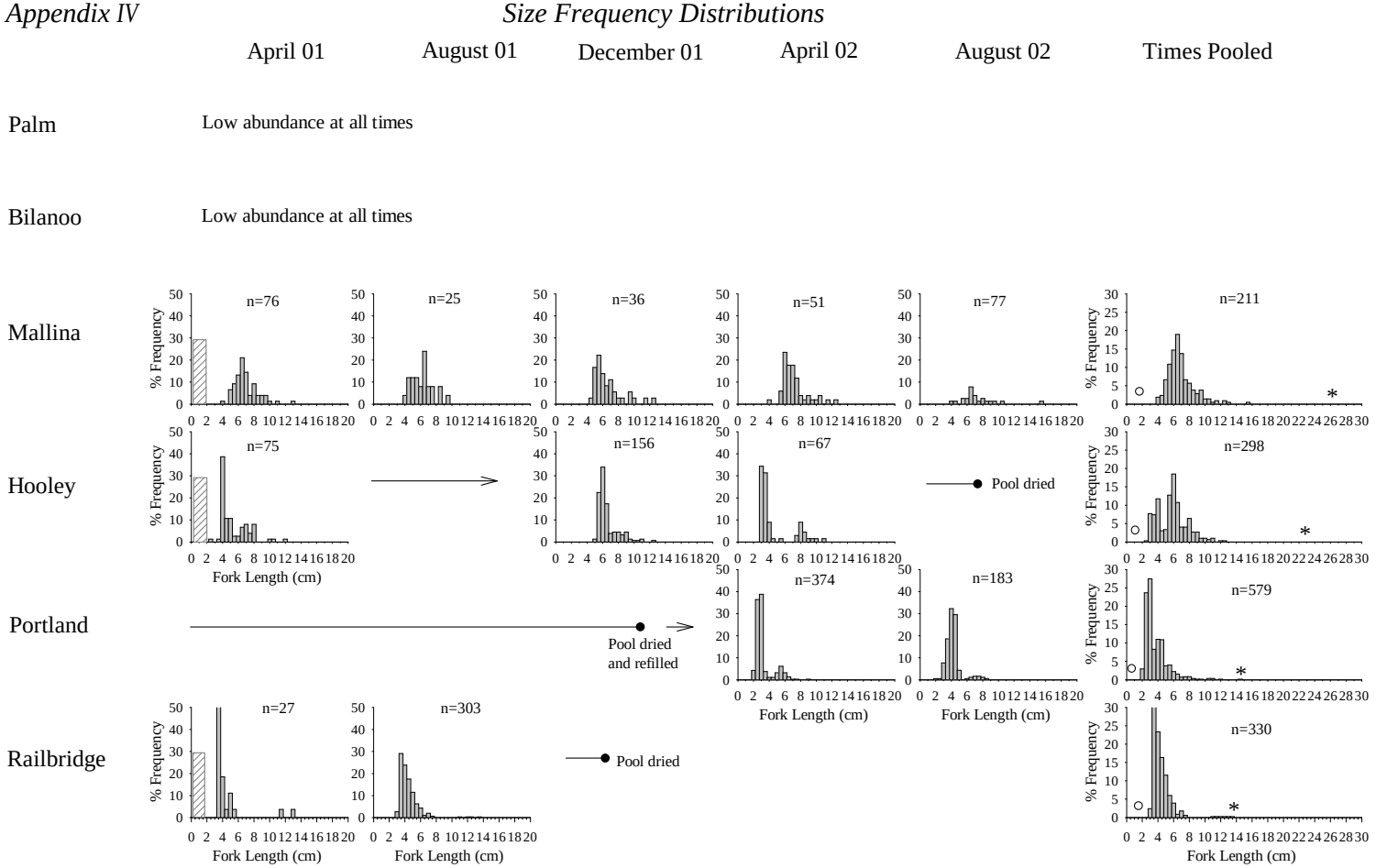


Figure IV.1. *Leiopotherapon unicolor* size frequency (%) distributions. Fish size was measured using fork length (cm). Graphs are shown for the six study sites over the five sampling dates and have been pooled for all dates. When abundance was low (<20 fish) no graph is shown. Lines ending with arrows were used to show persistence of a pool when fish abundance was low, and a line ending in a stop indicated when a pool dried. The maximum (*) and minimum (o) size classes of fish collected at a site are shown, together with the sample size (n). The size frequency distributions were constructed using fish collected with the drop-net. Gill nets and light trap data was only included to extend the size range. Size classes < 2 cm in April 2001 were hashed out as the larger mesh used on the drop-net at this time failed to collect these size classes.

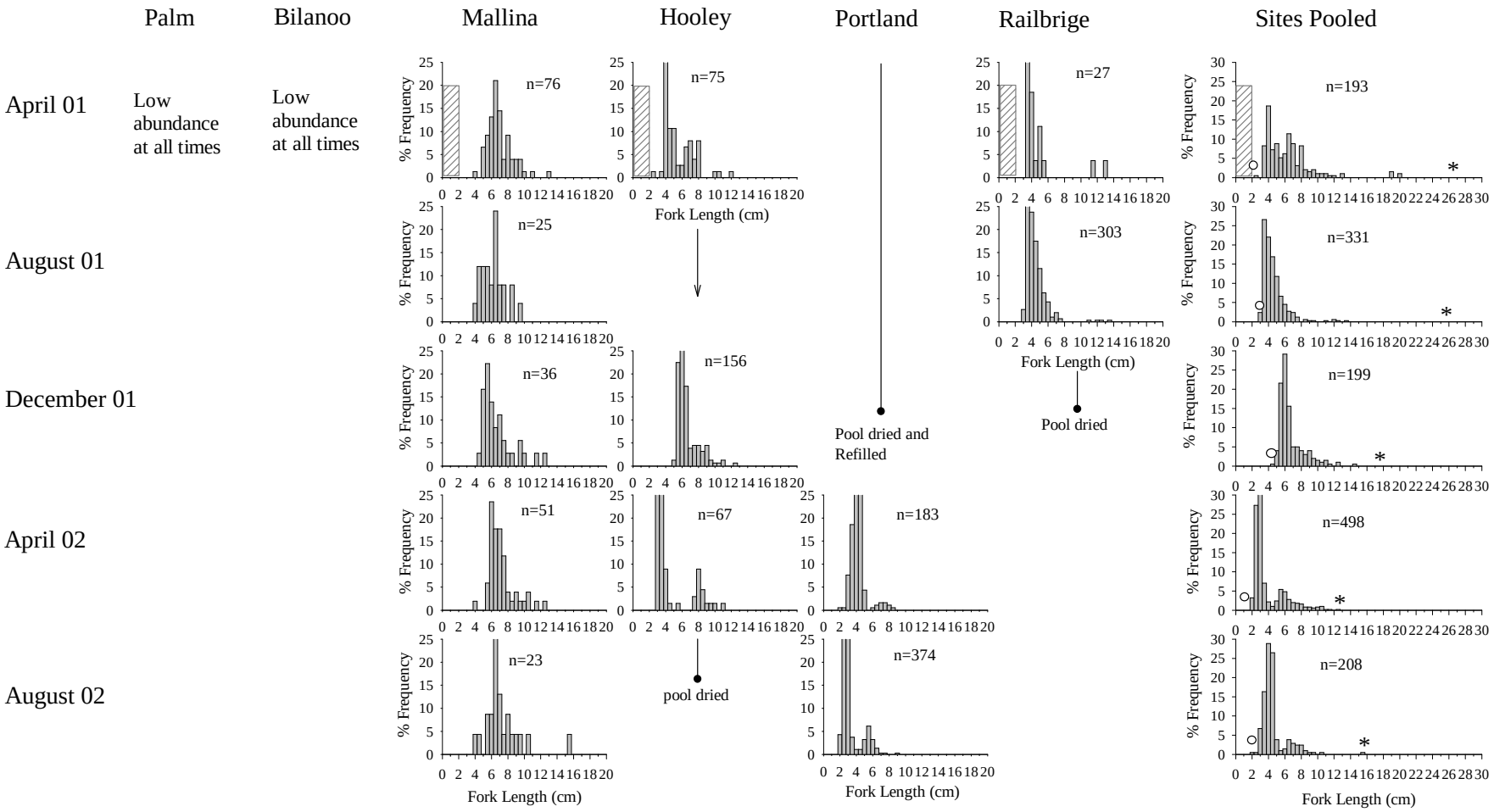


Figure IV.2. *L. unicolor* size frequency (%) distributions. Fish size was measured using fork length (cm). Graphs are shown for the five sampling dates over the six study pools, and have been pooled for all sites. For all other details refer to Figure IV.1.

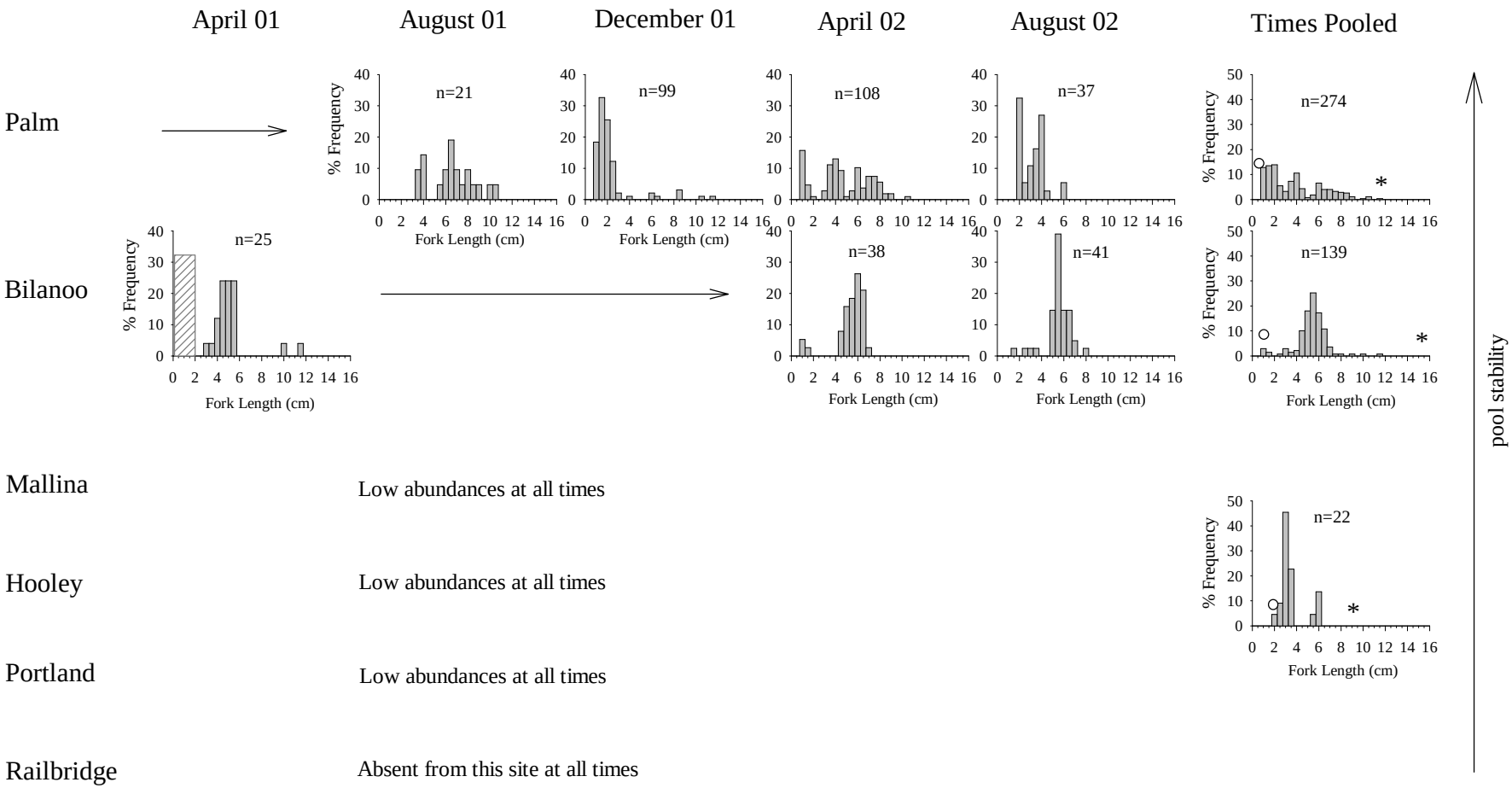


Figure IV.3. *Leiopotherapon aheneus* size frequency (%) distributions. Fish size was measured using fork length (cm). Graphs are shown for the six study sites over the five sampling dates and have been pooled for all dates. For all other details refer to Figure IV.1.

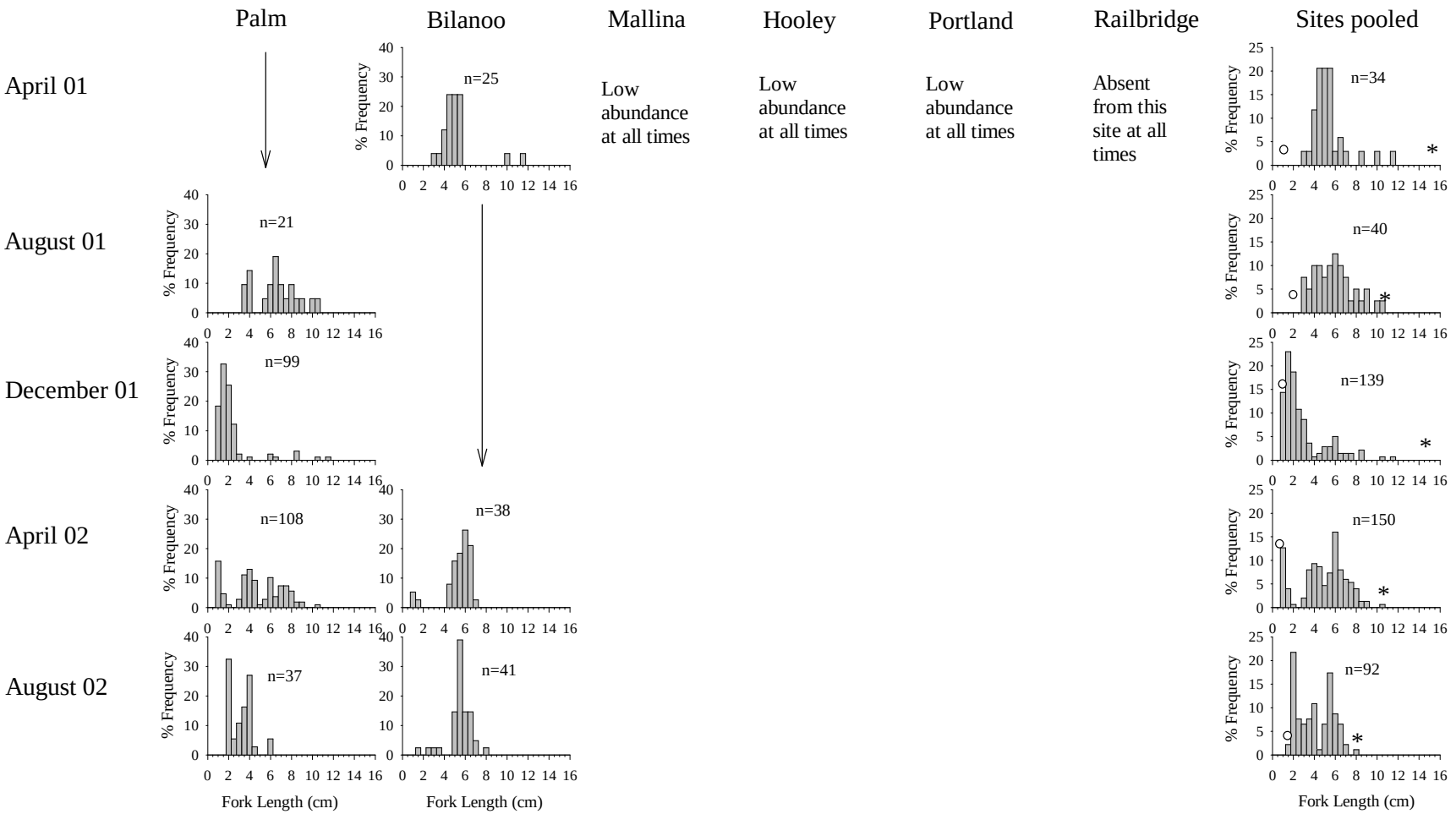


Figure IV.4. *L. aheneus* size frequency (%) distributions. Fish size was measured using fork length (cm). Graphs are shown for the five sampling dates over the six study pools, and have been pooled for all sites. For all other details refer to Figure IV.1.

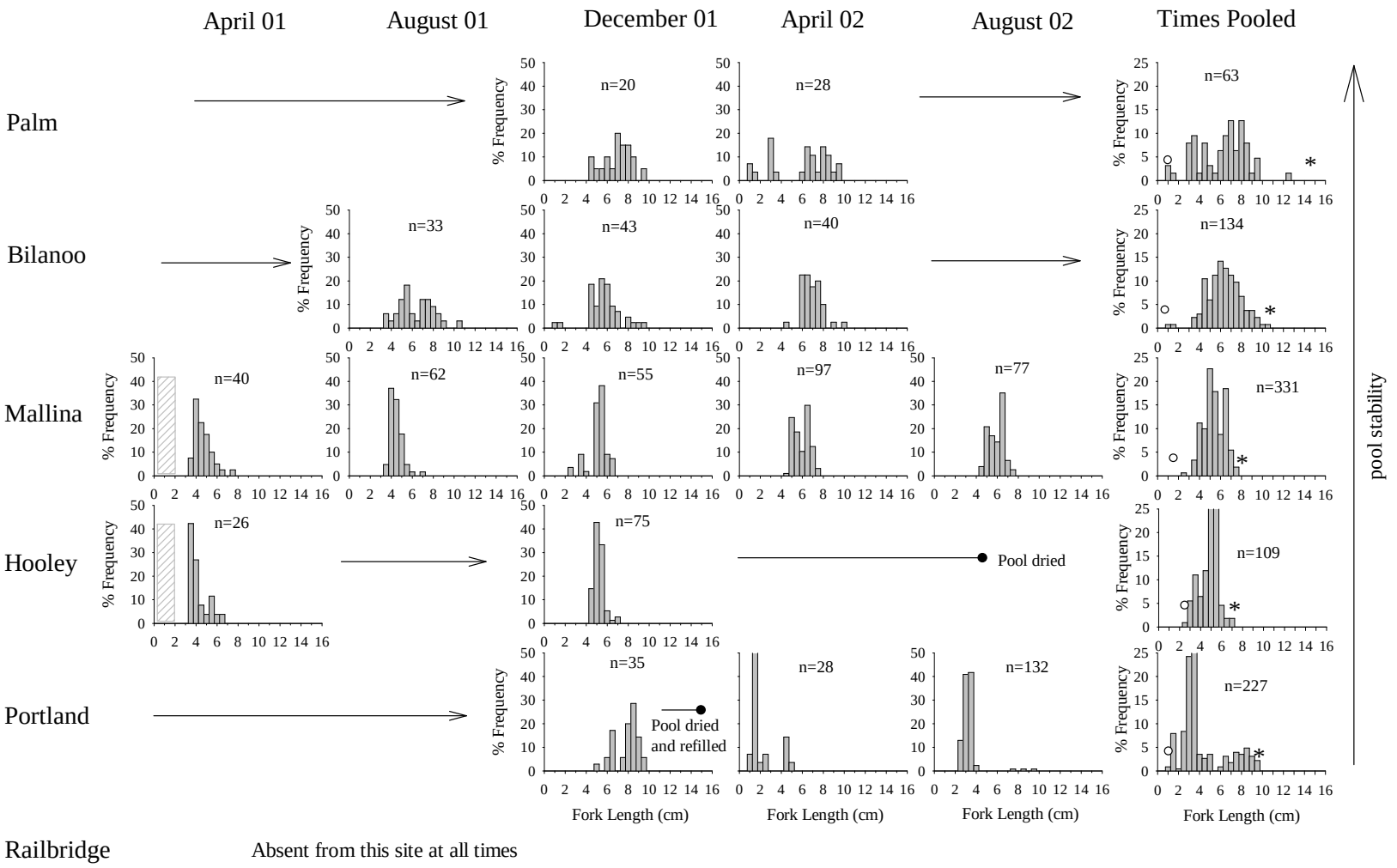


Figure IV.5. *Amniataba percoides* size frequency (%) distributions. Fish size was measured using fork length (cm). Graphs are shown for the six study sites over the five sampling dates and have been pooled for all dates. For all other details refer to Figure IV.1.

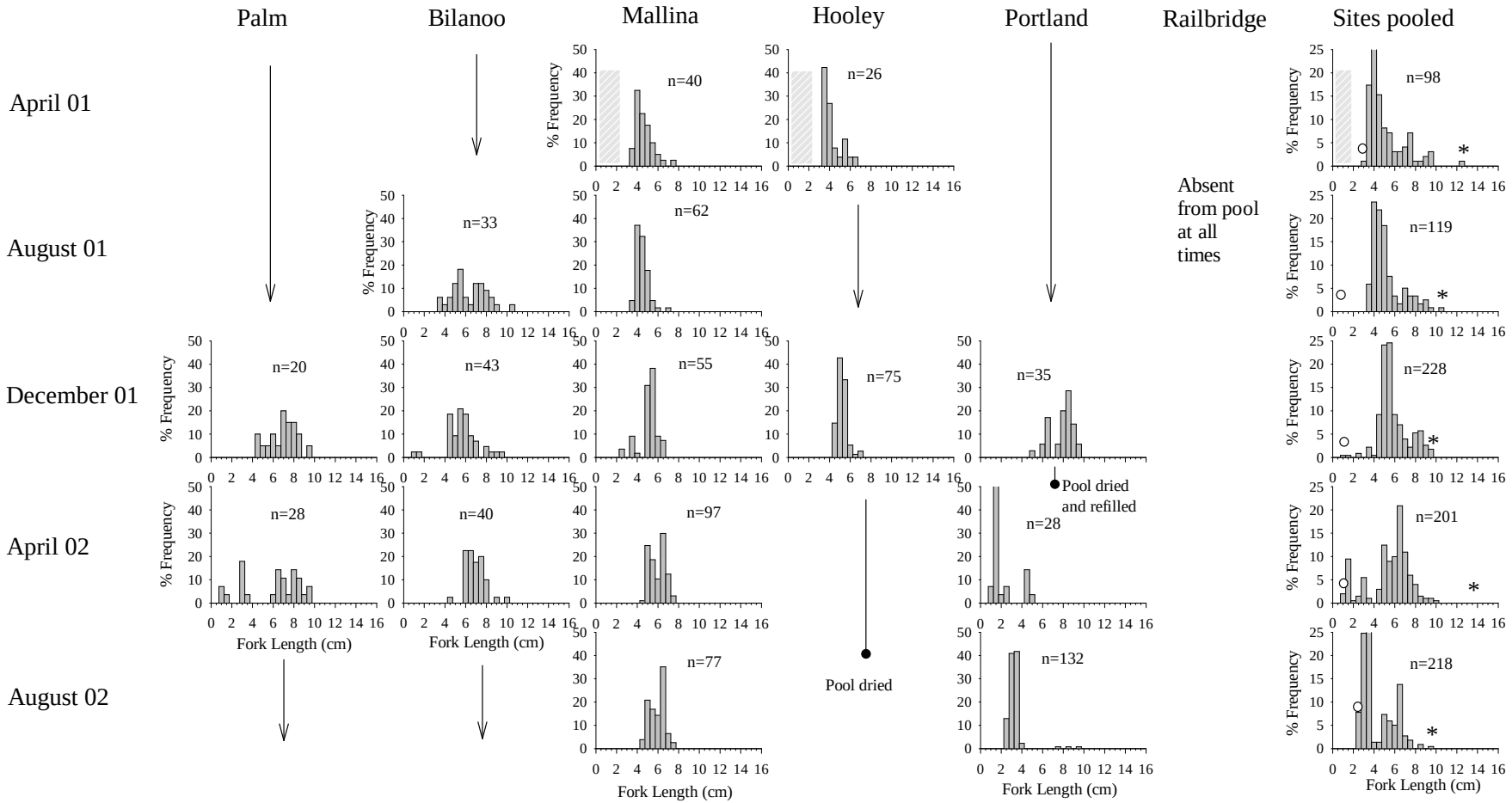


Figure IV.6. *A. percoides* size frequency (%) distributions. Fish size was measured using fork length (cm). Graphs are shown for the five sampling dates over the six study pools, and have been pooled for all sites. For all other details refer to Figure IV.

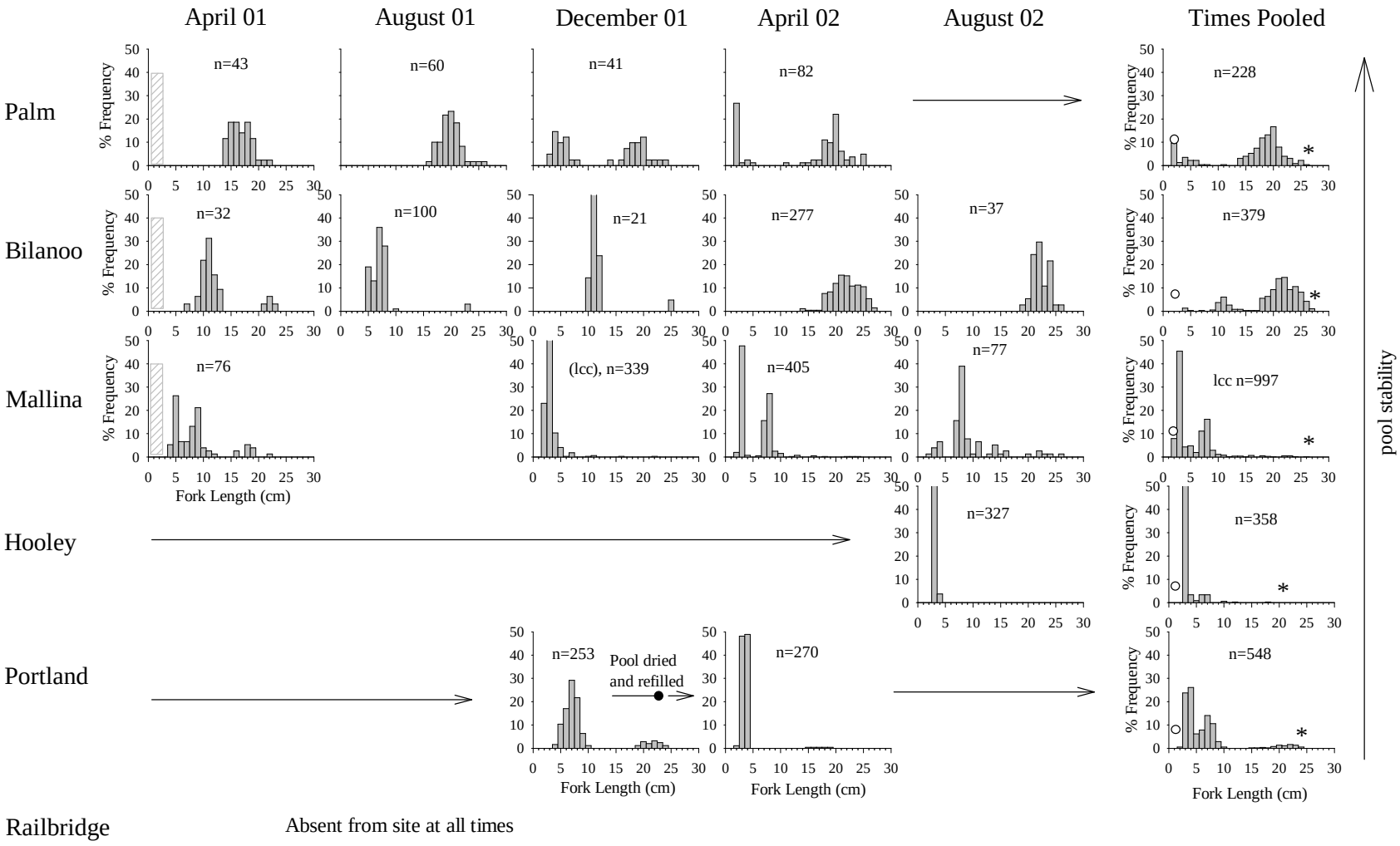


Figure IV.7. *Nematalosa erebi* size frequency (%) distributions. Fish size was measured using fork length (cm). Graphs are shown for the six study sites over the five sampling dates and have been pooled for all dates. . For all other details refer to Figure IV.

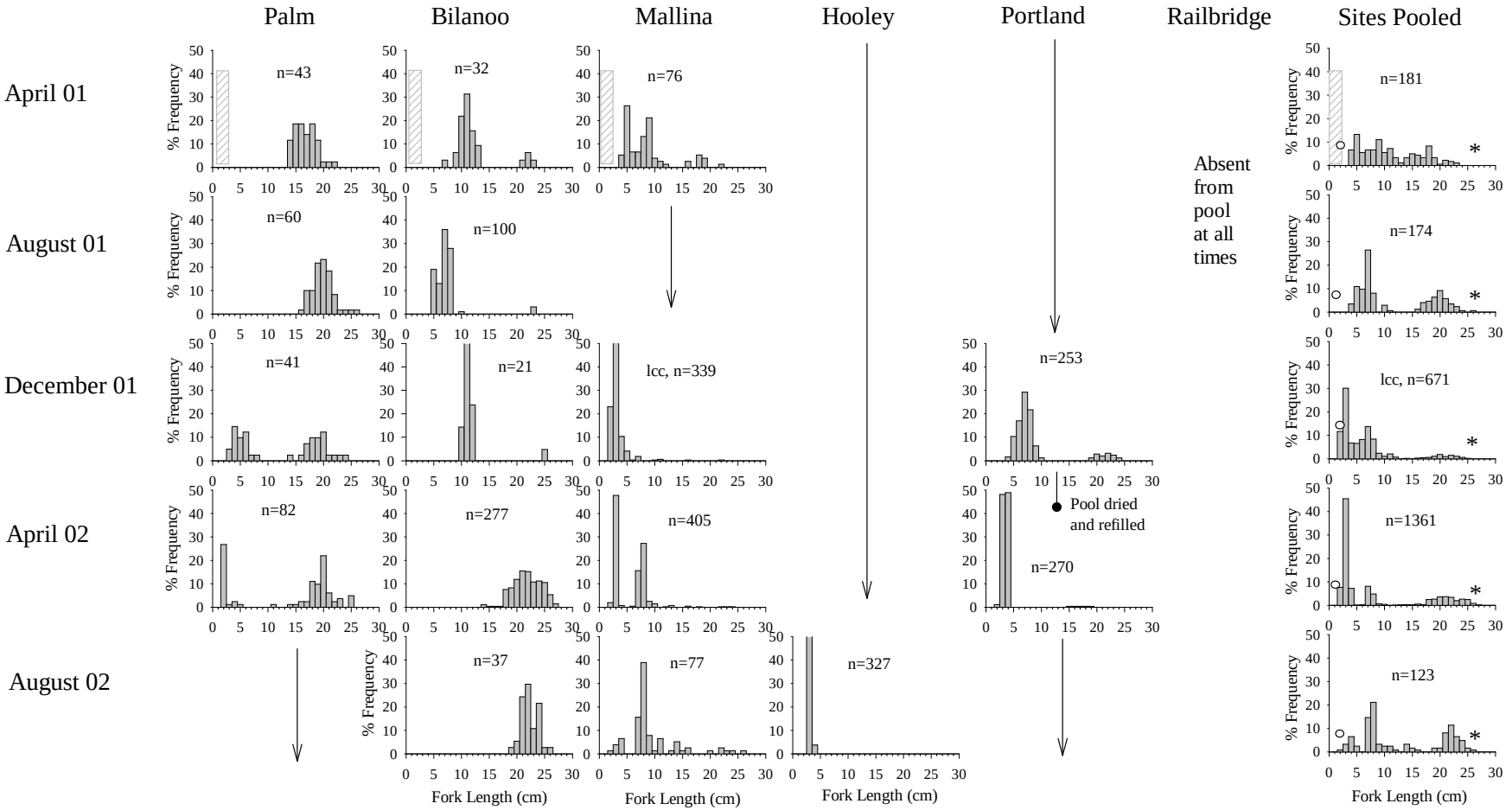


Figure IV.8. *N. erebi* size frequency (%) distributions. Fish size was measured using fork length (cm). Graphs are shown for the five sampling dates over the six study pools, and have been pooled for all sites. For all other details refer to Figure IV.

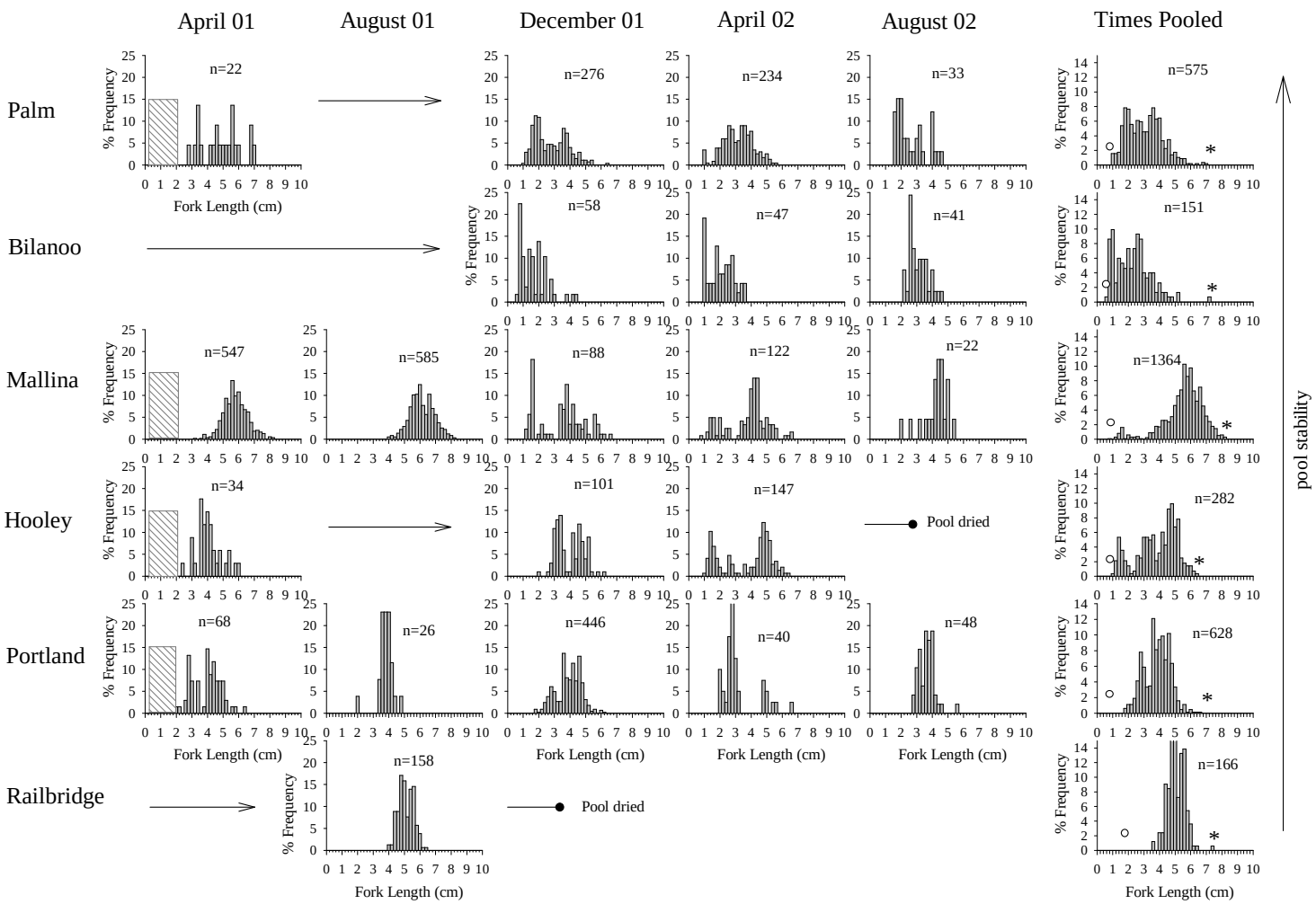


Figure IV.9. *Melanotaenia australis* size frequency (%) distributions. Fish size was measured using fork length (cm). Graphs are shown for the six study sites over the five sampling dates and have been pooled for all dates. For all other details refer to Figure IV.

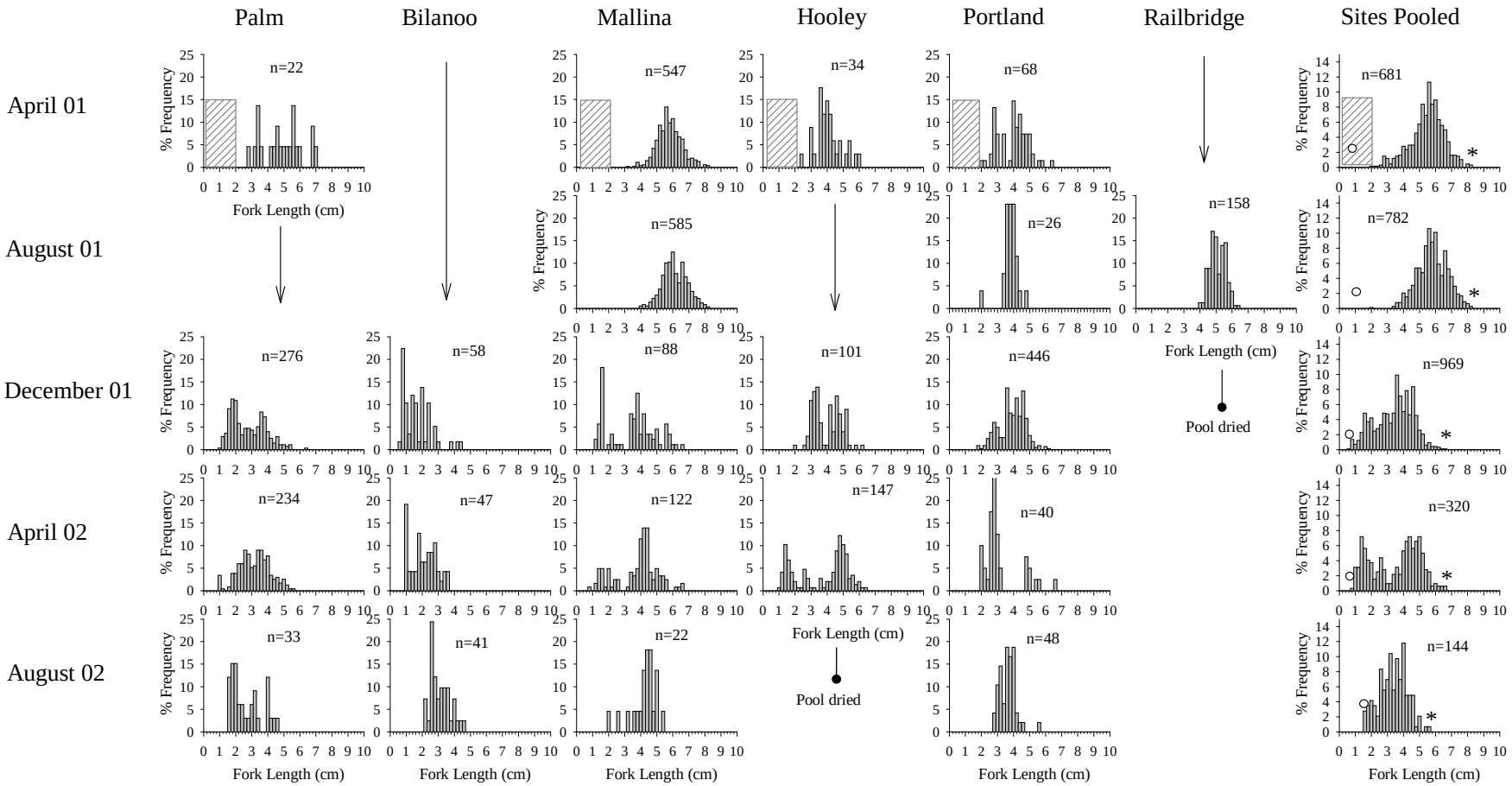


Figure IV.10. *M. australis* size frequency (%) distributions. Fish size was measured using fork length (cm). Graphs are shown for the five sampling dates over the six study pools, and have been pooled for all sites. For all other details refer to Figure IV.

Appendix V **Abundance (density) and Biomass of Fish per-unit-area versus Pool Variability in Depth: Intra-specific patterns**

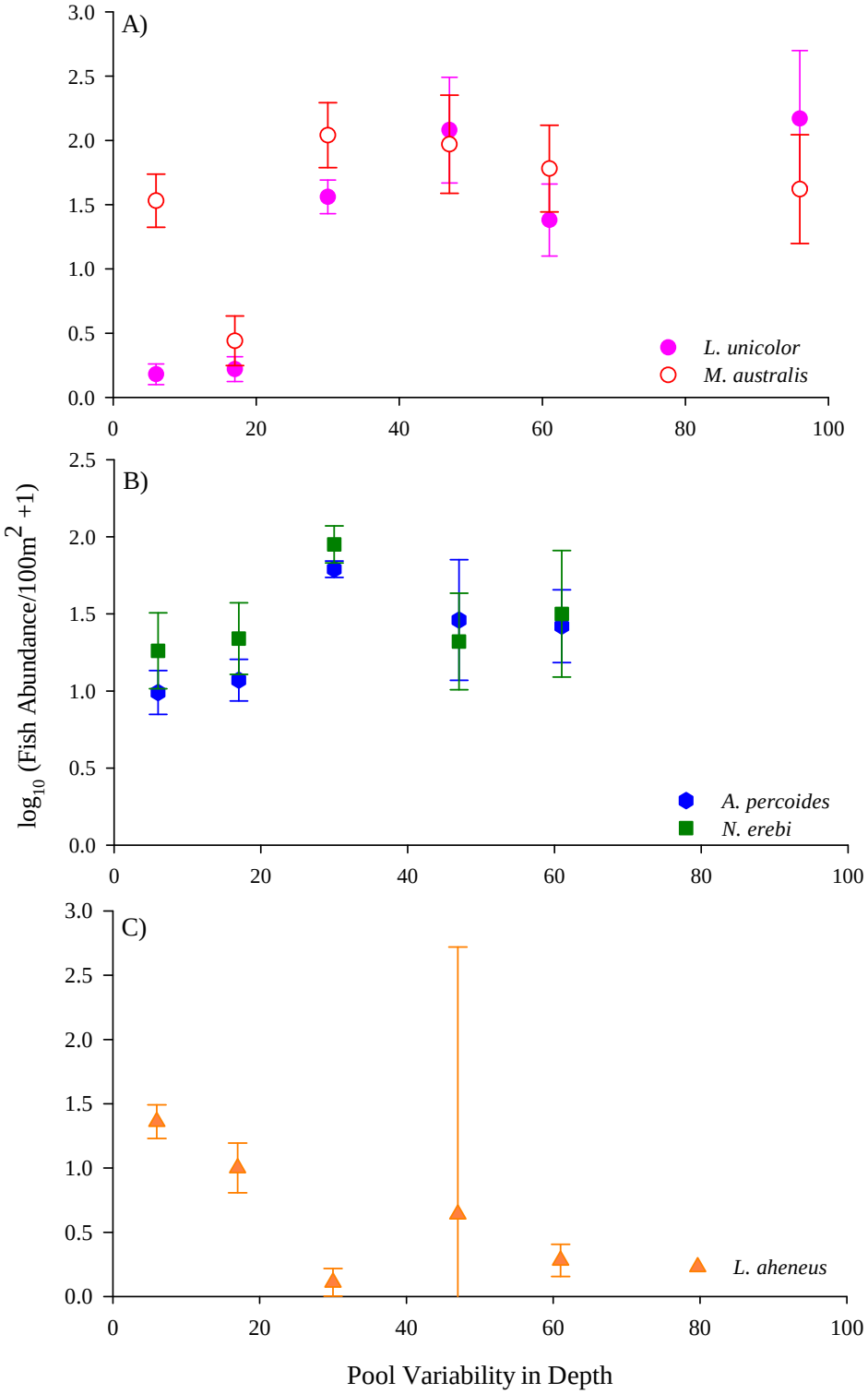


Figure V.1. Log_{10} (n+1) average (± SE) abundance of fish/100m^2 versus pool variability in depth. The three graphs show patterns for the five focal species. Fish abundance was standardized for habitat and fish < 3 cm were omitted, see the methods section of Chapter 4 for details.

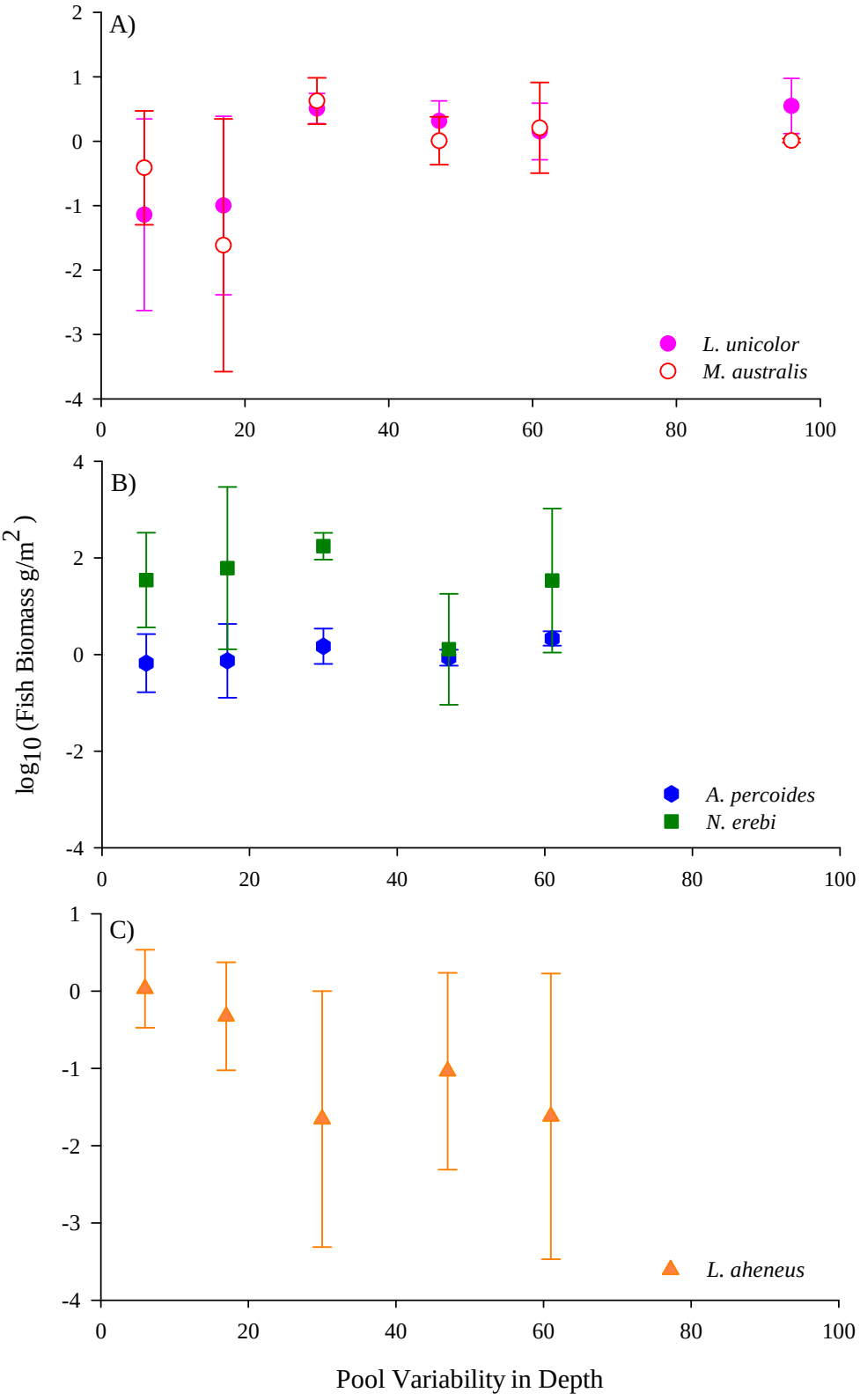


Figure V.2. Log_{10} average (± SE) biomass of fish (g/m^2) versus pool variability in depth. Graphs A to C show patterns for the five focal species. Fish biomass was standardized for habitat, see the methods section of Chapter 4 for details. All fish sizes were included.

Appendix VI **Food Web Structure and Fish diet**

Introduction

This appendix describes the food web structure of the pools of the Fortescue River, to examine whether the fish species utilise similar resources. Fish evolving within unstable systems are predicted to be resource generalists (Poff and Ward 1989).

Gut contents analysis is typically used to investigate dietary patterns, as it provides considerable amount of detail in resource partitioning; however, stable isotopic analysis of body tissue was preferred in this study. This was because, while stable isotopic analysis can describe only the general source(s) of carbon supporting fish growth, it is not prone to errors such as the confusion between food particles which are consumed and those which are actually assimilated, as is the case with gut content analysis (Rounick and Winterbourn 1986). The longer time scale of stable isotopic analysis also means that fine scale variation in feeding will not sway general patterns. It also provides a description of the trophic status of species, that is, if species (or size classes of a species) are higher up the food web than others (Peterson and Fry 1987).

Methods

Food web structure was examined for three pools: Hooley, Palm and Bilanoo, the location of these pools is shown in Chapter 2 Figure 2.1.

Sample Collection and Preparation

The food web was described by sampling sources of primary (autotrophic) and secondary (heterotrophic) productivity. Primary sources were collected from within the stream (autochthonous) and outside the stream (allochthonous).

Primary productivity: Autochthonous sources included aquatic macrophytes, algae, and phytoplankton. While macrophytes were easy to sample, benthic algae and phytoplankton were harder to obtain. Benthic algae were sampled from rocks and macrophytes using a scalpel and phytoplankton was collected by filtering water through a GF/C filter paper. Macrophytes were rinsed and their surfaces scraped to remove contaminants, however this was not possible for algae samples, therefore these samples did not represent pure sources. Allochthonous sources included riparian and fringing vegetation. Leaves were collected in a manner representative of the abundance of the species. Detritus was also sampled within the stream. In most cases this largely consisted of decaying terrestrial sources, but also would have contained in-stream sources and bacteria.

Secondary productivity: Macroinvertebrates were sampled from the littoral zone using hand nets (250 μm) and from the benthic zone using a kick net. It is recommended to place invertebrates into clear water for several hours to allow them to void their gut contents (Bunn *et al.* 1997); however this was not possible due to time constraints. Fish were collected using seine nets, gill nets and a drop trap. Individuals were identified to species, measured and had a section of their lateral musculature removed. Sponges were also collected.

All samples were stored immediately in liquid nitrogen and returned to the laboratory for processing. In the laboratory, specimens were rinsed with deionised water, and macroinvertebrates were sorted to order. Macroinvertebrates were pooled to the

taxonomic level of order (n ranged from 3-50, varying on size) in order to obtain enough material for analysis. As fish were much larger, muscle tissue was used in the analysis. Material was placed into an oven (60 ºC) and dried for one (heterotrophs) or two (autotrophs) days. Dried matter was homogenised with a mortar and pestle or a ball-grinder, and prepared for stable isotope analysis.

Stable Isotope Analysis
Samples were oxidised and the resultant CO_2 and N_2 analysed with a continuous-flow isotope-ratio mass spectrometer. Ratios of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ were expressed as the relative per mil ($^{o}/_{oo}$) difference between the sample and a standard. Standards were Pee Dee Belemnite (PDB) carbonate for C, and air N_2 for N.

$\delta X\ (‰) = (R_{sample} / R_{standard} - 1) * 1000$
where X = ^{13}C or ^{15}N and R = $^{13}C/^{12}C$ or $^{15}N/^{14}N$

Source determination and Trophic Position
Determination of the carbon source of a consumer is relatively straightforward if the consumer is utilizing only one source, and if sources do not overlap. This is because there is relatively little fractionation of $^{13}C/^{12}C$ isotopes during heterotrophic incorporation (DeNiro and Epstein 1978). Studies report a ~$\delta 1^{o}/_{oo}$ increases in ^{13}C (enrichment) with each trophic level (DeNiro and Epstein 1978, Tieszen *et al.* 1983, Fry and Sherr 1988). However, France (1996) noted that these aforementioned studies were carried out either in the laboratory or within marine systems. France and Peters (1997) review of freshwater literature revealed that ^{13}C enrichment is $0.2^{o}/_{oo}$ per trophic level. Therefore, any autotroph with neigh on the same signature is a potential source, assuming that its nitrogen signature is appropriate.

Unlike carbon, there is considerably more fractionation of nitrogen isotopes during heterotrophic incorporation (Peterson and Fry 1987). Studies report an increase of 2-$5^{o}/_{oo}$ ^{15}N with each trophic step (France *et al.* 1998, Bunn *et al.* 2003). Consequently, potential sources must have lower $\delta^{15}N$ values than consumers. Nitrogen isotopes can help to separate sources with identical carbon ratios, and also provide information on the trophic position of consumers within the food web. That is, consumers with higher $\delta^{15}N$ values (assuming a similar source) are feeding on sources higher up the food web. However, this should only be used as a guide rather than a definitive answer, as omnivory has the potential to complicate things.

Results and Discussion
The amount of variation between fish diets varied between pools and this appeared to be related to the diversity of food sources. For example, the isotopic signatures of different fish species (*Leiopotherapon unicolor, L. aheneus, Amniataba percoides, Glossogobius giurus, Nematalosa erebi, Melanotaenia australis*) were very similar in Hooley Pool (Figure AVI.1.A) where the macroinvertebrate community was relatively depauparate and the habitat relatively simple. Species' signatures were distinct at Bilanoo Pool (Figure AVI.1.C), which had dense stands of macrophytes, supporting diverse and abundant macroinvertebrate communities. Species' signatures were intermediate at Palm Pool (Figure AVI.1.B). This pool contained a wide array of macroinvertebrate species; however, most were restricted to the emergent reed beds, and may have been inaccessible to many fish.

These results show that while most species are able to survive on similar carbon sources, that is, they are generalists, that they do have preferences, and that given the opportunity they will diverge in their dietary intake.

Two species of fish (catfish), *Arius graeffei* and *Neosilurus hytrlii* could not be included in the above summation. This was because tissue from these species was collected only from one pool (Palm) (N.B. *A. graeffe*i was not present within Hooley Pool). The low delta N value of *N. hyrtlii* at Palm Pool indicated that this species has a lower trophic status than all of the other fish species. *N. hyrtlii's* isotopic signature was also considerably more enriched in ^{13}C than all other species (Figure AVI.1.B**)**. While this information was only based on only one individual it suggests that this species feeds of a greater proportion of epilithic algal material than the others. *A. graeffei* had a similar trophic level to the other species, but was more enriched in ^{13}C than the remaining species. *A. graeffei's* delta ^{13}C value was nearly identical to the signature of fine particulate organic matter (FPOM) within Palm Pool, suggesting that it may be a detritivore.

References

Bunn, S.E., Davies, P.M. and Kellaway, D.M. (1997) Contributions of sugar cane and invasive pasture grass to the aquatic food web of a tropical lowland stream. *Marine and Freshwater Research* **48**: 173-179.

Bunn, S.E., Davies, P.M. and Winning, M. (2003) Sources of organic carbon supporting the food web of an arid zone floodplain river. *Freshwater Biology* **48**: 1-17.

DeNiro, M.J. and Epstein, S. (1978) Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta*. **42**: 495-506.

France, R.L. (1996) Absence or masking of metabolic fractionations of 13C in a freshwater benthic food web. *Freshwater Biology* **36**: 1-6.

France, R.L., Chandler, M. and Peters, R. (1998) Mapping trophic continua of benthic foodwebs: body size - δ15N relationships. *Marine Ecology Progress Series* **174**: 301-306.

France, R.L. and Peters, R. (1997) Ecosystem differences in the trophic enrichment of 13C in aquatic food webs. *Canadian Journal of Fisheries and Aquatic Sciences* **54**: 1255-1258.

Fry, B. and Sherr, E.B. (1988) δ13C measurements as indicators of carbon flow in marine and freshwater ecosystems. In: P. W. Rundel, J. R. Ehleringer & K. A. Nagy (Eds.). *Stable isotopes in ecological research*. Springer-Verlag. U.S.A.

Peterson, B.J. and Fry, B. (1987) Stable isotopes in ecosystem studies. *Annual Review of Systematics* **18**: 293-320.

Poff, N.L. and Ward, J.V. (1989) Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. *Canadian Journal of Fisheries and Aquatic Sciences* **46**: 1805-1818.

Rounick, J.S. and Winterbourn, M.J. (1986) Stable carbon isotopes and carbon flow in ecosystems. *Biosciences* **36**: 171-177.

Tieszen, L.L., Boutton, T.W., Tesdahl, K.G. and Slade, N.A. (1983) Fractionation and turnover of stable carbon isotopes in animal tissues: implications for δ13C analysis of diet. *Oecologia* **57**: 32-37.

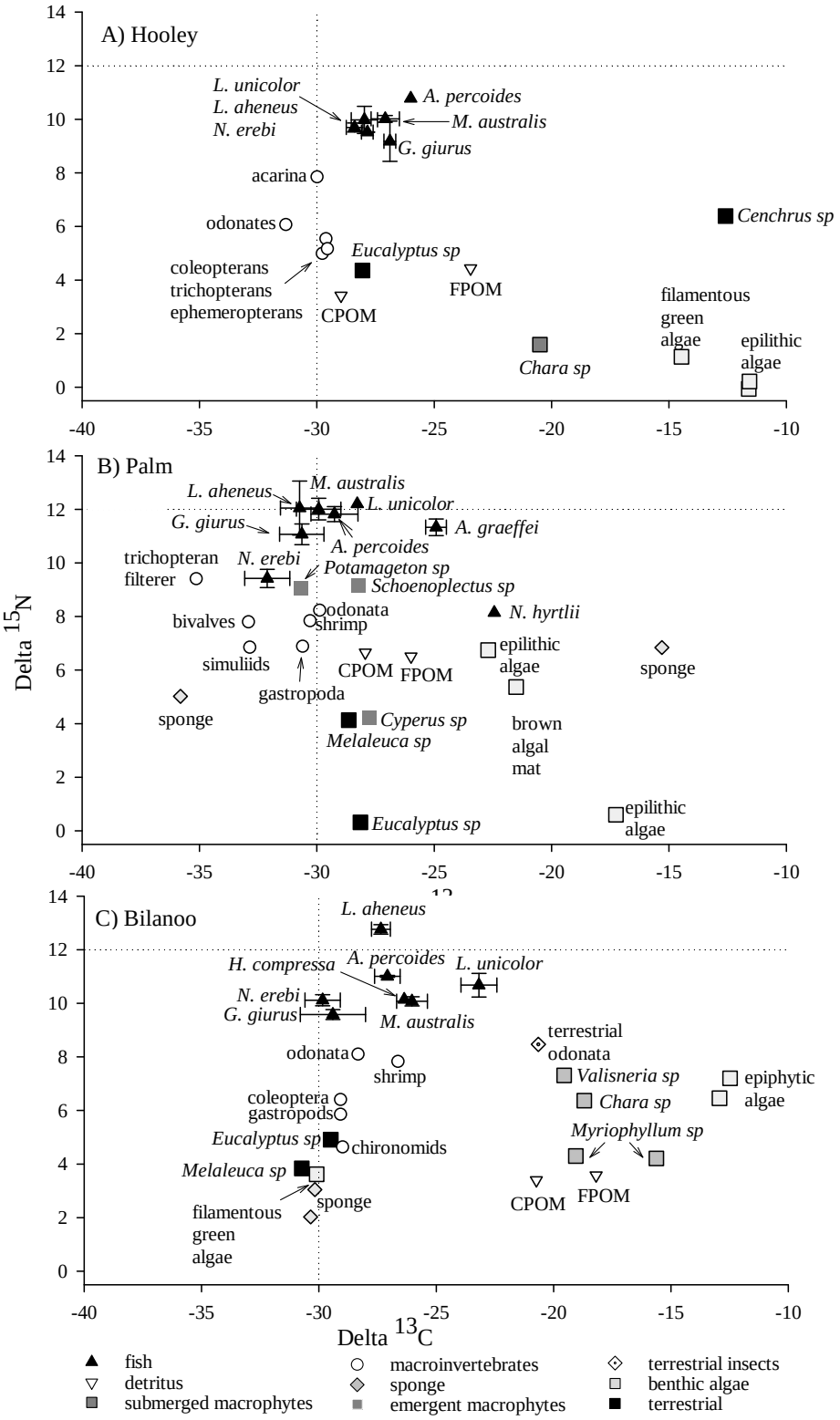


Figure VI.1. Stable Carbon ($\delta^{13}C$) and Nitrogen ($\delta^{15}N$) ratios for A) Hooley. B) Palm, and C) Bilanoo pools on the Fortescue River, during April 2002 (during a drought). Reference lines have been added to facilitate spatial comparison.

Appendix VII: **Is Otolith Weight a Predictor of Growth Rate in *Leiopotherapon unicolor*?**

Introduction

Once the size of a fish is known, age information is all that is required for an estimate of average growth rate. Unfortunately, aging fish is not a simple process. Typically the ear bones (otoliths) are used (Williams and Bedford 1974, Weatherley and Gill 1987). A fish hatches with a nucleus of otolith that grows daily by the laying down of calcium carbonate and protein (Williams and Bedford 1974). In larval and juvenile fish, the daily depositions (termed bands) are often visible and can be counted to estimate age (Pannella 1971). The width of daily bands can also be measured to provide a comparison of growth rate between similarly aged individuals (Bradford and Geen 1987, Secor and Dean 1989). In adult fish, however, daily bands are difficult to see because growth rate (band width) has decreased significantly (Campana and Neilson 1985). Age in adults is inferred from seasonal differences, as the bands will be stacked close together during periods of low growth (winter) and spread further apart during periods of high growth (summer) (Williams and Bedford 1974). When seasonal bands are visible they can be used to apply a broad age (i.e. 0+, 1+, 2+ …) to individuals. Growth curves (Von Bertalanffy) can be constructed based on size at age data and used to compare growth rates between populations (Quinn 1999).

Estimations of growth rate based on annual age information will always have some degree of inaccuracy because individuals classified as 1+ may have just turned one or maybe approaching two. This inaccuracy will be exacerbated in short lived species, as the error in aging will be relatively large. Furthermore, if the date of birth for an individual is not precisely known (i.e. in protracted spawning or multiple spawning species), this also has the potential to increase the inaccuracy. An alternative method, which compares otolith weight in similar sized fish, as a measure of growth rate, could avoid some of these problems.

Slow-growing fish have been found to have relatively heavier otoliths than their similar sized, fast-growing counterparts (Templeman and Squires 1956, Marshall and Parker 1982, Reznick *et al.* 1989, Secor and Dean 1989). This phenomenon can be explained by the 'Daily Increment Packing' hypothesis proposed by Secor and Dean (1989). They suggest that the daily-band of an otolith consists of two components; an increment that is independent of somatic growth, and one that is related to somatic growth. As slower-growing fish take longer to reach the same size as fast-growing fish, their otoliths have a greater number of daily bands, whose additive weight exceeds the otolith weight of the fast-growing fish.

While support for the association between otolith weight and growth rate has been wide-spread, most evidence has been gained indirectly (Templeman and Squires 1956, Boehlert 1985, Pawson 1990). There have been relatively few controlled experiments (Marshall and Parker 1982, Reznick *et al.* 1989, Secor and Dean 1989), and several studies have revealed that the dimensions of an otolith may be a poor indicator of growth rate (Neilson and Geen 1982, Rice *et al.* 1985, Schafer 2000). Indeed, research on daily bands has reported instances where otolith growth has been uncoupled from somatic growth (Mosegaard *et al.* 1988, Wright *et al.* 1990, Milicich 1991). These conflicting results indicate the need to validate the relationship between

somatic growth rate and otolith weight for a given species. The results of an experimental study using one of the abundant and widespread species within the Fortescue River, *Leiopotherapon unicolor,* are presented in this appendix.

To assess the suitability of using otolith weight to predict growth rate, growth rate was altered by manipulating diet. This produced fish of different ages but equal size. If otolith weight was a good predictor of growth rate, then the older or slower-growing fish would have heavier otoliths than their younger or faster-growing counterparts.

Methods

The fish were sourced from an ephemeral pool (location 21º30'18"S 117º0.2'30"E) within the Fortescue catchment. Juvenile fish from the same cohort (3-4 cm) were collected in September of 2002, and transported to aquaria in the School of Animal Biology (University of Western Australia, Perth). Fish were held in communal aquaria until the trial commenced on the 12th of February 2003.

Experimental Design

A paired design was used to examine the effects of growth rate on otolith weight for 18 pairs of fish (36 in total). Fish within each pair were matched for size and sex, and were housed within a common 6 L aquarium. Within each aquarium, fish were separated by a fine mesh partition and one was randomly assigned to the high-growth treatment and the other to the low-growth treatment. Pairs of fish were randomly assigned to the 18 aquaria.

Fish receiving the high-growth treatment grew until the 6th of June (114 days), when they were anaesthetised by immersion in a 40 ppm solution of clove oil, euthanased, measured, weighed, and sexed. Their otoliths were removed, dried, and stored in an eppendorf. Fish receiving the low-growth treatment continued to grow until they reached the same length that their high-growth pair had been on the 6th of June. They were then sacrificed in the same manner as the high-growth fish.

Fish size at the start of the experiment ranged from 48 to 69 mm in length (fork length). By this stage fish were approximately one year of age and reproductively active. Fish were sexed by applying pressure to their abdomen and looking for milt, which identified male fish. This method of sexing correctly identified the sex of 35 out of the 36 fish. Reproductive status did not alter during the course of the experiment, as males were still milting in October and all females collected were gravid. The prolonged period (February–October) of reproductive activity outside the normal time range (December-March) was probably due to the constant temperature and day length. No fish were observed to display signs of spawning behaviour.

Growth and Maintenance

Growth was manipulated using diet. High-growth fish were fed ~2 % of their body weight (which approximated *ad libitum* conditions) and low-growth fish were fed ~1% of their body weight. Fish were fed using Nutrafin complete care fish pellets, which contained sufficient calcium and phosphorus to ensure that bone growth was not limited. Fish were fed twice a day (9 am and 5 pm), 6 days a week. Fish were measured and weighed every 3 to 4 weeks to monitor growth and guide adjustments in food intake. Prior to measurements, fish were anaesthetised in a 40 ppm solution of

clove oil for 20-30 seconds (depending on size). Fish were measured using a fish ruler (to 1 mm) and weighed in water (to 0.1 g, using a portable balance, A&D HL 400g x 0.1 g) to minimise stress, allowed to recover, and then returned to their aquarium.

Each aquarium was connected to the common biological filtration system. A piece of mesh was placed over the outlet pipe to prevent food from being sucked away. Although the biological filter kept the water clean, aquaria were cleaned once every two months to remove any scum that had built up.

Temperature was held constant (25±1 °C) over the 8 month course of the experiment. A high temperature was chosen to help maximise the growth rate of the high-diet treatment. This temperature also approximated field conditions, as temperatures in the Fortescue River range between 20 to 30 °C. A 12 h light/dark cycle was established.

Otolith Measurements

Prior to weighing, otoliths were examined under a dissecting microscope (6 X magnification) to ensure that they were clean and not chipped. Each otolith was weighed (mg) using a Sartorius 4503 microbalance (d=0.001 mg). The average weight of the two otoliths was used for all analyses.

Statistical Analyses

All statistics were executed using JMP (SAS Institute 2001). Prior to the analyses outliers were removed (see results). A paired one tailed t-test was used to examine if the slow-growing fish had heavier otoliths than their fast-growing counterparts. Regression analysis was used to investigate the extent to which variation in fish size accounted for variation between pairs. Fish size at the end of the experiment was used. The time taken for low-growth fish to reach the size of their high-growth counterpart (extra age) was proposed as an additional regressor, but was highly correlated (r=0.92) with fish size and was omitted from the regression to avoid problems associated with colinearity (Zar 1999).

Differences in the paired t-tests were normally distributed (Zar 1999). Assumptions of homogeneity of variance and normality were met for all analyses.

Results

Manipulating growth rate was considerably more difficult than expected. Some fish on high-diets refused to eat all of their food and so grew much slower than expected, while others on low-diets grew faster than anticipated. In one instance a high- and low-growth pair displayed no difference in growth rate. As this study was interested in the relationship between growth rate and otolith weight, not the relationship between food and growth rate, this pair was omitted from the data analysis. One fish also escaped, reducing the total number of pairs to 16.

Fish in the high-growth treatment grew from on average 59.1 ± 0.82 mm at the start of the experiment to 87.9 ± 0.86 mm, which was an increase of 50.2 % of their initial length. The growth rate of this treatment was on average 0.253 ± 0.053 mm per day. Fish in the low-growth treatment started at the same size (on average 58.6 ± 0.80 mm) and took between 40 to 198 days to catch up to the size of their partner (at the end of

the experiment they were on average 87.9 ± 0.80 mm). The growth rate of this treatment was on average 0.126 ± 0.034 mm per day.

For fish of the same size, those grown at a low rate had otoliths that were on average 0.61±0.127 mg heavier than those grown at a high rate (paired t-test: df=15, t=4.81, p=0.0001) (Figure 6.1A). Larger fish showed a greater difference in otolith weight between high- and low-growing pairs than smaller fish (linear regression: df=15, R^2=0.56, F=17.91, p=0.0008) (Figure 6.1B).

Discussion

Otolith weight can be used as a predictor of growth rate when comparing *L. unicolor* of the same size. This study, like that of Reznick *et al.* (1989) and Secor and Dean (1989), found that slower-growing fish had heavier otoliths than fast-growing individuals.

A method that compares average growth conditions, such as otolith weight, will have advantages in certain situations and disadvantages in others. It should be advantageous for large-scale investigations, as it will provide a robust and general comparison of growth rates; it will not be skewed by short-term fluctuations. Conversely, it will be disadvantageous for fine-scale investigations; individuals experiencing periods of high- and low-growth will be impossible to distinguish from individuals experiencing average growth (Jenkins *et al.* 1993).

One way to enhance or diminish the advantages and disadvantages of the method is to select the age class of fish being studied. Comparisons of young (juvenile) fish will restrict the capacity for historical patterns of growth to affect current patterns; allowing greater insight into the relationship between current physical/biotic parameters and growth. Researchers are cautioned about making correlations with very young (larval) fish, as studies by several authors (Molony and Choat 1990, Paperno *et al.* 1997, Johnson *et al.* 2002) have revealed that time lags occur in the response of an otolith to changing growth conditions. Comparisons using adult fish will reveal long-term trends in growth and will be advantageous if growth differences between individuals are small. Comparisons using very large adult fish, where growth rate has declined considerably, may reveal more about the longevity of individuals than their growth rates, and care should be taken when interpreting such data.

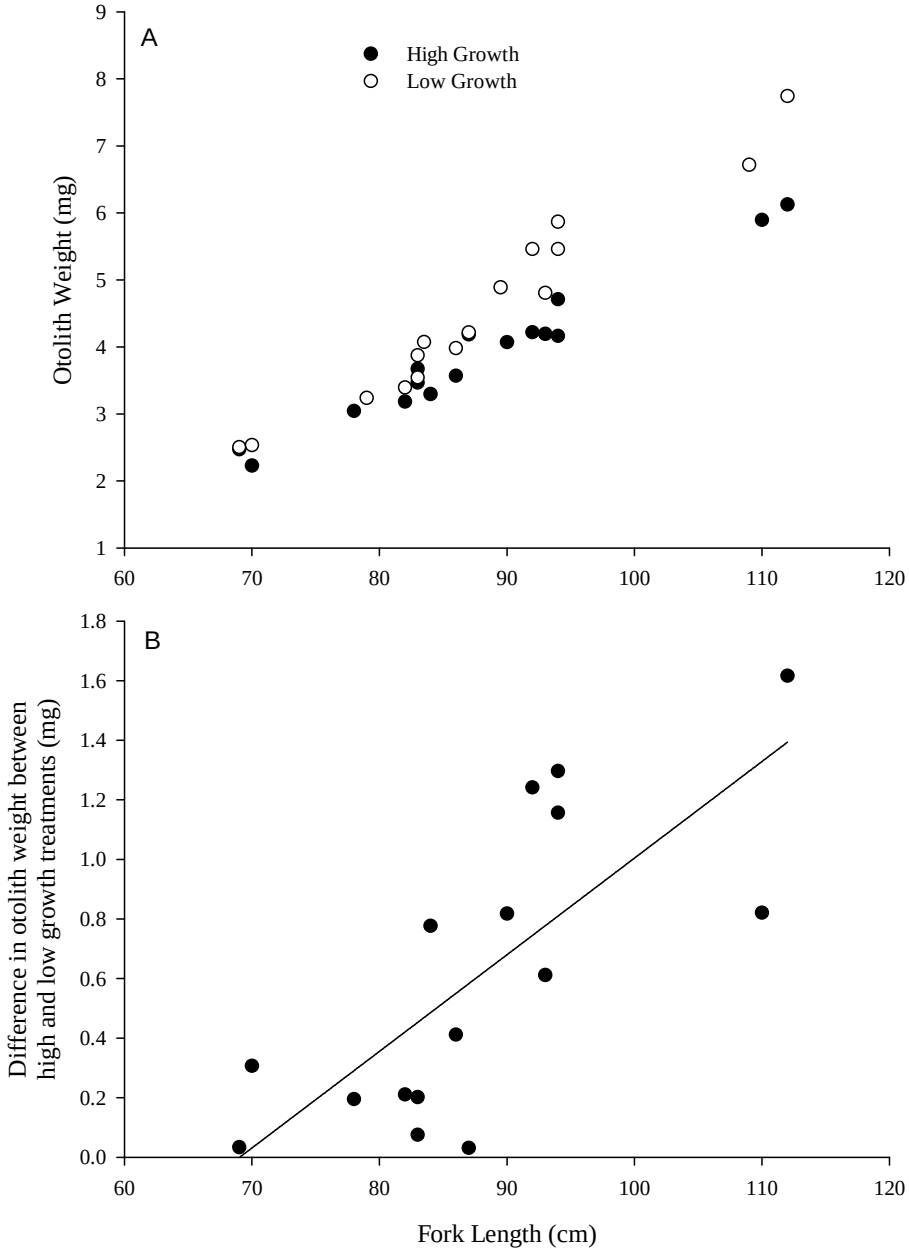


Figure VII.1 A) Otolith weight at size for the two growth treatments. B) Linear regression of difference in otolith weight versus fish size (Difference= 0.032*Fork Length – 2.24, R^2 =0.56).

References

Boehlert, G.W. (1985) Using objective criteria and multiple regression models for age determination in fishes. *Fishery Bulletin* **83**: 103-117.

Bradford, M.J. and Geen, G.H. (1987) Size and growth of juvenile chinook salmon back-calculated from otolith growth increments. In: R. C. Summerfelt & G. E. Hall (Eds.). *The age and growth of fish*. The Iowa State University Press, Ames, Iowa.

Campana, S.E. and Neilson, J.D. (1985) Microstructure of fish otoliths. *Canadian Journal of Fisheries and Aquatic Sciences* **42**: 1014-1032.

Jenkins, G.P., Shaw, M. and Stewart, B.D. (1993) Spatial variation in food-limited growth of juvenile greenback flounder, *Rhombosolea tapiina*: evidence from otolith daily increments and otolith scaling. *Canadian Journal of Fisheries and Aquatic Sciences* **50**: 2559-2566.

Johnson, M.W., Rooker, J.R., Gatlin, D.M. and Holt, G.J. (2002) Effects of variable ration levels on direct and indirect measures of growth in juvenile red drum (*Sciaenops ocellatus*). *Journal of Experimental Marine Biology and Ecology* **274**: 141-157.

Marshall, S.L. and Parker, S.S. (1982) Pattern identification in the micro-structure of sockeye salmon (*Oncorhynchus nerka*) otoliths. *Canadian Journal of Fisheries and Aquatic Sciences* **39**: 542-547.

Milicich, M.J. (1991) Do otoliths record changes in somatic growth rate? - conflicting evidence from a laboratory and field study of a temperate reef fish, *Parika scaber*. *Bureau of Rural Resources Proceedings* **15**: 59-61.

Molony, B.W. and Choat, J.H. (1990) Otolith increment widths and somatic growth rate: the presence of a time-lag. *Journal of Fish Biology* **37**: 541-551.

Mosegaard, H., Svedang, H. and Taberman, K. (1988) Uncoupling of somatic and otolith growth rates in Arctic char (*Salvelinus alpinus*) as an effect of differences in temperature response. *Canadian Journal of Fisheries and Aquatic Sciences* **45**: 1514-1524.

Neilson, J.D. and Geen, G.H. (1982) Otoliths of Chinook Salmon (*Oncorhynchus tshawytscha*): daily growth increments and factors influencing their production. *Canadian Journal of Fisheries and Aquatic Sciences* **39**: 1340-1347.

Pannella, G. (1971) Fish otoliths: daily growth layers and periodical patterns. *Science* **173**: 1124-1127.

Paperno, R., Targett, T.E. and Grecay, P.A. (1997) Daily growth increments in otoliths of juvenile weakfish, *Cynoscion regalis*: experimental assessment of changes in increment width with changes in feeding rate, growth rate, and condition factor. *Fishery Bulletin* **95**: 521-529.

Pawson, M.G. (1990) Using otolith weight to age fish. *Journal of Fish Biology* **36**: 521-531.

Quinn, T.J. (1999) *Quantitative fish dynamics*, Oxford University Press, New York.

Reznick, D., Lindbeck, E. and Bryga, H. (1989) Slower growth results in larger otoliths: an experimental test with guppies (*Poecilia reticulata*). *Canadian Journal of Fisheries and Aquatic Sciences* **46**: 108-111.

Rice, J.A., Crowder, L.B. and Binkowski, F.P. (1985) Evaluating otolith analysis for bloater, *Coregonus hoyi*: do otoliths ring true? *Transactions of the American Fisheries Society* **114**: 532-539.

SAS Institute (2001) JMP IN, statistical discovery software, version four. Duxbury Thomson Learning.

Schafer, D.J. (2000) Evaluation of periodic and aperiodic otolith structure and somatic-otolith scaling for use in retrospective life history analysis of a tropical marine goby, *Bathygovius coalitus*. *Marine Ecology Progress Series* **199**: 217-229.

Secor, D.H. and Dean, J.M. (1989) Somatic growth effects on the otolith-fish size relationship in young pond-reared striped bass, *Morone saxatilis*. *Canadian Journal of Fisheries and Aquatic Sciences* **46**: 113-121.

Templeman, W. and Squires, H.J. (1956) Relationship of otolith lengths and weights in the haddock *Melanogrammus aeglefinus* (L.) to the rate of growth of the fish. *Journal of the Fisheries Research Board of Canada* **13**: 467-487.

Weatherley, A.H. and Gill, H.S. (1987) *The biology of fish growth*, Academic Press, London.

Williams, T. and Bedford, B.C. (1974) The use of otoliths for age determination. In: T. B. Bagenal (Ed.) *Aging of Fishes, Proceedings of an International Symposium*. Unwin Brothers Ltd., Reading, England.

Wright, P.J., Metcalfe, N.B. and Thorpe, J.E. (1990) Otolith and somatic growth rates in Atlantic salmon parr, Salmo salar L: evidence against coupling. *Journal of Fish Biology* **36**: 241-249.

Zar, J.H. (1999) *Biostatistical analysis,* fourth edition. Prentice-Hall Inc., New Jersey.

Appendix VIII **Diurnal Fluctuations in Water Temperature in a Stable and Unstable Pool**

A detailed comparison of diurnal fluctuations in water temperature was carried out during the dry season of 2002. A data logger was placed 1.5 m below the waters surface at a permanent (Palm) and an unstable pool (Portland), and water temperatures were monitored once every hour until the variable pool dried. The stable and unstable pools had similar average water temperatures but the unstable pool underwent significantly greater diurnal fluctuations in temperature (Figure VIII .1).

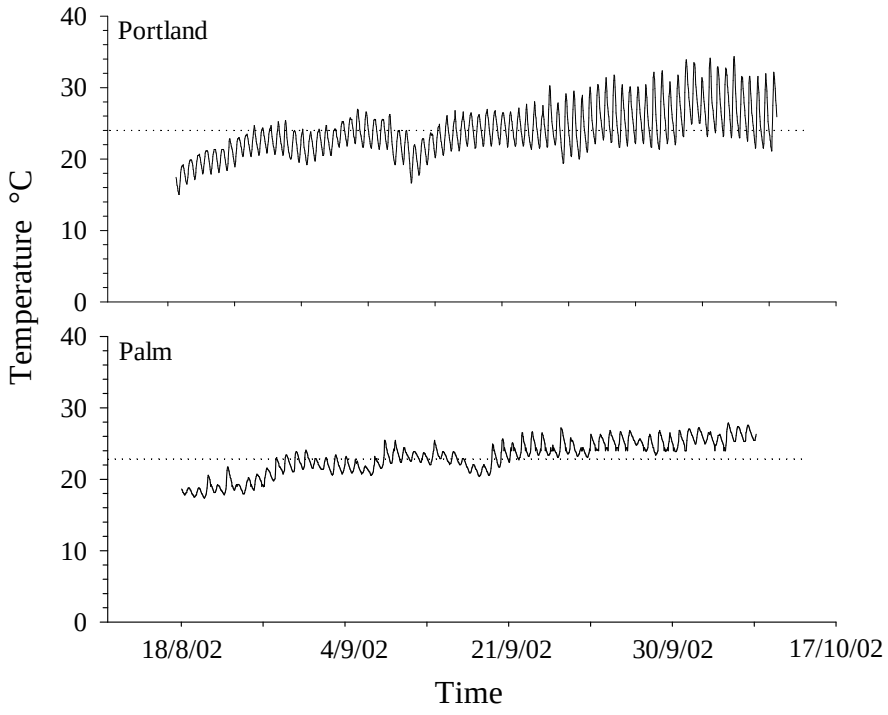


Figure VIII.1. Water temperature over time within a stable (Palm Pool) and an unstable pool (Portland River). The average water temperature in each pool is displayed by the dotted line. The water temperature was on average 23.0°C at Palm Pool, and 23.9°C at Portland River.

References

Alkins-Koo, M. (2000) Reproductive timing of fishes in a tropical intermittent stream. *Environmental Biology of Fishes* **57**: 49-66.

Allen, G.R., Midgley, S.H. and Allen, M. (2002) *Field guide to the freshwater fishes of Australia*, Western Australian Museum, Perth.

Allen, M.S., Hale, M.M. and Pine, W.E. (1999) Comparison of trap nets and otter trawls for sampling black crappie in two Florida lakes. *North American Journal of Fisheries Management* **19**: 977-983.

Andrew, N.L. and Mapstone, B.D. (1987) Sampling and the description of spatial patterns in marine ecology. *Oceanography and Marine Biology: an Annual Review* **25**: 39-90.

Angermeier, P.L. and Karr, J.R. (1983) Fish communities along environmental gradients in a system of tropical streams. *Environmental Biology of Fishes* **9**: 117-135.

Angermeier, P.L. and Schlosser, I.J. (1989) Species-area relationships for stream fishes. *Ecology* **70**: 1450-1462.

Arthington, A.H., Balcombe, S.R., Wilson, G.A., Thoms, M.C. and Marshall, J. (2005) Spatial and temporal variation in fish-assemblage structure in isolated waterholes during the 2001 dry season of an arid-zone floodplain river, Cooper Creek, Australia. *Marine and Freshwater Research* **56**: 25-35.

Auty, E.H. (1978) Reproductive behaviour and early development of the empire fish, *Hypseleotris compressus* (Eleotridae). *Australian Journal of Marine and Freshwater Research* **29**: 285-297.

Bagenal, T.B. (1974) *The proceedings of an international symposium on the aging of fish*, University of Reading, Surrey, England, Unwin Brothers Limited.

Baird, D.J., Linton, L.R. and Davies, R.W. (1987) Life-history flexibility as a strategy for survival in a variable environment. *Functional Ecology* **1**: 45-48.

Baker, J.A. and Foster, S.A. (2002) Phenotypic plasticity for life history traits in a stream population of the threespine stickleback, *Gasterosteus aculeatus* L. *Ecology of Freshwater Fish* **11**: 20-29.

Baltz, D.M. (1984) Life history variation among female surfperches (Perciformes: Embiotocidae) *Environmental Biology of Fishes* **10**: 159-171.

Bart, H.L. (1989) Fish habitat association in an Ozark stream. *Environmental Biology of Fishes* **24**: 173-186.

Bayley, P.B. (1988) Factors affecting growth rates of young tropical floodplain fishes: seasonality and density-dependence. *Environmental Biology of Fishes* **21**: 127-142.

Bayley, P.B. and Austen, D.J. (1988) Comparison of detonating cord and rotenone for sampling fish in warmwater impoundments. *North American Journal of Fisheries Management* **8**: 310-316.

Bayley, P.B. and Li, H.W. (1992) Riverine fishes. In: P. Calow & G. E. Petts (Eds.). *The river handbook: hydrological and ecological principles*, volume 1. Blackwell Scientific, Oxford.

Begon, M. and Mortimer, M. (1986) *Population ecology: a unified study of animals and plants*, second edition, Sinauer Associates, Massachusetts.

Belbin, L. (1992). *PATN: pattern analysis package*. Reference Manual. Division of Wildlife and Rangelands Research. Canberra, Australia, CSIRO.

Beumer, J.P. (1979) Reproductive cycles of two Australian freshwater fishes: the spangled perch, *Therapon unicolor* Gunther, 1859 and the east Queensland rainbowfish, *Nematocentris splendida* Peters, 1866. *The Journal of Fish Biology* **15**: 111-134.

Bishop, K.A., Allen, S.A., Pollard, D.A. and Cook, M.G. (2001) *Ecological studies of the freshwater fishes of the Alligator Rivers region, Northern Territory: autecology*. Supervising Scientist report 145. Supervising Scientist, Darwin.

Boulton, A.J. and Brock, M.A. (1999) *Australian freshwater ecology: processes and management*, Gleneagles Publishing, South Australia.

Breder, C.M. and Rosen, D.E. (1966) *Modes of reproduction in fishes*, T.F.H. Publicatons, Jersey.

Briggs, I.C. (1980) Herrings. In: R.M. McDowall (Ed.). Freshwater fishes of south-eastern Australia. A.H. & A.W. Reed Pty. Ltd., Sydeny.

Brown, K.M. (1985) Intraspecific life history variation in a pond snail: the roles of population divergence and phenotypic plasticity. *Evolution* **39**: 387-395.

Brown, L.R. (2000) Fish communities and their associations with environmental variables, lower San Joaquin River drainage, California. *Environmental Biology of Fishes* **57**: 251-269.

Campana, S.E. and Neilson, J.D. (1985) Microstructure of fish otoliths. *Canadian Journal of Fisheries and Aquatic Sciences* **42**: 1014-1032.

Capone, T.A. and Kushlan, J.A. (1991) Fish community structure in dry-season stream pools. *Ecology* **72**: 983-992.

Cargnelli, L.M. and Gross, M.R. (1996) The temporal dimension in fish recruitment: birth date, body size, and size-dependent survival in a sunfish (bluegill: *Lepomis Macrochirus*). *Canadian Journal of Fisheries and Aquatic Sciences* **53**: 360-367.

Casselman, J.M., Penczak, T., Carl, L., Mann, R.H.K., Holcik, J. and Woitowich, W.A. (1990) An evaluation of fish sampling methodologies for large river systems. *Polskie Archiwum Hydrobiologii* **37**: 521-551.

Chick, J.H., Jordan, F., Smith, J.P. and McIvor, C.C. (1992) A comparison of four enclosure traps and methods used to sample fishes in aquatic macrophytes. *Journal of Freshwater Ecology* **7**: 353-361.

Clarke, K.R. and Warwick, R.M. (2001) *Changes in marine communities: an approach to statistical analysis and interpretation*, second edition. PRIMER-E, Plymouth, United Kindom.

Closs, G.P. and Lake, P.S. (1996) Drought, differential mortality and the coexistence of a native and an introduced fish species in a south east Australian intermittent stream. *Environmental Biology of Fishes* **47**: 17-25.

Copp, G.H. and Penaz, M. (1988) Ecology of fish spawning and nursery zones in the flood plain, using a new sampling approach. *Hydrobiologia* **169**: 209-224.

Copp, I. (2005) *Geology and landforms of the Pilbara*, Department of Conservation and Land Management, Perth, Western Australia.

Dames and Moore (1984). *Millstream water management programme*, Engineering Division, Public Works Department, Western Australia.

Davies, W.D. and Shelton, W.L. (1983) Sampling with toxicants. In: L. A. Neilson & D. L. Johnson (Eds.). *Fisheries Techniques Manual*. American Fisheries Society special publication, Bethesda, Maryland.

Delucchi, C.M. (1988) Comparison of community structure among streams with different temporal flow regimes. *Canadian Journal of Zoology* **66**: 579-586.

Dobzhansky, T. (1950) Evolution in the tropics. *American Scientist* **38**: 209-221.

Dunning, J.B., Danielson, B.J. and Pulliam, H.R. (1992) Ecological processes that affect populations in complex landscapes. *Oikos* **65**: 169-175.

Ebert, T.A. (1981) Estimating mortality from growth parameters and a size distribution when recruitment is periodic. *Limnology and Oceanography* **26**: 764-769.

Espegren, G.D. and Bergersen, E.P. (1990) Quantitative sampling of fish populations with a mobile rising net. *North American Journal of Fisheries Management*. **10**: 469-478.

Fausch, K.D. and Bramblett, R.G. (1991) Disturbance and fish communities in intermittent tributaries of a western great plains river. *Copeia* **1991**: 659-674.

Fernandez-Delgado, C. and Herrera, M. (1995) Age structure, growth and reproduction of *Rutilus lemmingii* in an intermittent stream of the Guadalquivir river basin, southern Spain. *Hydrobiologia* **299**: 207-213.

Fowler, A.J. and Short, D.A. (1996) Temporal variation in the early life-history characteristics of the king george whiting (*Sillaginodes punctata*) from analysis of otolith microstructure. *Journal of Marine and Freshwater Research* **47**: 809-818.

Fox, M.G. and Keast, A. (1991) Effect of overwinter mortality on reproductive life history traits of pumpkinseed (*Lepomis gibbosus*) populations. *Canadian Journal of Fisheries and Aquatic Sciences* **49**: 1792-1799.

Freeman, B.J., Greening, J.S. and Oliver, J.D. (1984) Comparison of three methods for sampling fishes and macroinvertebrates in a vegetated freshwater wetland. *Freshwater Ecology* **2**: 603-609.

Freeman, M.C., Crawford, M.K., Barrett, J.C., Facey, D.E., Flood, M.G., Hill, J., Stouder, D.J. and Grossman, G.D. (1988) Fish assemblage structure in a southern Appalachian stream. *Canadian Journal of Fisheries and Aquatic Sciences* **45**: 1949-1958.

Gehrke, P.C. (1991) Implications of water quality for larval fish metabolism, activity and growth in extensive rearing conditions. *Bureau of Rural Resources Proceedings* **15**: 84-87.

Gelwick, F.P. (1990) Longitudinal and temporal comparisons of riffle and pool fish assemblages in a northeastern Oklahoma Ozark stream. *Copeia* **1990**: 1072-1082.

Gillanders, B.M., Ferrell, D.J. and Andrew, N.L. (1999) Size at maturity and seasonal changes in gonad activity of yellowtail kingfish (*Seriola lalandi*; Carangidae) in New South Wales, Australia. *New Zealand Journal of Marine and Freshwater Research* **33**: 457-468.

Gilliam, J.F., Fraser, D.F. and Alkins-Koo, M. (1993) Structure of a tropical stream fish community: a role for biotic interactions. *Ecology* **74**: 1856-1870.

Glover, C.J.M. (1982) Adaptations of fishes in arid Australia. In: W. R. Barker & P. J. M. Greenslade (Eds.). *Evolution of the flora and fauna of arid Australia*. Peacock Publications, South Australia.

Gorman, O.T. and Karr, J.R. (1978) Habitat structure and stream fish communities. *Ecology* **59**: 507-515.

Goto, A. (1998) Life-history variations in the fluvial sculpin, *Cottus nozawae* (Cottidae), along the course of a small mountain stream. *Environmental Biology of Fishes* **52**: 203-212.

Gottelli, N.J. and Pyron, M. (1991) Life history variation in North American freshwater minnows: effects of latitude and phylogeny. *Oikos* **62**: 30-40.

Grossman, G.D., Dowd, J.F. and Crawford, M. (1990) Assemblage stability in stream fishes: a review. *Environmental Management* **14**: 661-671.

Grossman, G.D., Freeman, M.C., Moyle, P.B. and Whitaker, J.O. (1985) Stochasticity and assemblage organization in an Indiana stream fish assemblage. *The American Naturalist* **126**: 275-285.

Grossman, G.D., Moyle, P.B. and Whitaker, J.O. (1982) Stochasticity in structural and functional characteristics of an Indiana stream fish assemblage: a test of community theory. *The American Naturalist* **120**: 423-454.

Grossman, G.D., Ratajczak, R.E., Crawford, M. and Freeman, M.C. (1998) Assemblage organization in stream fishes: effects of environmental variation and interspecific interactions. *Ecological Monographs* **68**: 395-420.

Hellier, T.R. (1958) The drop-net quadrat, a new population sampling device. *Publications of the Institute of Marine Science University of Texas* **5**: 165-168.

Henley, J.P. (1967) *Evaluation of rotenone sampling with scuba gear*. Proceedings of the Annual Conference of the Southeastern Association of Game and Fish Commissioners.

Hjelm, J., Persson, L. and Christensen, B. (2000) Growth, morphological variation and ontogenetic niche shifts in perch (*Perca fluviatilis*) in relation to resource availability. *Oecologia* **122**: 190-199.

Hockin, D.C., O'Hara, K., Cragg-Hine, D. and Eaton, J.W. (1985) Fish population estimation: the use of rotenone to evaluate the reliability of a removal technique. *Aquaculture and Fisheries Management* **16**: 349-357.

Hoeinghaus, D.J., Layman, C.A., Arrington, D.A. and Winemiller, K.O. (2003) Spatiotemporal variation in fish assemblage structure in tropical floodplain creeks. *Environmental Biology of Fishes* **67**: 379-387.

Holmgren, K. and Appelberg, M. (2001) Effects of environmental factors on size-related growth efficiency of perch, *Perca fluviatilis*. Ecology of Freshwater Fish **10**: 247-256.

Horwitz, R.J. (1978) Temporal variability patterns and the distributional patterns of stream fishes. *Ecological Monographs* **48**: 307-321.

Humphrey, C., Klumpp, D.W. and Pearson, R. (2003a) Early development and growth of the eastern rainbowfish, *Melanotaenia splendida splendida* (Peters) 11. Otolith development, increment validation and larval growth. *Marine and Freshwater Research* **54**: 105-111.

Humphrey, C., Klumpp, D.W. and Pearson, R. (2003b) Early development and growth of the eastern rainbowfish, *Melanotaenia splendida splendida* (Peters) I. morphogenesis and ontogeny. *Marine and Freshwater Research* **54**: 17-25.

Hunter, J.R. and Macewicz, B.J. (1985) Measurement of spawning frequency in multiple spawning fishes. In: R. Lasker (Ed.) *An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, Engraulis mordax*. U.S. Department of Commerce, NOAA Technical Report 36.

Hunter, J.R., Macewicz, B.J., Lo, N.C.H. and Kimbrell, C.A. (1992) Fecundity, spawning, and maturity of female dover sole, *Microstomus pacificus*, with an evaluation of assumptions and precision. *Fisheries Bulletin* U.S. **90**: 101-128.

Hutchings, J.A. (1993) Adaptive life histories effected by age-specific survival and growth rate. *Ecology* **74**: 673-684.

Hutchings, J.A. (1997) Life history responses to environmental variability in early life. In: R. C. Chambers & E. A. Trippel (Eds.). *Early life history and recruitment in fish populations*. Chapman and Hall, London.

Jackson, D.A., Peres-Neto, P.R. and Olden, J.D. (2001) What controls who is where in freshwater fish communities - the roles of biotic, abiotic, and spatial factors. *Canadian Journal of Fisheries and Aquatic Sciences* **58**: 157-170.

Jacobsen, T. and Kushlan, J.A. (1987) Sources of sampling bias in enclosure fish trapping: effects on estimates of density and diversity. *Fisheries Research Board of Canada* **5**: 401-412.

Jenkins, G.P., Shaw, M. and Stewart, B.D. (1993) Spatial variation in food-limited growth of juvenile greenback flounder, *Rhombosolea tapiina*: evidence from otolith daily increments and otolith scaling. *Canadian Journal of Fisheries and Aquatic Sciences* **50**: 2559-2566.

Jobling, M. (1995) *Environmental biology of fishes*, Chapman and Hall, London.

John, K.R. (1964) Survival of fish in intermittent streams of the Chiricahua mountains, Arizona. *Ecology* **45**:112-119.

Kawasaki, T. (1979) Fundamental relations among the selections of life history in the marine teleosts. *Bulletin of the Japanese Society of Scientific Fisheries* **46**: 289-293.

Kjelson, M.A. and Johnson, N. (1973) Description and evaluation of a portable drop-net for sampling nekton populations. *Proceedings of the Southeast Association of Game and Fisheries Commissioners* **27**: 653-662.

Knight, J.G. and Bain, M.B. (1996) Sampling fish assemblages in forested floodplain wetlands. *Ecology of Freshwater Fish* **5**: 76-85.

Kramer, D.L. (1978) Reproductive seasonality in the fishes of a tropical stream. *Ecology* **59**: 976-985.

Krebs, C.J. (1999) *Ecological methodology*, second edition. Addison-Wesley Educational Publishers, Benjamin/Cummings imprint, Menlo Park.

Kushlan, J.A. (1974) Quantitative sampling of fish populations in shallow freshwater environments. *Transactions of the American Fisheries Society* **103**: 348-352.

Lake, J.S. (1967) *Freshwater fishes of the Murray-Darling River system*. Research Bulletin of New South Wales State Fisheries, 7.

Lake, J.S. (1971) *Freshwater fishes and rivers of Australia*, Thomas Nelson (Australia) Ltd., Melbourne.

Lake, J.S. (1978) *Australian freshwater fishes: an illustrated field guide*. Thomas Nelson Australia Pty. Ltd., Melbourne, Australia.

Lewis, W.M.J. (1970) Morphological adaptations of cyprinodontoids for inhabiting oxygen deficient waters. *Copeia* **2**: 319-325.

Lewontin, R.C. (1965) Selection for colonizing ability. In: H. G. Baker & G. L. Stebbins (Eds.). *The genetics of colonizing species*. Academic Press, New York.

Llewellyn, L.C. (1973) Spawning, development, and temperature tolerance of the spangled perch, *Madigania unicolor* (Gunther), from inland waters in Australia. *Australian Journal of Marine and Freshwater Research* **24**: 73-94.

Llewellyn, L.C. (1983) *The distribution of fish in New South Wales*. The Australian Journal for Limnology: Special Publication No. 7.

Lockman, P.M. and Young, G. (2000) Induced spawning and early ontogeny of New Zealand freshwater eels (*Anguilla dieffenbachii* and *A. australis*). *New Zealand Journal of Marine and Freshwater Research* **34**: 135-145.

Lowe-McConnell, R.H. (1975) *Fish communities in tropical freshwaters*. Longman, New York.

Lyons, J. (1986) Capture efficiency of a beach seine for seven freshwater fishes in a north-temperate lake. *North American Journal of Fisheries Management* **6**: 288-289.

MacArthur, R.H. and Wilson, E.O. (1967) *The theory of island biogeography*, Princeton University Press, Princeton, New Jersey.

Mackie, M. and Lewis, P. (2001) *Assessment of gonad staging systems and other methods used in the study of the reproductive biology of narrow-barred spanish mackerel, Scomberomorus commerson, in Western Australia*.

Fisheries research report No. 136. Department of Fisheries, Western Australia.

Mahon, R. (1980) Accuracy of catch-effort methods for estimating fish density and biomass in streams. *Environmental Biology of Fish* **5**: 343-360.

Mahon, R. and Balon, E.K. (1980) Quantitative collection of fishes from small fast flowing streams. *Arch. Hydrobiologia* **90**: 324-329.

Mahon, R., Balon, E.K. and Noakes, D.L.G. (1979) Distribution, community structure and production of fishes in the upper Speed River, Ontario: a preimpoundment study. *Environmental Biology of Fishes* **4**: 219-244.

Marsh-Matthews, E. and Matthews, W.J. (2000) Spatial variation in relative abundance of a widespread numerically dominant fish species and its effect on fish assemblage structure. *Oecologia* **125**: 283-292.

Marshall, S.L. and Parker, S.S. (1982) Pattern identification in the micro-structure of sockeye salmon (*Oncorhynchus nerka*) otoliths. *Canadian Journal of Fisheries and Aquatic Sciences* **39**: 542-547.

Masini, R.J. (1988) *Inland waters of the Pilbara, Western Australia* (Part 1). Environmental Protection Authority, Perth, Western Australia.

Matthews, W.J. (1986) Fish faunal structure in an Ozark stream: stability, persistence and a catastrophic flood. *Copeia* **1986**: 388-397.

Matthews, W.J. (1987) Physicochemical tolerance and selectivity of stream fishes as related to their geographic ranges and local distributions. In: W. J. Matthews & D. C. Heinz (Eds.). *Community and evolutionary ecology of North American stream fishes*. University of Oklahoma Press, Norman.

Matthews, W.J. (1998) *Patterns in freshwater fish ecology*, Chapman and Hall, New York.

Matthews, W.J., Cashner, R.C. and Gelwick, F.P. (1988) Stability and persistence of fish faunas and assemblages in three midwestern streams. *Copeia* **1988**: 945-955.

Matthews, W.J. and Maness, J.D. (1979) Critical thermal maxima oxygen tolerances, and success of cyprinid fishes in a south-western river. *American Midland Naturalist* **24**: 374-377.

Matthews, W.J. and Marsh-Matthews, E. (2003) Effects of drought on fish across axes of space, time and ecological complexity. *Freshwater Biology* **48**: 1232-1253.

Matthews, W.J. and Styron, J.T. (1981) Tolerance of headwater vs. mainstream fishes for abrupt physicochemical changes. *American Midland Naturalist* **105**: 149-158.

McMahon, T.A. (1979) *Hydrological characteristics of arid zones*. Proceedings of the Canberra Symposium, Canberra, IAHS-AISH Publication no. 128.

Medeiros, E.S.F. and Maltchik, L. (2001) Fish assemblage stability in an intermittently flowing stream from the Brazilian semiarid region. *Austral Ecology* **26**: 156-164.

Media Cybernetics. Image Pro Plus, image analysis software, version 5. Silver Springs, Maryland, U.S.A.

Meffe, G.K. and Berra, T.M. (1988) Temporal characteristics of fish assemblage structure in an Ohio stream. *Copeia* **1988**: 684-690.

Meffe, G.K. and Minkley, W.L. (1987) Persistence and stability of fish and invertebrate assemblages in a repeatedly disturbed Sonoran Desert stream. *American Midland Naturalist* **117**: 177-191.

Merrick, J.R. and Schmida, G.E. (1984) *Australian freshwater fishes - biology and management*. John R. Merrick.

Morgan, D.L., and Gill, H.S. (2004) Fish fauna in inland waters of the Pilbara (Indian Ocean) drainage division of Western Australia – evidence for three subprovinces. *Zootaxa* **636**: 1-43.

Morgan, R.P., Killgore, K.J. and Douglas, N.H. (1988) Modified popnet design for collecting fishes in varying depths of submersed aquatic vegetation. *Freshwater Biology* **4**: 533-539.

Moseley, F.N. and Copeland, B.J. (1969) A portable drop-net for representative sampling of nekton. *Marine Science* **14**: 37-45.

Moyle, P.B. and Vondracek, B. (1985) Persistence and structure of the fish assemblage in a small California stream. *Ecology* **66**: 1-13.

Murphy, G.I. (1968) Pattern in life history and the environment. *The American Naturalist* **102**: 391-403.

Murua, H., Kraus, G., Saborido-Rey, F., Witthames, P.R., Thorsen, A. and Junquera, S. (2003) Procedures to estimate fecundity of marine fish species in relation to their reproductive strategy. *Journal of Northwest Atlantic Fisheries Science* **33**: 33-54.

Murua, H. and Saborido-Rey, F. (2003) Female reproductive strategies of marine fish species of the north Atlantic. *Journal of Northwest Atlantic Fisheries Science* **33**: 23-31.

Napier, J. and van Leeuwen, S. (1996) *Common plants of the Pilbara*, Department of Conservation and Land Management, Perth, Western Australia.

Nichols, D.G. and Acuna, E.I. (2001) Annual and batch fecundities of yellowfin sole, *Limanda aspera*, in the eastern Bearing Sea. *Fisheries Bulletin* **99**: 108-122.

Oliva-Paterna, F.J., Minano, P.A. and Torralva, M. (2003) Habitat quality affects the condition of *Barbus sclateri* in Mediterranean semi-arid streams. *Environmental Biology of Fishes* **67**: 13-22.

Orr, T.M. and Milward, N.E. (1984) Reproduction and development of *Neosilurus ater* (Perugia) and *Neosilurus hyrtlii* Steindachner (Teleostei: Plotosidae) in a tropical Queensland stream. *Australian Journal of Marine and Freshwater Research* **35**: 187-195.

Osborne, L.L. and Wiley, M.J. (1992) Influence of tributary spatial position on the structure of warmwater fish communities. *Canadian Journal of Fisheries and Aquatic Sciences* **49**: 671-681.

Ostrand, K.G. and Marks, D.E. (2000) Mortality of prairie stream fishes confined in an isolated pool. *Texas Journal of Science* **52**: 255-258.

Ostrand, K.G. and Wilde, G.R. (2002) Seasonal and spatial variation in a prairie stream-fish assemblage. *Ecology of Freshwater Fish* **11**: 137-149.

Pannella, G. (1974) Otolith growth patterns: an aid in age determination in temperate and tropical fishes. In: T. B. Bagenal (Ed.) *Aging of Fishes, Proceedings of an International Symposium*. Unwin Brothers Ltd., Reading, England.

Perrow, M.R., Jowitt, A.J.D. and Gonzalez, L.Z. (1996) Sampling fish communities in shallow lowland lakes: point-sample electric fishing vs electric fishing within stop-nets. *Fisheries Management and Ecology* **3**: 303-313.

Pianka, E.R. (1970) On r- and K-selection. *The American Naturalist* 104: 592-597.

Poff, N.L. (1996) A hydrogeography of unrelated streams in the United States and an examination of scale-dependence in some hydrological descriptors. *Freshwater Biology* **36**: 71-91.

Poff, N.L. (1997) Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *The North American Benthological Society* **16**: 391-409.

Poff, N.L. and Allan, J.D. (1995) Functional organization of stream fish assemblages in relation to hydrological variability. *Ecology* **76**: 606-627.

Poff, N.L. and Ward, J.V. (1989) Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. *Canadian Journal of Fisheries and Aquatic Sciences* **46**: 1805-1818.

Post, J.R., Parkinson, E.A. and Johnston, N.T. (1999) Density-dependent processes in structured fish populations: interaction strengths in whole-lake experiments. *Ecological Monographs* **69**: 155-175.

Pot, W., Noakes, D.L.G., Ferguson, M.M. and Coker, G. (1984) Quantitative sampling of fishes in a simple system: failure of conventional methods. *Hydrobiologia* **114**: 249-254.

Power, M.E., Matthews, W.J. and Stewart, A.J. (1990) Grazing catfish, fishing birds, and attached algae in a Panamanian stream. *Environmental Biology of Fishes* **26**: 285-294.

Puckridge, J.T. (1992) Bony bream: the story of a survivor. *SAfish* **16**: 19-22.

Puckridge, J.T. and Drewien, M. (1988) The aquatic fauna of the north-western branch of Cooper Creek. In: J. R. Reid & J. Gillen (Eds.). *The Coongie Lakes study*. South Australian Department of Environment and Planning, Adelaide.

Puckridge, J.T., Sheldon, F., Walker, K.F. and Boulton, A.J. (1998) Flow variability and the ecology of large rivers. *Marine and Freshwater Research* **49**: 55-72.

Puckridge, J.T. and Walker, K.F. (1990) Reproductive biology and larval development of a gizzard shad, *Nematalosa erebi* Gunther Dorosomatinae Teleostei, in the River Murray, *South Australia Australian Journal of Marine and Freshwater Research* **41**: 695-712

Pulliam, H.R. (1988) Sources, sinks, and population regulation. *The American Naturalist* **132**: 652-661.

Pusey, B.J. and Arthington, A.H. (1993) Spatial and temporal variation in fish assemblage structure in the Mary River, south-eastern Queensland: the influence of habitat structure. *Environmental Biology of Fishes* **37**: 355-380.

Pusey, B.J., Arthington, A.H., Bird, J.R. and Close, P.G. (2001) Reproduction in three species of rainbowfish (Melanotaeniidae) from rainforest streams in northern Queensland, Australia. *Ecology of Freshwater Fish* **10**: 75-87.

Pusey, B., Arthington, A.H. and Read, M.G. (1995) Species richness and spatial variation in fish assemblage structure in two rivers of the wet tropics of northern Queensland, Australia. *Environmental Biology of Fishes* **37**: 355-380.

Pusey, B.J., Arthington, A.H. and Read, M.G. (1998) Freshwater fishes of the Burdekin River, Australia: biogeography, history and spatial variation in community structure. *Environmental Biology of Fishes* **53**: 303-318.

Pusey, B.J., Kennard, M.J. and Arthington, A.H. (2000) Discharge variability and the development of predictive models relating stream fish assemblage structure to habitat in northeastern Australia. *Ecology of Freshwater Fish* **9**: 30-50.

Pusey, B., Kennard, M. and Arthington, A.H. (2004) *The freshwater fishes of north-eastern Australia*, CSIRO Publishing, Collingwood, Victoria.

Quinn, G. and Keough, M. (2002) *Experimental design and data analysis for biologists*, Cambridge University Press, Cambridge.

Quist, M.C. and Guy, C.S. (2001) Growth and mortality of prairie stream fishes: relations with fish community and instream habitat characteristics. *Ecology of Freshwater Fish* **10**: 88-96.

Rahel, F.J., Lyons, J.D. and Cochran, P.A. (1984) Stochastic or deterministic regulation of assemblage structure? It may depend on how the assemblage is defined. *The American Naturalist* **124**: 583-589.

Reynolds, J.B. (1983) Electrofishing. In: L. A. Neilson & D. L. Johnson (Eds.). *Fisheries techniques manual*. American Fisheries Society Special Publication, Bethesda, Maryland.

Reznick, D.A., Bryga, H. and Endler, J.A. (1990) Experimentally induced life-history evolution in a natural population. *Nature* **346**: 357-359.

Reznick, D. and Endler, J.A. (1982) The impact of predation on life history evolution in Trinidadian guppies (*Poecilia reticulata*). *Evolution* **36**: 160-177.

Reznick, D., Lindbeck, E. and Bryga, H. (1989) Slower growth results in larger otoliths: an experimental test with guppies (*Poecilia reticulata*). *Canadian Journal of Fisheries and Aquatic Sciences* **46**: 108-111.

Reznick, D. and Yang, A.P. (1993) The influence of fluctuating resources on life history: Patterns of allocation and plasticity in female guppies. *Ecology* **74**: 2011-2019.

Richter, B.D., Baumgartner, J.V., Powell, J. and Braun, D.P. (1996) A method for assessing hydrologic alteration within ecosystems. *Conservation Biology* **10**: 1163-1174.

Richter, B.D., Baumgartner, J.V., Wigington, R. and Braun, D.P. (1997) How much water does a river need? *Freshwater Biology* **37**: 231-249.

Rimmer, M.A. (1985a) Reproductive cycle of the fork-tailed catfish *Arius graeffei* Kner and Steindachner (Pisces: Ariidae) from the Clarence River, New South Wales. *Australian Journal of Marine and Freshwater Research* **36**: 23-32.

Rimmer, M.A. (1985b) Growth, feeding and condition of the fork-tailed catfish *Arius graeffei* Kner and Steindachner (Pisces: Ariidae) from the Clarence River, New South Wales. *Australian Journal of Marine and Freshwater Research* **36**: 33-39.

Rimmer, M.A. (1985c) Early development and buccal incubation in the fork-tailed catfish *Arius graeffei* Kner & Steindachner (Pisces: Ariidae) from the Clarence River, New South Wales. *Australian Journal of Marine and Freshwater Research* **36**: 405-411.

Rincon, P.A., Hughes, N.F. and Grossman, G.D. (2000) Landscape approaches to stream fish ecology, mechanistic aspects of habitat selection and behavioural ecology. Introduction and commentary. *Ecology of Freshwater Fish* **9**: 1-3.

Roberts, T.R. (1978) An ichthyological survey of the fly river in Papua New Guinea with descriptions of new species. *Smithsonian Contributions to Zoology* **78**: 405-418.

Rodd, F.H. and Reznick, D.N. (1997) Variation in the demography of guppy populations: the importance of predation and life histories. *Ecology* **78**: 405-418.

Rodriguez, M.A. and Lewis, W.M. (1994) Regulation and stability in fish assemblages of neotropical floodplain lakes. *Oecologia* **99**: 166-180.

Ross, S.T., Matthews, W.J. and Echelle, A.A. (1985) Persistence of stream fish assemblages: effects of environmental change. *The American Naturalist* **126**: 24-40.

Saint-Paul, U., Zuanon, J., Villacorta, C., Garcia, M., Noemi Fabre, N., Berger, U. and Junk, W. (2000) Fish communities in central Amazonian white- and blackwater floodplains. *Environmental Biology of Fishes* **57**: 235-250.

Sale, P.F. and Douglas, W.A. (1984) Temporal variability in the community structure of fish on coral patch reefs and the relation of community structure to reef structure. *Ecology* **65**: 409-422.

Sall, J., Lehman, A. and Creighton, L. (2001) *JMP start statistics, a guide to statistics and data analysis using JMP and JMP IN software*, SAS Institute Inc., Second edition, Duxbury Thomson Learning, Canada.

SAS Institute (2001) JMP IN, statistical discovery software, version four. Duxbury Thomson Learning.

Schlosser, I.J. (1985) Flow regime, juvenile abundance, and the assemblage structure of stream fishes. *Ecology* **66**: 1484-1490.

Schlosser, I.J. (1987a) A conceptual framework for fish communities in small warmwater streams. In: W. J. Matthews & D. C. Heinz (Eds.). *Community and evolutionary ecology of North American stream fishes*. University of Oklahoma Press, Norman.

Schlosser, I.J. (1987b) The role of predation in age- and size-related habitat use by stream fishes. *Ecology* **68**: 651-659.

Schlosser, I.J. (1991) Stream fish ecology: a landscape perspective. *Bioscience* **4**1: 704-712.

Schlosser, I.J. (1995a) Dispersal, boundary processes, and trophic-level interactions in streams adjacent to beaver ponds. *Ecology* **76**: 908-925.

Schlosser, I.J. (1995b) Critical landscape attributes that influence fish population dynamics in headwater streams. *Hydrobiologia* **303**: 71-81.

Schlosser, I.J. (1998) Fish recruitment, dispersal, and trophic interactions in a heterogeneous lotic environment. *Oecologia* **113**: 260-268.

Secor, D.H. and Dean, J.M. (1989) Somatic growth effects on the otolith-fish size relationship in young pond-reared striped bass, *Morone saxatilis*. *Canadian Journal of Fisheries and Aquatic Sciences* **46**: 113-121.

Secor, D.H., Dean, J.M. and Hansbarger, J. (1992a) Modification of the quatrefoil light trap for use in hatchery ponds. *The Progressive Fish-Culturist* **54**: 202-205.

Secor, D.H., Dean, J.M. and Laban, E.H. (1992b) Otolith removal and preparation for microstructural examination. *Canadian Journal of Fisheries and Aquatic Sciences*, **117**: 19-57.

Sheldon, A.L. (1968) Species diversity and longitudinal succession in stream fishes. *Ecology* **49**: 193-198.

Shireman, J.V., Colle, D.E. and DuRant, D.F. (1981) Efficiency of rotenone sampling with large and small block nets in vegetated and open-water habitats. *American Fisheries Society* **110**: 77-80.

Siegel, S. and Castellan, J.J. (1988) *Nonparametric statistics for the behavioral sciences*, Second edition. McGraw-Hill, New York.

Sinclair, A.F., Swain, D.P. and Hanson, J.M. (2002) Disentangling the effects of size-selective mortality, density, and temperature on length-at-age. *Canadian Journal of Fisheries and Aquatic Sciences* **59**: 372-382.

Sloane, R.D. (1984) Distribution, abundance, growth and food of freshwater eels (*Anguilla* spp.) in the Douglas River, Tasmania. *Australian Journal of Marine and Freshwater Research* **35**: 325-339.

Smale, M.A. and Rabeni, C.F. (1995) Influences of hypoxia and hyperthermia on fish species composition in headwater streams. *Transactions of the American Fisheries Society* **124**: 711-725.

Snodgrass, J.W., Bryan, A.L., Lide, R.F. and Smith, G.M. (1996) Factors affecting the occurrence and structure of fish assemblages in isolated wetlands of the upper coastal plain, U.S.A. *Canadian Journal of Fisheries and Aquatic Sciences* **53**: 443-454.

Sogard, S.M. and Olla, B.L. (2001) Growth and behavioural responses to elevated temperatures by juvenile sablefish, *Anoplopoma fimbria*, and the interactive role of food availability. *Marine Ecology Progress Series* **217**: 121-134.

Southwood, T.R.E., May, R.M., Hassell, M.P. and Conway, G.R. (1974) Ecological strategies and population parameters. *The American Naturalist* **108**: 791-803.

Spranza, J.J. and Stanley, E.H. (2000) Condition, growth, and reproductive styles of fishes exposed to different environmental regimes in a prairie drainage. *Environmental Biology of Fishes* **59**: 99-109.

Stanley, E.H., Fisher, S.G. and Grimm, N.B. (1997) Ecosystem expansion and contraction in streams. *Bioscience* **47**: 427-435.

Starrett, W.C. (1951) Some factors affecting the abundance of minnows in the Des Moines River, Iowa. *Ecology* **32**: 13-27.

Stearns, S.C. (1976) Life -history tactics: a review of the ideas. *The Quarterly Review of Biology* **51**: 3-47.

Stearns, S.C. (1989) The evolutionary significance of phenotypic plasticity. *Bioscience* **39**: 436-445.

Stearns, S.C. (1992) *The evolution of life histories*, Oxford University Press, Oxford.

Stearns, S.C. and Koella, J.C. (1986) The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size at maturity. *Evolution* **40**: 893-913.

Taylor, C.M. (1997) Fish species richness and incidence patterns in isolated and connected stream pools: effects of pool volume and spatial position. *Oecologia* **110**: 560-566.

Taylor, C.M., Winston, M.R. and Matthews, W.J. (1996) Temporal variation in tributary and mainstem fish assemblages in a great plains stream system. *Copeia* **1996**: 280-289.

Templeman, W. and Squires, H.J. (1956) Relationship of otolith lengths and weights in the haddock *Melanogrammus aeglefinus* (L.) to the rate of growth of the fish. *Journal of the Fisheries Research Board of Canada* **13**: 467-487.

Todd, P.R. (1981a) Morphometric changes, gonad histology, and fecundity estimates in migrating New Zealand freshwater eels (*Anguilla* spp.). *New Zealand Journal of Marine and Freshwater Research* **15**: 155-170.

Todd, P.R. (1981b) Timing and periodicy of migrating New Zealand freshwater eels. *New Zealand Journal of Marine and Freshwater Research* **15**: 225-235.

Trammer, E.J. (1977) Catastrophic mortality of stream fishes trapped in shrinking pools. *American Midland Naturalist* **97**: 469-478.

Trexler, J.C., Loftus, W.F., Jordan, F., Lorenz, J.J., Chick, J.H. and Kobza, R.M. (2000) Empirical assessment of fish introductions in a subtropical wetland: an evaluation of contrasting views. *Biological Invasions* **2**: 265-277.

Unmack, P.J. (2001) Fish persistence and fluvial geomorphology in central Australia. *Journal of Arid Environments* **49**: 653-669.

Vaux, P.D., Whittier, T.R., De Cesare, G. and Kurtenbach, J.P. (2000) Evaluation of a backpack electrofishing unit for multiple lake surveys of fish assemblage structure. *North American Journal of Fisheries Management* **20**: 168-179.

Wanzenbock, J. and Keresztessy, K. (1995) Zonation of a lentic ecotone and its correspondence to life history strategies of fish. *Hydrobiologia* **303**: 247-255.

Weatherley, A.H. and Gill, H.S. (1987) *The biology of fish growth*, Academic Press, London.

Werner, E.E. and Gilliam, J.F. (1984) The ontogenetic niche and species interactions in size structured populations. *Annual Review of Ecology Systematics* **15**: 395-425.

West, G. (1990) Methods of assessing ovarian development in fishes: a review. *Australian Journal of Marine and Freshwater Research* **41**: 199-222.

Wilbur, H.M. (1980) Complex life cycles. *Annual Review of Ecology Systematics* 11: 67-94.

Wilbur, H.M., Tinkle, D.W. and Collins, J.P. (1974) Environmental certainty, trophic level, and resource availability in life history evolution. *The American Naturalist* **108**: 805-817.

Winemiller, K.O. (1989) Patterns of variation in life history among South American fishes in seasonal environments. *Oecologia* **81**: 225-241.

Winemiller, K.O. (1992) Life-history strategies and the effectiveness of sexual selection. *Oikos* **63**: 318-327.

Winemiller, K.O. and Rose, K.A. (1992) Patterns of life-history diversification in North American fishes: implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences* **49**: 2196-2218.

Wooton, R.J. (1992) *Fish ecology*. Chapman and Hall, New York.

WRAP (1997) *The state of the northern rivers*, Water and Rivers Commission. WRAP 10.

Yant, P.R., Karr, J.R. and Angermeier, P.L. (1984) Stochasticity in stream fish communities: an alternative interpretation. *The American Naturalist* **124**: 573-582.

Zar, J.H. (1999) *Biostatistical analysis*, fourth edition. Prentice-Hall Inc., New Jersey.

Zaret, T.M. and Rand, A.S. (1971) Competition in tropical stream fishes: support for the competitive exclusion principle. *Ecology* **52**: 336-342.

This page has been left blank intentionally.