

**Muresk Institute of Agriculture  
Department of Applied Biosciences**

**Ethology and production of freshwater crayfish in  
aquatic polysystems in Western Australia**

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**This thesis is presented for the degree of  
Doctor of Philosophy  
of  
Curtin University of Technology**

**December 2005**

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Aquatic polyculture has been recognised as a potential way of increasing the cost-effectiveness of farming marron (*Cherax tenuimanus*), as it can lower average costs of production, increase system yields, and reduce economic risks associated with monoculture operations. Polyculture also increases ecological stability and assists recycling processes, which can result in synergistic benefits to participating species. In aquaculture, this synergism can result in increased profitability through advanced growth rates and/or reduced feed input. However, many of the inherent advantages of aquatic polyculture rely on cohabitants occupying distinct ecological niches within the system. In Western Australia, opportunities to multi-crop aquatic species are limited by species choice due to low natural diversity and strict translocation policies. This creates a situation where available aquaculture species exhibit overlaps in occupied niches. Effects of this overlap can include direct predation, increased intraspecific conflict, and competition for resources such as shelter and food.

Prior to this study, silver perch (*Bidyanus bidyanus*) were identified as a prime candidate for duoculture with marron, based on favourable schooling and feeding characteristics, and preliminary trials demonstrated commercial benefits, including synergistic growth advantages to marron. However, investigations also showed that silver perch will predate on both small and moulting crayfish under certain conditions, and that growth of silver perch was inhibited when held in cages to prevent predation. The work reported in this thesis was undertaken to address the niche overlap existing between marron and silver perch, and therefore assist the marron industry in Western Australia in implementing appropriate management strategies for diversification. Research focussed on investigating the ecological issues underlying interspecific interactions in marron polysystems, with the eventual aim of presenting information that could assist system managers in determining optimal conditions required to reduce antagonistic relationships and maximise synergism, ultimately leading to higher yields.

Seven trials were conducted in three culture systems (54L aquaria, 250L aquaria and 720m<sup>2</sup> experimental ponds) examining the ability of marron to detect, recognise and respond to a range of information cues (chemical, visual, tactile) from two potential predators (silver perch and Murray cod), with and without competition from conspecific and heterospecific crayfish (*Cherax albidus*). The ability of marron to interpret and respond appropriately to these variables was tested under a range of system-specific

conditions, including stocking density, stocking size, shelter/habitat complexity, food availability, light intensity and life stage. Cage culture conditions were also examined to determine if the addition of shelter would mediate growth inhibition previously recorded, and to determine the desired stocking regime to return market sized fish in one growth season (8 months).

Results from laboratory research and field-based trials did not support the free-range culture of marron and silver perch, even where turbidity and habitat complexity is high. Although both male and female marron (various sizes) demonstrated an ability to detect and differentiate between chemical and visual cues from potential predators, avoidance responses were only displayed upon attack from predators, or following predation of conspecifics; and avoidance strategies employed by marron were relatively ineffective. Although marron showed some capacity to recognise an impending predatory threat, high initial mortalities and growth inhibition due to reduced foraging, would greatly reduce system yields. In addition, intraspecific competition between marron is likely to increase as avoidance responses would lead to high relative densities within shelters.

The lack of avoidance behaviour displayed by marron when only visual and chemical cues from predators are present strongly supports cage culture of silver perch in marron ponds. As marron did not appear to alter their general behaviour (e.g. foraging) based on cues associated with silver perch held in cages they stand to benefit from cohabitation. Field-trials examining the pond culture of marron and caged silver perch demonstrated synergistic growth advantages to marron, compared to monoculture, and also identified several system variables that appear to improve polyculture production. The addition of bank shelters (within 1m of waters edge) was suggested to give marron a competitive advantage when moulting, expressed through growth and survival. Survival of marron was also increased in caged polyculture ponds, compared to monoculture, most likely due to increased health status (due to improved recycling) and/or increased habitat complexity owing to the presence of fish cages. Growth inhibition previously reported when silver perch are held in cages was mediated to some degree by cage shelters, which appeared to increase feeding behaviour, reduce general anxiety and resulted in increased growth. The introduction of advanced silver perch fingerlings in order to produce market-sized fish in one growth season was also supported. However, it is recommended that cage culture dynamics require further elucidation if

silver perch are to be commercially successful as a stand-alone crop using this grow-out strategy. Significantly, the synergistic growth advantages experienced by marron when grown with fish demonstrate value from polyculture even if fish are not depended on as a secondary income. In this case, other species may also provide similar advantages, and a native candidate such as freshwater cobbler (*Tandanus bostocki*) would also redress problems associated with translocation laws restricting the use of silver perch in some areas of Western Australia. As no density effects were recorded in any of the trials conducted for either species, further investigation into increased system loads is required. In addition, as nutrient loads, and thus phytoplankton density, usually increases proportionately with pond biomass it is recommended that an additional herbivorous species, for example white eye mullet (*Mugil cephalus*), be examined in conjunction with increased density trials.

Field research reported in this thesis was carried out in earthen ponds utilising remediated water from a acidified mine lake. Over a three-year period water quality parameters were maintained within optimal ranges for marron and silver perch, and survival and growth of both species was comparable to industry levels. These results validate the effectiveness of mine-water treatment technology; and accordingly, results support commercial viability of crayfish polyculture utilising remediated acid mine water. The large water resources offered by the numerous artificial lakes created from open cut mining has the potential to sustain a large successful aquaculture industry for Collie (Western Australia), and in other areas with extension of water treatment technology.

The incorporation of caged silver perch into marron ponds not only takes advantage of the inherent economic and risk-spreading benefits from a diversified management strategy, but also incorporates a number of within-system benefits due to synergism between species. The ecological approach to aquatic polyculture research reported in this thesis has elucidated key communication factors underlying interactions within crayfish polysystems, which is critical to a knowledge-based approach to system management.

**This thesis is dedicated to my grandfather  
Stan Storer**

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## **STATEMENT OF SOURCES**

### **DECLARATION**

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution of tertiary education. Information derived from published or unpublished sources has been acknowledged in the text and a list of references is given.

**Tim Storer**

**17th November 2005**

### **STATEMENT OF ACCESS TO THESIS**

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**Tim Storer**

**17th November 2005**

## ***Acknowledgements***

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*Some perspective...* trials in this thesis involved the construction of seven 0.072 ha ponds and twelve 15m long fish cages; the set-up of over 150 aquaria and 20 large tanks, the assembling of 6 paddlewheels and over 500 marron hides; almost 100 pond harvests (half of these in conditions postal workers wouldn't consider); gross measurements on over 20,000 individual crayfish and almost 14,000 fish; and 24,160 separate water quality data points (imagine the data entry and statistics!!!). It wasn't until I began writing the acknowledgements for this thesis that I realised the astounding amount of help I have had along the way, without which none of this would be possible.

I would firstly like to acknowledge funding from the Centre for Sustainable Mine Lakes, representing input from mining companies throughout Australia. In particular, I would like to thank Wesfarmers Premier Coal for their dedicated funding for the investigation into aquaculture end-uses for mine lake closure. Wesfarmers input included building the water treatment system and ponds, and my research scholarship. I would also like to make special mention of Peter Ashton for his commitment, drive, support, friendship and level head, without Peter this project would have been dead before it began.

An army of people helped me to conduct the trials in this thesis, however with literally hundreds of students (both willing and commandeered) from the South-West Regional College of TAFE, Curtin University and the Collie Senior High School, over more than three years, there are too many to mention individually – you know who you are, thankyou! I would like to make particular acknowledgement of Paul Irving for his help with a large part of the work conducted for this thesis, as both a student and colleague – your unnerving love for cobbler inspires us all, and thank god for your fondness for freezing, muddy ponds!

Many friends and colleagues from TAFE and Curtin University have supported me throughout this 'ordeal'. In particular, I would like to thank my proxy mums, Mary Ingram and Terri Gianola, for their endless support in the face of extreme adversity, and Kerri Rioux - the true power behind the man. I would also like to thank Kerry and Terri for getting their hands wet (what a team!), Jaime and Dr Jane for their shoulders to whinge on, Dr Ravi – perhaps the best hallway cricketer this world has ever seen, Prayadt for teaching me the secrets of the fish-bag, Debra Ryan (for all the nights... dissecting), Luke 'redfin' Spencer for his help and... umm... anger! To Cliff and Fiona Mac for their help on and off the field and Scotty for forcing me to learn statistics.



## ***Acknowledgements***

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I would particularly like to recognise the support of my friends, to Mike, Kell, Wattsie, Joel, Dan, Byron, Simo and the crew for stress relief and help with top-down studies into nature conservation, to the midget and Kinky Inky for Monday-Friday drinks! Benjamin for keeping me grounded, Baby-Huey for taking me in! and the mighty Georgia Salmon for her perspective. I would like to make special mention of Patrick Ridley, whose friendship over many years has been invaluable, and his help with everything from monitoring to harvesting to statistics is appreciated. I am also thankful for his special skills in white-water sinking, and honestly believing that I was the true inventor of the cheesy crust pizza.

Thanks also to Rick Scott for donation of Murray cod, Rod and Sue Bamess for all the marron and perch, Alexandra Hoschke for her comments on the final manuscript, and Michelle Ingram for wading through the lit. review.

To my family: Jo (or the less cool, Jodi), Paul and Vicky, grandparents Stan and Grace Storer and those happy parasites Gage and Hunter, who loved getting me up early to 'study'. I would like to thank everyone for everything. I would especially like to thank my parents Joan and Lynton for their 'constructive nagging' and endless love and support.

My final acknowledgement is to my supervisors who have taught me much more than involved within the bounds of this thesis. To Louis Evans for her initial faith in me, without which I would probably be still working at Pizza Hut (making millions off my stuffed crust pizza idea), and also for comments on my literature review. Most importantly, thanks to Glen Whisson, whose expertise, guidance, card counting abilities, patience, and countless hours editing were invaluable... P.S. sorry for any grey hairs.

Without the help of my friends and colleagues I could not have completed any of the work in this thesis, and their efforts cannot be understated or forgotten (If I have forgotten anyone along the way I apologise!).

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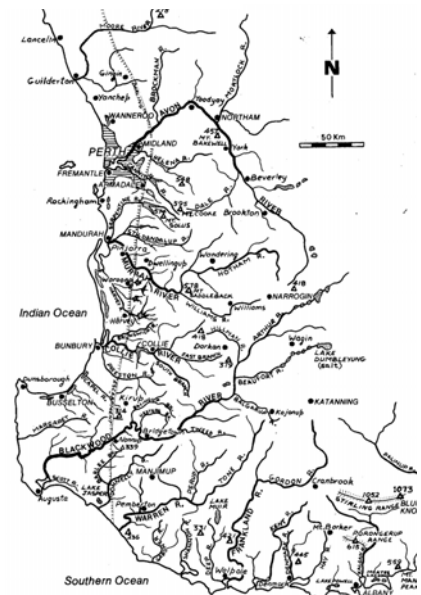
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# Chapter one

---



## **Introduction**

*This introductory chapter examines the state of world aquaculture, the freshwater crayfish industry in Australia, and the benefits of diversified production strategies for the marron industry in Western Australia*

## 1.1 State of the world's fisheries

World capture fishing is a US \$81 billion/y industry, employing 28 million fishers and 4.1 million vessels in 2000/2001 (FAO 2003).

Commercial harvesting of the world's oceans reached a plateau in the early 1990s (FAO 2002, 2004) attributed to unsustainable anthropogenic pressure on global fish populations (Pafit 1995, Kurlansky 1997,). Overfishing, illegal and unregistered fishing activities and habitat destruction have contributed to the present situation (Moore 1999). Currently, 60% of traditional fisheries are considered at-limit or over exploited (Kurlansky 1997, Wainwright and Kirkness 1997, Moore 1999), with catch reductions in many major fisheries and complete failure of others (Table 1.1).

**Table 1.1** Examples of world capture fisheries in decline or collapse (2004)

Decline	Collapsed
Alaskan halibut (1)	Canadian fishery (1)
Orange roughy – 96% loss (2,3)	Atlantic cod (2)
Southern bluefin tuna – 82% loss (4)	Haddock (5)
Patagonian toothfish (5)	Redfish (5)
Northern bluefin tuna (5)	...
Dories (5)	...
Afonsinos (5)	...

1. Pafit 1995, 2. Kurlansky 1997, 3. Mascher, 1997, 4. Wainwright and Kirkness 1997, 5. FAO 2003

## 1.2 The role of aquaculture

With expanding world populations demanding quality fish products, the deficit between supply and demand is increasing. To address this growing shortfall, aquaculture production has increased steadily over the past decade, growing 9-10%/y between 1990 (13.1 million tonnes) and 2001 (37.5 million tonnes), and currently employing around 7 million people (FAO 2003). Of the total cultured product, inland aquaculture contributed almost two thirds of volume and over half of total supply was from finfish, predominantly freshwater species (FAO 2003).

Aquaculture production is currently estimated at over 41% of total fisheries production (FAOSTAT 2004). When compared with production of 29.1% in 2001 (FAO 2003), 27.3% in 2000 (FAO 2002), 16.2% in 1990 (FAO 1997), and 3.9% in 1970 (FAO 2002) the industry stands as one of the worlds fastest growing sectors, expanding more rapidly than all other animal food producing industries (FAO 2003). However, even with current levels of production the need for further expansion of the aquaculture sector is emphasised (Bangkok Declaration and Strategy - NACA/FAO 2002) in order to successfully ameliorate the increasing shortfall in supply.

### **1.3 Status of Australian aquaculture**

In Australia, the aquaculture industry has developed rapidly over the past decade and appears likely to make a major contribution to the future growth of Australia's food production and exporting industries. In 2002/03, Australia's total aquaculture production was valued at AUD \$743 million, 32% of the total gross value of production from Australian fisheries (ABARE 2003a), and followed a 14% nominal average growth rate over the past decade (ABARE 2003b).

In 2001/2002, over 44 thousand tonnes of aquacultured product were harvested in Australia and over 15 million juveniles produced (mostly finfish) (AATD 2003). Species cultured commercially, in order of worth, included southern blue fin tuna, pearl oysters, salmonoids, edible oysters, prawns, barramundi, mussels, freshwater crayfish, microalgae, native freshwater fish, aquarium fish, crocodiles, abalone, miscellaneous marine finfish, eels, brine shrimp, freshwater prawns, scallops and aquatic worms. Over two-thirds of total production in Australia came from tuna and oysters (pearl and edible), with the freshwater crayfish industry considered the 8th most valuable aquaculture sector (AADT 2003).

It has been estimated by the aquaculture industry that sales could treble to AUD \$2.5 billion by 2010 if competitive advantages to meet increasing domestic and global demand for aquaculture products can be successfully exploited (ABARE 2003b).

One of the key groups of animals targeted for aquaculture expansion in Australia is freshwater crayfish (AADT 2003, ABARE 2003b), especially as culture technology is easily adaptable within existing farming practices.

## 1.4 Freshwater crayfish aquaculture

The culture of freshwater crayfish is an established and lucrative industry worldwide. Globally, freshwater crayfish aquaculture contributed 685 thousand tonnes to the seafood industry in 2002/02, worth over AUD \$3.7 billion (FAO-FIGIS 2005).

## 1.5 Freshwater crayfish aquaculture in Australia

In Australia, aquaculture production of freshwater crayfish is centred on three species; marron (*Cherax tenuimanus*), redclaw (*Cherax quadricarinatus*), and yabbies (*Cherax albidus*). Production from these species has been increasing over the past 10 years, and with improvements in production guidelines (Wingfield 2000), stronger and more unified grower associations (Wingfield 2000), cooperative marketing ventures, and increasing demand for aquacultured products (Wingfield 2000, ABARE 2003b), this trend is expected to continue (Piper 2000, ABARE 2003b).

In 2001/2002, production of Australian freshwater crayfish was 297 tonnes, valued at AUD \$4.4 million (farm gate), comprised of yabbies - AUD \$2.0 million, redclaw - AUD \$1.0 million, and marron - AUD \$1.4 million (ABARE 2003a). Based on expected improvements in artificial diets, reduction in predation, improved water supply and increased capitalisation (O'Sullivan and Roberts 1999, O'Sullivan and Dobson 2000) commercial production of yabbies, redclaw and marron was predicted to increase by 293%, 239% and 381%, respectively, between 1998-99 and 2004-05 (Piper 2000, ABARE 2003b).

Market prices of Australian freshwater crayfish are expected to remain stable regardless of forecast increases in production (Lawrence 1998, Piper 2000), due to:

- their uniqueness, high quality and rarity in overseas markets, thus, higher volumes are likely to find ready acceptance at current prices in Europe, Japan, Korea and south-east Asia and in the larger coastal cities on the eastern and western side of USA (Piper 2000);
- local markets absorbing increased volumes of product without diminution in price as increased production leads to regular availability of quality product in retail and restaurant outlets (Piper 2000);

- the larger end of the freshwater crayfish production compares favourably on price and quality grounds with the smaller end of the marine crayfish product (Piper 2000);
- Australian crayfish being significantly larger (100-300g+) than the main international competitors (Lawrence et al. 1995) (i.e. adult red swamp crayfish - 30-35g; Huner and Lindqvist 1995).

The freshwater crayfish industry within Australia has expanded, intensified and made minor but encouraging technological advances over the past two decades, and with a stable global demand for quality product, the freshwater crayfish industry has a very high potential for future expansion (Bennison and Whisson 1992, Lawrence 1998, Piper 2000). One of the expected major contributors to industry expansion in freshwater crayfish is marron (Lawrence 1998).

## **1.6 Marron industry in Western Australia**

Marron are regarded as a gourmet product by chefs, attracting a higher unit price than both yabbies and redclaw (FWA 2002a). Within Western Australia, commercial marron production is generally confined to the south-west of Western Australia, although an expanding industry exists in Kangaroo Island, South Australia (Piper 2000). Previous unsuccessful translocations of marron overseas have occurred in South Africa, Zimbabwe, Japan, China, USA and the Caribbean (Morrissy et al. 1990).

Marron farming has received significant attention from researchers, farmers and investors over the past 30 years and consequently, there is now a more complete understanding of general biology and culture technology. However, monoculture practices in Western Australia have not lived up to predicted expectations, due to either lower than expected growth rates, environmental impediments such as drought, high costs of production and a lack of scientific approach (Bennison and Whisson 1992, Morrissy et al. 1995a, O'Sullivan and Roberts 1999, ABARE 2003a).

Commercial sensitivities mean that accurate information on income and operating costs in commercial farms is not readily available. Based on information from producers and processors, value and production figures for the marron industry in

2001/02 were calculated by the Australian Bureau of Agriculture and Resources Economics (2003a) (Table 1.2).

**Table 1.2** Value and production of marron (2001/2002) (ABARE 2003a)

Australian marron production	58 tonnes
Western Australian production	46 tonnes
Net worth	AUD \$1.4M (farm gate)

The Western Australian Department of Fisheries reported 2001/02 production from 187 producers (FWA 2003a), however anecdotal evidence suggests that a large percentage of production stems directly from a small number of farmers with 'best practice' operations (How and Lawrence 2004). Average farm production is estimated at around 600/kg/ha/y, however levels of up to 4000/kg/ha/y have been achieved (Morrissy et al. 1995a). The WA Department of Fisheries state that for well-designed and managed commercial ponds, 2000 kg/ha/y of marketable product is considered commercially viable and a realistic goal (MGA 2002, FWA 2004). These figures are based on market price, with current farm gate returns of AUD \$23.8/kg (ABARE 2003b) and wholesale prices increasing with unit size (AUD \$16-\$30) (S. Bamess pers. comm. 2004). Retail prices for live marron are reported to fluctuate between AUD \$110-140/kg (RIRDC 2002a), depending on market, supply and season.

### **1.7 Impediments to expansion of the marron industry**

With average farm production estimates falling well below figures considered to be commercially attractive (How and Lawrence 2004) there are a number of production aspects that require elucidation and investigation. The fact that some farms have returned production figures in excess of 2000/kg/ha/y (Morrissy et al. 1995a, FWA 2004) illustrates that industry potential is realistic, and progress requires greater communication and research.

The marron industry also faces a number of micro and macro-economic factors forming major obstacles to development. These obstacles relate predominantly to inherent problems associated with monoculture production, and for a product that is open to temporal fluctuations in factors ranging from culture environment to market status. Specifically, these problems include:

**Micro-economic factors (rural farming community, on-farm)**

- Reliance on one seasonal income source/y;
- Fluctuations in market demand (Smailes 1997);
- Lack of continuity of supply (Morrissy 1990, Whisson 2000);
- Low industry volumes;
- Competition (Whisson 2000);
- Lack of industry communication;
- Customer perception - inability to attract investors/finance (Whisson 2000);
- Variation in product quality (Whisson 2000);
- Distribution problems (Whisson 2000);
- Processor capacity;
- Pricing (Whisson 2000).

**Macro-economic factors (international, national, regional, state)**

- Fluctuating world economies - declining returns (Taylor 1996, Tonts et al. 2000, Whisson 2000), rising input costs (Taylor 1996, Smailes 1997);
- Import tariffs and trade restrictions (live product) (RIRDC 2002b);
- Translocation policies-restrictions (Whisson 2000);
- General instability in world markets (Whisson 2000);
- Reduction in government support (Higgins 1999);
- Unstable global marketplace position due to minor contribution of Australian freshwater crayfish.

These factors represent a relatively high level of business risk and uncertainty confronting investors and existing operations looking towards expansion (Whisson 2000, RIRDC 2002a). One of the tools available to farmers is to turn to risk spreading strategies such as diversification (Whisson 1993, Kraus 1995, RIRDC 2002a/b).

## 1.8 Diversification options in aquaculture

Farm diversification is a valid form of rural adjustment where additional, complementary industries are added to existing operations (Anosike and Coughenour 1990, Tonts et al. 2000, RIRDC 2002a, RIRDC 2002b). Essentially, business risk is spread by removing reliance on one income source through increasing product range (Whisson 1993, Kraus 1995). In primary industry, the risk posed by a single revenue stream is exacerbated as it not only relies on economic status but also favourable environmental conditions (Hardaker et al. 1997). The range of options for mixed farming enterprises are commonly divided into two sectors based of the nature of associated industries:

### **Agricultural**

The combination of additional agricultural output options to traditional farming ventures (McMurty et al. 1997, RIRDC 2002a). This could be adding lamb production to a pre-existing wool enterprise, or less traditional options, such as combining fruit crops with aquaculture or tree plantations on livestock leases (RIRDC 2002a).

### **Non-agricultural**

Non-agricultural diversification options include enterprises such as, ecotourism - farm based accommodation and recreation (Saunders and O'Sullivan 1998); on-farm processing and marketing; and 'passive diversification' options where land or infrastructure is leased for non-agricultural purposes (RIRDC 2002a).

Farmers looking at diversification options in aquaculture have to consider the effect that existing or additional industries would have on water quality. Diversification of traditional farming operations in Australia has demonstrated successful implementation of aquaculture (RIRDC 2002a, Gooley and Gavine 2003). In a recent study by the Rural Industries Research and Development Commission (2002a) into the cost and benefits of farm diversification a number of case studies were profiled. This study included two examples involving aquaculture. Firstly, the addition of trout aquaculture to a sheep farm in NSW which yielded a cost-benefit ratio of 1.2 over 7 years, and secondly, a sheep-cropping enterprise diversified with marron aquaculture in WA, resulting in a cost benefit ratio of 1.5 over 5 years. Other forms of aquaculture



diversification include value-adding, such as on-farm processing and marketing of stock. An example of this is the production of gourmet lemon or chilli yabbies (Cambinata yabbies, Western Australia). In this case, 200g jars containing 14 small yabby tails with an approximate net weight of 60g are sold at AUD \$17.00/jar. This activity not only adds value to product, but allows the sale of small stock, not generally accepted by market.

A diversification option which is practised extensively overseas (e.g. Scott et al. 1988, Pillay 1993, Brummett and Alon 1994, Milstein 1997) and has been recently explored in Western Australia for its 'within system' benefits is **aquatic polyculture** (Whisson 2000, Whisson and Storer 2003, Storer et al. 2004a).

### 1.9 Aquatic polysystems in Western Australia

Aquatic polyculture is the combination of multiple aquatic crops in the same pond. The original technology and models for aquatic polyculture were developed in areas such as Israel (Peterson 2000) and China (Pillay 1993), where water resources are scarce and expensive, and multiple use is essential. Although the technology for aquatic polyculture was spawned out of necessity, intrinsic benefits have lead to technology being pursued around the world for economic, social and environmental advantages. The term '**aquatic polysystem**' is used in this thesis to describe a system approach to aquatic polyculture research. This terminology was utilised to explain the combination of biological, chemical and physical processors that influence the functioning of a polyculture system, or polysystem, and the holistic approach required in order to optimise culture technology.

A system view of aquatic polyculture would address many of economic problems confronting marron growers, whilst incorporating production advantages stemming from the use of complementary species. The benefits include:

- Increased net productivity and profitability (e.g. Cohen et al. 1983, Swift 1993, Wahab et al. 1995, Gooley and Gavine 2003);
- Income spreading across year;

- Reduced capital outlay and cost-effectiveness through resource sharing (Gooley 2000, McKinnon et al. 2000, Whisson 2000, Gooley and Gavine 2003);
- Offsetting management and maintenance costs (Harris and Glatz 2002, Whisson 2000, Gooley and Gavine 2003);
- Increased nutrient cycling through increased food web complexity (Cohen 1984, Gooley and Gavine 2003);
- Lower net water usage (Gooley and Gavine 2003);
- Improved water quality (Rouse et al. 1987);
- Synergistic benefits including increased growth and condition of component species (Whisson 2000, Whisson and Storer 2003, Storer et al. 2004a).

Although results from aquatic polysystems are encouraging, technology needs development and modification for each area of implementation, as site-specific variations in culture conditions alters system dynamics and thus, management needs. The key element for successful implementation of polyculture technology in new areas relies on the selection of component species. Species have to be chosen based on water quality and environmental conditions, and selection requires consideration of economic factors, government policy, regulatory restrictions and market opportunity (Spencer 2000). However, paramount to the success of aquatic polyculture is the selection of species displaying complementary niche occupations, to reduce competition or predation and maximise synergistic benefits (Rouse et al. 1987, Whisson 2000)

### **1.10 Factors governing production in crayfish polysystems**

Marron are the base species for culture in Western Australian polysystems, as existing production and infrastructure is centred on pond culture of marron, and the marron industry stands to gain from risk spreading strategies (Section 1.7). Marron have demonstrated potential for duoculture with finfish (Whisson 1997, 1998, 2000, Storer and Whisson 2003, Storer et al. 2004a) and pelagic finfish species are the most likely polyculture candidate as they occupy a separate space in the water column.

In Western Australia, the selection of species displaying favourable qualities for integration into existing marron ponds is limited (Jones and Ruscoe 1996, Lambert 1998, Whisson 1998, Whisson 2000). This is primarily due to the lack of acceptable native species and strict translocation policies preventing exotic introductions. The choice of a complementary finfish for duoculture with marron is made more difficult due to the evolution of marron in a relatively predator-free environment (Morrissy 1997, FWA 1999, Allen et al 2002). As marron are the dominant invertebrate in their natural environment they have not been exposed to predation pressure, and therefore it is unlikely that they have evolved effective avoidance strategies. The introduction of exotic finfish in other parts of the world has resulted in heavy predation on benthic macroinvertebrates (Stoddard 1987, Bradford et al. 1998, Knapp et al. 2001), and it is likely marron would suffer similarly.

Production strategies for Western Australian polysystems need to consider ways to reduce overlaps in niche selection between component species in order to optimise production.

## **1.11 Key species for culture in Western Australian polysystems**

### **1.11.1 Marron, *Cherax tenuimanus***

Marron are a large freshwater crayfish native to permanent forested rivers in high-rainfall areas in the south-west of Western Australia (Lawrence 1995). Marron are well recognised as a species with aquaculture potential (Morrissy 1992a, Jussila and Evans 1997), being the third largest freshwater crayfish in the world (largest aquaculture species), having one of the highest 'tail-with-shell' recovery rates (42-43%, comparable with marine rock lobsters), and are rated as one of the finest-flavoured crustaceans available (Morrissy et al. 1990).

The monoculture of marron is semi-intensive, carried out in purpose built ponds approximately 1.8m deep (standpipe). Pond depth was determined through investigations, promoting optimum temperature conditions (FWA 1999), although the marron occupy only the benthos, with pelagic regions empty. The addition of pelagic finfish utilises this space.

### 1.11.2 Silver perch, *Bidyanus bidyanus*

A number of species have been investigated for polyculture potential with marron (Lambert 1998, Whisson 2000, Storer et al. 2004a). Of these, silver perch appear to have schooling and feeding characteristics (Rowland and Barlow 1991) most conducive to cohabitation with marron (Jones and Ruscoe 1996, Whisson 1998, Whisson 2000).

Silver perch are a freshwater fish with native range extending through most of the Murray Darling Basin, including the western drainage of New South Wales. Silver perch are predominantly produced using semi-intensive pond cultures (Rowland 2002). Production of silver perch is principally centred in New South Wales (278 tonnes @ \$8.81/kg (farm gate), net value - \$2.45 million) (NSW Fisheries 2003) and Queensland (44 tonnes @ \$7.66/kg (farm gate) - net value \$0.34 million) (DPI 2003), with small quantities produced in Victoria and South Australia (PIRSA 1999). Silver perch were introduced into Western Australia around 1950 for aquaculture (FWA 2005), and since then the Silver Perch Growers' Association has been working towards developing a code of practice and marketing strategies for exporting their product (FWA 2002a). In 2001/2002 approximately 26 tonnes of silver perch valued at around \$0.26 million were produced (ABARE 2003a). Production across the three major states in 2001-02 was 348 tonnes valued at \$3.05 million at the farm gate, and in addition to grow-out production, hatchery production of silver perch was 921,000 in 2001/2002, worth over \$0.22 million (ABARE 2003a).

The baseline technology for dual cropping of marron and silver perch was developed by Whisson (2000), with management centring on the production of silver perch within floating cages and culturing marron free-range in ponds. Results from these initial studies have shown a synergistic advantage to marron, represented by increased growth rates and an encouraging net increase in productivity. The recommendations from this preliminary investigation include the need to investigate growth-density relationships, habitat complexity and light intensity in order to optimise synergy.

## 1.12 Ecology and ethology of crayfish polysystems

### **Ecology**

The study of the interrelationships between organisms and their environment (Macquarie 1996)

### **Ethology**

The behavioural study of animals in their natural habitat (Macquarie 1996)

In nature, organisms have to manage conflicting demands of food gathering, predator avoidance and favourable abiotic environment (oxygen, temperature, shelter etc.) in order to maximise their fitness. Optimal foraging theory suggests that decisions are based on these demands through their influence on net energy gain, and predicts that species will evolve under natural selection to enhance fitness (Charnov 1976, Krebs and Davies 1978). In artificial systems, such as aquatic polyculture, where many environmental factors are novel and dynamic, species have to adapt rapidly, which results in varying levels of success and often at the consequence of fitness. In these situations, an understanding of pond ecology and ethology of component species is imperative in order to successfully manipulate system variables to optimise interplay between species, reducing negative interactions and maximising synergy.

Many authors have identified the importance of studying behaviour and interactions between organisms and their environment in order to optimise production (i.e. Appelberg and Odelstrom 1988, Diaz et al. 1995a/b, Liu and Cai 1998, Schneider et al. 2004). Research suggests that the outcomes from interaction are a function of communication, interpretation of environmental information (visual, chemical, audio, tactile, electrical) and the associated behavioural responses (Ringleberg et al. 1991, Ringleberg 1997, Li et al. 2000, Listerman et al. 2000). The ecological basis governing communication and interaction incorporates the influence of the abiotic environment (shelter, turbidity, temperature) and temporal changes (diurnal, seasonal).

### 1.13 Thesis rationale

Financial risk and uncertainty has characterised the Australian farming sector since the early 1980s (RIRDC 2002a) and marron farming has been no exception. Aquatic polyculture strategies address the risks associated with marron monoculture through diversification of product line, resource and input sharing and higher total yields (Whisson 2000).

Successful implementation of aquatic polyculture relies on the development of appropriate management strategies suiting area and site-specific conditions, resource availability, enterprise mix and individuals concerned. The challenge of integrating polyculture technology in Western Australian conditions is, however, compounded by the lack of appropriate complementary species for duoculture with marron. Of species examined, silver perch has been identified as having the greatest potential, although the dual cropping of marron and silver perch is an example where polyculture species do not occupy distinctly separate niches. For the marron industry to take advantage of the potential rewards of marron-perch polysystems, a customised management strategy needs to be developed to target niche overlaps. This requires examination of the ecological processes governing production in these systems, including ethology of component species, the nature and intensity of interactions, and the influence of system dynamics on interrelationships. A sound understanding of keystone processes will enable better prediction of system requirements, whilst developing more flexible production guidelines, which can be utilised in situations using alternate component species and in operations outside of Western Australia.

The work carried out in this thesis will assist the marron industry in Western Australia in providing a competitive edge through the use of polyculture technology to increase viability (production and profitability) of marron ponds. The research will aid farmers through identifying a more holistic, system level approach where ecology and ethology are paramount to decision processes and management strategies.

### 1.14 Aim and specific objectives

To investigate the cognitive architecture of marron, that is, its ability to receive, process and utilise environmental information; the sensory modalities involved in intra and interspecific communication; how system specific factors can influence the nature and extent of interactions; and how each of these areas relates to production. The underlying goal of research is to use knowledge of species ethology and system ecology to shape management strategies, which will reduce antagonism and maximise synergism within aquatic polysystems in Western Australia.

**Specific objectives** are divided into four study areas centred on investigating the basis for communication, interaction and response between fish and crayfish and the effects of interactions on production. The study areas were chosen to confront three levels of questioning; responses to simple cues, responses to multiple stimuli, and responses to multiple stimuli contingent on variations in system conditions. The research questions addressed in this thesis were:

#### **Study area one: Interspecific chemical communication**

1. Do marron detect and respond to food odour?
2. Are marron able to detect novel chemical signals (pheromones) from silver perch?
3. Is foraging or other behaviour influenced by chemical detection of silver perch?
4. Does response of marron to chemical cues from silver perch and food vary depending on crayfish size and age?

#### **Study area two: Multiple exteroceptive cues**

1. Do marron detect visual cues from silver perch?
2. Do marron demonstrate a cumulative or varied response to multiple information cues (visual and chemical)?
3. Do marron differentiate exteroceptive cues regarding food and potential predation risk?
4. Is foraging influenced by the detection of chemical and/or visual cues from silver perch?

5. How does general behaviour and avoidance strategies compare between marron and invasive crayfish species?
6. Does the presence of exteroceptive cues from silver perch influence interaction behaviour between marron and other species of crayfish?
7. Is individual and interaction behaviour between marron and other crayfish species altered between daytime and night-time conditions?

**Study area three: Interaction responses to novel cues**

1. What interaction response occur between marron and a novel predatory fish?
2. What impact does shelter and light intensity have on interaction between marron and a novel predatory fish?
3. Do marron exhibit innate avoidance strategies in response to a novel predator?
4. Do marron display recognition and learned responses to the presence of a novel predator? and are inducible defences effective?

**Study area four: System variables**

1. How does stocking regime (relative stocking size, stocking time, density) of marron affect population dynamics, growth and survival of marron in ponds?
2. How does stocking regime (relative stocking size, stocking time, density) of silver perch in cages affect population dynamics, growth and survival of marron in ponds?
3. How does shelter complexity affect marron production in polyculture in ponds with caged silver perch?
4. Does manipulation of cage culture dynamics affect silver perch condition? and does this affect marron production?
5. Does polyculture produce any off-season benefits to either species, in terms of growth and survival?

The questions within each study area are primarily addressed in subsequent chapters of this thesis, that is, study area one is examined in Chapter 4, area two in Chapter 5, area three in Chapter 6 and study area four in Chapter 7.



## Chapter two

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### **Literature Review**

*This chapter provides an overview of aquatic polyculture, focusing on Western Australian technology and species. Discussion includes ecology of multi-species pond aquaculture and research relating to interspecific and intraspecific communication.*

*In particular, predator-prey interactions are addressed due to niche overlaps existing between species available for culture in Western Australian polysystems*

***'This is an extended review to disseminate a broad research area and provide a solid base for future researchers'***

## 2.1 Introduction

In nature, aquatic systems are comprised of multiple species in virtually every case. In an artificial system, through informed management based on an understanding of the ecological processes occurring in nature, a multiple species strategy can provide several benefits including: increased water quality (Rouse et al. 1987, Azim and Wahab 2003), improved nutrient cycling (Riise and Roos 1997, Liu and Cai 1998, RIRDC 2002b), soil enhancement (RIRDC 2002b), and nitrogen fixing (RIRDC 2002b, Langdon et al. 2004). These benefits can equate to substantial increases in profitability for animal and plant based farming industries (e.g. Rouse and Stickney 1982, Cohen et al. 1983, Scott et al. 1988, Swift 1993, Wahab et al. 1995). However, as the number of species increases, the complexity of the system increases disproportionately (Rouse 1987), presenting a trade off to the proponent of a multi-species culture strategy seeking the benefits of mimicking the variety (and associated stability) in nature's aquatic systems. Taking advantage of these benefits requires a knowledge-gathering exercise that combines observation and experimentation of variables known to be involved (based on natural theories and understood ecosystem processes). Only then can the potential economic benefits of such a strategy be ascertained for aquaculture (Dailey 1997, Cork and Shelton 2000).

An optimal environment is generally considered as one that promotes maximum production of the cultured animal. In practice, however, optimal environments often cannot be obtained economically. This leads to the need for balancing environment and production in an economic framework. In the case of marron polyculture in Western Australia, aquaculturalists are required to manipulate biotic and abiotic parameters within pond environments to reduce niche overlaps between component species (Whisson 2000). To do this aquaculturalists need to understand the ecology of integrated production systems and more specifically the behavioural ecology of cultured species. This is demonstrated historically with the complex multi-species cultures of China (Shepherd 1992), Asia and Europe (Milstein 1997, Reddy et al. 2002) and Israel (Pillay 1993), where production gains stem from the selection of species which fill distinct synergistic niches within the system.

This chapter examines the biological dynamics of multi-species systems, focusing on communication and interaction behaviour between conspecifics and heterospecifics,

and the influence of system-specific abiotic conditions. In an unstable marketplace, this information is vital for equipping farmers with the tools required to augment production through ecological management of systems and species, which may give them a competitive edge.

## 2.2 World review - polyculture

Polyculture is a multi-faceted business approach where more than one product is targeted within the same location (Whisson 2000). In addition to business advantages, polyculture can also provide benefits associated with advanced ecological stability and function (McKinnon et al. 2000, Gooley and Gavine 2003). One industry that has proven well suited to this technology is aquaculture (O'Sullivan 1996, Haroon and Pittman 1997, Prein 2002).

Traditionally, integrated aquaculture has been viewed as the combination of terrestrial and aquatic farming, where the output of the terrestrial crop becomes the input for the aquatic system. Typically, effluent from terrestrial crops is used to increase production of water plants and fish (Preston 2000, Barbara 2000), such as in the production of tilapia (*Oreochromis niloticus*) in ponds, which has been increased by effluent from adjacent pig farms (Thy and Preston 2003). In this example, pig manure is converted into biogas and effluent by biodigestors (Botero and Preston 1995), and the effluent is delivered to ponds resulting in increased phytoplankton - feed for tilapia. Aquaculture has been successfully integrated with a number of diverse enterprises, including:

- Integration into land-based horticulture–agriculture systems (Sharma and Olah 1996, McMurty et al. 1997, Prein 2002);
- Dual-cropping complementary species (Brunson and Griffin 1988, Haroon and Pittman 1997);
- Generation of valuable bi-products (O'Sullivan 1996, Scott et al. 1998);
- Crop rotation (Brown et al. 1974), where seasonal use of same system by alternate species can offer synergistic rewards;
- Tourism-based services (O'Sullivan 1996, Saunders and O'Sullivan 1998);
- Aquatic polyculture - culture of complementary aquatic species in the same system where niche overlaps are minimised (Brown and Gratzek 1980, Tucker and Robinson 1990, Milstein 1997, RIRDC 2002b).

Aquatic polyculture, is integrated aquaculture within a single aquatic system (Whisson 2000), whereby outputs from one crop become inputs for another crop wholly within the same aquatic system. Examples of polycultures include the culture of catfish, carp, eels and pond snails in macrophyte ponds (World News 2005), or growing crayfish in rice paddies during re-flooding after summer-fall harvest of rice (Mitsch and Gooselink 1993), where crayfish feed on detritus and crayfish-effluent increases production of rice crop in the subsequent season.

### **2.2.1 Aquatic polyculture**

Aquatic polyculture has been practiced throughout the world for over a thousand years (Pillay 1993, Milstein 1997) and contributes a significant amount of product to world aquaculture production (FAO 2004). Increasing the number of species cultured not only takes advantage of the inherent economic and risk spreading benefits from a diversified industry (Section 1.8) but also incorporates a number of within-system benefits due to synergistic alliances formed between species. Advantages from aquatic polyculture include (Whisson 2000):

- Greater combined production – even if individual species' production is lower than achieved through monoculture (Brick and Stickney 1979, Hopher and Pruginin 1981, Tuten and Avault 1981, Rouse and Stickney 1982, Pillay 1993);
- Improved system management, where secondary species are deliberately stocked to improve system conditions, with a view to increase production of the primary species (Brown and Gratzek 1980, Tucker and Robinson 1990, Medley et al. 1993, RIRDC 2002b, Luong et al. 2005); examples include, increased nutrient cycling through addition of nitrogen fixing crops such as legumes, water ferns and other floating plants (RIRDC 2002b);
- Increased cost-effectiveness, where costs can be spread between more than one crop (Brown and Gratzek 1980, Huner 1986, Pillay 1993);
- Population control, where a secondary species is stocked purely to control the number of a primary species in an effort to improve marketable yield (Chervinski 1975, Dunseth and Bayne 1978, Hopher and Pruginin 1981, Pillay 1993, Fischer and Grant 1994);

- A more diverse and stable ecosystem, where niches are filled by compatible species, both plant and animal, for increasing aesthetics/ tourism value (O'Sullivan 1996, Saunders and O'Sullivan 1998);
- A cost-effective and rich source of animal protein for the primary species (Tucker and Robinson 1990, Parker 1992, RIRDC 2002b) or the addition of aquatic plants for herbivorous fish (duckweed in carp polycultures in Bangladesh - Azim and Wahab 2003);
- An integrated permaculture system providing outputs for domestic consumption (O'Sullivan 1995, O'Sullivan 1996, Amand 1997).

The many benefits of multi-cropping aquatic species make polyculture an attractive research focus. However, the movement away from specialised monoculture practices does increase management concerns. Diversification often involves significant financial outlay, staff training for new skills required, access to new resources and most importantly an ability to create or respond to new market opportunities (RIRDC 2002b). The greater management needs of multi-species systems are further compounded if negative interactions exist between species. The selection of component species with distinct ecological requirements and with complementary feeding habitats is important for a properly functioning ecosystem, however this is often not possible. In most cases limited species selection results in some degree of overlap between occupants, as is the case with marron-silver perch duoculture in Western Australia (Whisson 2000). For aquatic polyculture to be successful in these situations the niche requirements of species must be identified and understood, and in order to mediate overlaps between species, a sound understanding of the ecological processes governing interactions is required.

There are many examples of successful species combinations from around the world, producing both substantial gains in profitability and improved system sustainability, compared with traditional monocultures.

### **2.2.2 Finfish polyculture**

Finfish polyculture is perhaps the most recognised and traditional form of multi-species aquatic systems, with examples dating back to China in the tenth century

(Pillay 1993, Milstein 1997). Numerous beneficial species combinations have been explored and reported and these include such ventures as the polyculture of:

- Marble goby (*Oxyeleotris marmorata*) and carps (Luong et al. 2005);
- Channel catfish (*Ictalurus punctatus*) and rainbow trout (*Oncorhynchus mykiss*) (Beem et al. 1988);
- Silver carp (*Hypthalmichthys molitrix*), grass carp (*Ctenopharyngodon idella*), bighead carp (*Aristichthys nobilis*), mud carp (*Cirrhinus molitorella*) and black carp (*Mylopharyngodon piceus*) in China (Shepherd 1992);
- The Indian major carps, catla (*Catla catla*), rohu (*Labeo rohita*), mrigal (*Cirrhina mrigala*) and calbasu (*Labeo calbasu*) in Asia and Europe (Milstein 1997, Reddy et al. 2002);
- Tilapia with carp and mullet (*Mugil cephalus*) in Israel (Pillay 1993);
- Tilapia with a range of predatory species (*Hemichromis fasciatis*, *Ophiocephalus obscuris*, *Micropterus salmonides*, *Channa striata*, *Cichla ocellaris*, *Elops hawaiiensis* and *Dicentrarchus* sp.) to reduce stunting due to overcrowding (Chervinski 1975, Dunseth and Bayne 1978, Fischer and Grant 1994, De Graaf et al. 1996);
- Channel catfish (*Ictalurus punctatus*) with tilapia as a protein rich food source in the United States (Brown and Gratzek 1980, Parker 1992);
- Baitfish in the United States (Brown and Gratzek 1980) including catfish (*I. Punctatus*) and minnows (*Pimephales promelas* and *P. notatus*), catfish with bluegill (*Lepomis macrochirus*) and bass (*Micropterus salmoides*), golden shiners (*Notemigonus crysoleucas*) and fathead minnows (*P. promelas*) with freshwater prawns;
- Milkfish (*Chanos chanos*) in southeast Asia (Milstein 1997), with species such as Penaeid shrimps, mullet (*Mugil tade* and *M. parsia*), sea bass (*Lates calcarifer*), carps, mudcrabs (*Scylla serrata*) and pearlspot (*Etroplus surarensis*) cultured in Taiwan, Hong Kong, Israel, Egypt and India (Pillay 1993); and
- Salmonoids (Brown et al. 1974), trout sp. and channel catfish (Brown et al. 1974, Beem et al. 1988).

There are also many examples of combinations that have not proven successful, often as a result of interspecific dynamics. Examples include: tilapia and freshwater prawns (*M. rosenbergii*), where yields of prawns were low (Brock 1988); channel catfish, silver

carp, bighead carp, paddlefish (*Polydon spathula*), freshwater prawns (*M. rosenbergii*) and freshwater crayfish (*Procambarus clarkii*), which resulted in reduced production of decapods (Green et al. 1979, Tucker and Robinson 1990); duoculture of turbot (*Scaphthalmus maximus*) and Atlantic salmon (*Salmo salar*), where species displayed limited potential due to climatic and economic constraints. These examples illustrate the importance of species choice and appropriate management where knowledge of species characteristics and system niches (spatial and temporal) are matched appropriately to maximise success.

In all polysystems, the selection of complementary component species is central to successful production, where appropriate choices can allow complex species rich systems. In the prominent carp cultures of China, where up to seven species are cultured *in situ*, the individual ecological roles of each species display synergistic qualities paramount to success. The five base species in these systems each fill an individual feeding niche, with phytoplankton consumed by silver carp, macrophytes by grass carp, macroplankton by bighead carp, detritus by mud carp and molluscs targeted by black carp (Pillay 1993). In addition, common carp (*Cyprinus carpio*) are often integrated as a scavenger. The same division of species with distinct ecological roles is seen in many other systems (e.g. Brown and Gratzek 1980, Tucker and Robinson 1990, Parker 1992, RIRDC 2002b, Luong et al. 2005), for example, mullet are used to control increased phytoplankton growth due to nutrients from milkfish culture, and crabs are incorporated in targeting macrovegetation and detritus (Pillay 1993).

### **2.2.3 Decapod-finfish freshwater polyculture**

Due to the distinct benthic niche occupied by large decapod crustaceans (crayfish, prawns and shrimp) they are a common choice for polyculture with pelagic finfish species (Eldani and Primavera 1981, Rouse and Stickney 1982, Cohen 1984, Rouse et al. 1987, Brummett and Alon 1994). For this reason they are often a successful addition to even established multi-species fish polycultures (Green et al. 1979, Malecha et al. 1981, Tuten and Avault 1981, Schroeder 1983), with improved yields, increased profit and increased ecological efficiency reported in many species combinations (Table 2.1).

**Table 2.1** Decapod polyculture combinations displaying improved yields in freshwater

Crustacean species	Polyculture species	Reference
Freshwater crayfish		
<i>Cherax tenuimanus</i> (marron)	Silver perch, <i>B. bidyanus</i>	Whisson 1998, 2000; Storer et al. 2004a
	Mullet ( <i>Mugil cephalus</i> ), mussels and shrimp.	O'Sullivan 1995
<i>Cherax quadricarinatus</i> (redclaw)	Red hybrid tilapia ( <i>Oreochromis</i> hybrid)	Barki et al. 2001
	Carp	Tucker and Robinson 1990
	Silver perch, <i>B. bidyanus</i>	Jones and Ruscoe 1996
<i>Procambrus clarki</i> (Red swamp crayfish)	Various Chinese fish sp.	Xinya 1995
	Numerous predaceous finfish	Huner 1976
Freshwater prawns and shrimp		
<i>Macrobrachium rosenbergii</i> (Freshwater prawn)	Channel catfish ( <i>Ictalurus punctatus</i> )	Huner et al 1983a; Miltner et al. 1983; Cange et al. 1986; D'Abramo et al. 1986; Heinen et al. 1987, 1989.
	Fathead minnows ( <i>Pimephales promelas</i> ) and golden shiners ( <i>Notemigonus crysoleucas</i> )	Perry and Tarver 1987
	Carp sp.	Malecha et al. 1981; Cohen et al. 1983; Miltner et al. 1983; Schroeder 1983; Fitzgerald 1988; Hulata et al. 1990; Sarig 1992.
	Tilapia sp.	Brick and Stickney 1979; Cohen et al 1983; Schroeder 1983; Meriwether et al. 1984; Martino and Wilson 1986; Rouse et al. 1987; Hulata et al. 1990; Sarig 1992; Sadek and Moreau 1996.
	Baitfish sp.	Crawford and Freeze 1982; Perry and Tarver 1987; Scott et al. 1988.
<i>Penaeus chinensis</i> (Chinese shrimp)	Taiwan red tilapia ( <i>Oreochromis mossabicus</i> and <i>O. niloticus</i> ) and constricted tangelus ( <i>Sinonovacula constricta</i> )	Tian et al. 2001



Many crustacean species have not proven amenable to polyculture (Karplus et al. 1995, Kotha and Rouse 1997, Rouse and Kahn 1998), such as many species of Penaeid prawns where polyculture has resulted in half the gross revenue of monoculture (Shang 1983). In these cases improved management practices can sometimes aid in overcoming negative effects (Huner et al. 1983b, Whisson 2000).

#### **2.2.4 Polyculture of Australian species**

Diversification of aquaculture industries in Australia is a relatively new trend (Saunders and O'Sullivan 1998) and as such, farmers wishing to explore possible combinations of species have few local examples in which the potential for successful aquatic polyculture can be examined. However, the use of Australian species for polyculture has attracted overseas interest (Medley et al. 1993, Brummett and Alon 1994, Karplus et al. 1995) and the outcomes from research carried out can be used to infer potential viability of similar systems in Australia.

Of the few Australian species combinations examined, the polyculture of Australian *Cherax* crayfish species with finfish appears to hold the highest potential in freshwater systems. Overseas aquaculturalists identified the potential of *Cherax* crayfish polycultures, with a number of investigations carried out throughout Israel and America, beginning in the early 1990s. These investigations were primarily focussed on *Cherax quadricarinatus* (redclaw), and demonstrated varied results. In Israel, Karplus et al. (1995) combined *C. quadricarinatus* (redclaw) with common and silver carp, tilapia hybrids, African catfish (*Clarias gariepinus*) and the carnivorous freshwater crab *Potamon potamonius*. Although fish species survived and grew well, crayfish survival was low (25%) with suggestions that climatic conditions were unfavourable to redclaw culture. These findings were supported in a study conducted in Alabama, USA, where redclaw were grown with tilapia (Rouse and Kahn 1998). In this study, a definitive comparison was made between redclaw monoculture and polyculture systems (not done in previous example), which revealed low survival in both systems (<25%). As continued studies in the region demonstrated higher survival of polycultured redclaw (Medley et al. 1993, Pinto and Rouse 1996, Kotha and Rouse 1997), the negative results from the initial trials conducted by Karplus et al. (1995) and Rouse and Kahn (1998) were assumed related to factors other than cohabitation with

fish, such as reduced stock quality related to shipping conditions. Redclaw-tilapia duoculture in South Carolina (USA) demonstrated antagonistic interactions between species (Brummett and Alon 1994). In this study, tilapia growth was significantly reduced, with production negatively affected through disruption of feeding and spawning behaviour by crayfish, although crayfish showed no negative effects from duoculture (growth, incidence of intersexuality and percentage of berried females) and feed conversion of tilapia was improved compared to monoculture.

In Australia, research into *Cherax* crayfish polyculture systems has been carried out over the past 10 years. Jones and Ruscoe (1996) introduced the Australian native silver perch to established redclaw ponds in Queensland. Although survival was greatly reduced by cormorant (*Phalacrocorax* sp.) predation and definitive conclusions were limited by insufficient replication, the authors reported that polyculture economics were favourable. In this study, a total yield of 2849 kg/ha was recorded from polyculture, including 2358 kg of crayfish, compared to 2285 kg in monoculture ponds (Jones and Ruscoe 1996). Since then, a number of *Cherax* duoculture ventures have demonstrated positive benefits. The most encouraging results have been with cohabitation of silver perch (*B. bidyanus*) and marron. In Victoria (O'Sullivan 1996) and in New South Wales (O'Sullivan 1998) production of over 300 kg/ha for marron and 10,000-20,000 silver perch/ha were reported (O'Sullivan 1998). The greatest amount of work on marron-silver perch polyculture systems has been conducted in Western Australia, where aquatic polyculture was identified as a future priority to enhance marron monoculture production (Lawrence 1999). The results of this work are discussed in the following section.

### **2.2.5 Marron polysystems**

The marron aquaculture industry is a prime candidate for aquatic polyculture. New industries, such as marron aquaculture, are more exposed to business risk due to evolving technologies and sudden shifts in product demand, and are therefore more likely to gain the greatest benefit from diversification of product lines (Whisson 2000). Furthermore, one of the major problems confronting marron monoculture production is variable growth and survival, which not only affects overall production but reduces the ability of farmers to quantify outputs, making meeting orders difficult. Continuity of

supply is a critical component for the long term success of industry, especially where young industries are trying to establish permanent markets (Morrissy 1990, Whisson 2000). Aquatic polyculture has proven to reduce variability of growth and survival (Rouse et al. 1987, Whisson 2000). The implementation of polyculture within the marron industry also takes advantage of existing infrastructure that can be utilised with little modification and without disruption of other activities.

Although polyculture may indeed hold the key to some of the problems faced by the marron industry, there are a few core aspects inhibiting wide-ranging implementation in Western Australia. Polyculture is a practice that focuses on increasing system yields by stocking species displaying complementary feeding characteristics (Rouse et al. 1987, Scott et al. 1988, Brummett and Alon 1994) and this is not the case in Western Australia, with species choice limited by strict translocation policies and little to no native candidates. The polyculture of marron and silver perch has demonstrated the highest potential of the limited species combinations available.

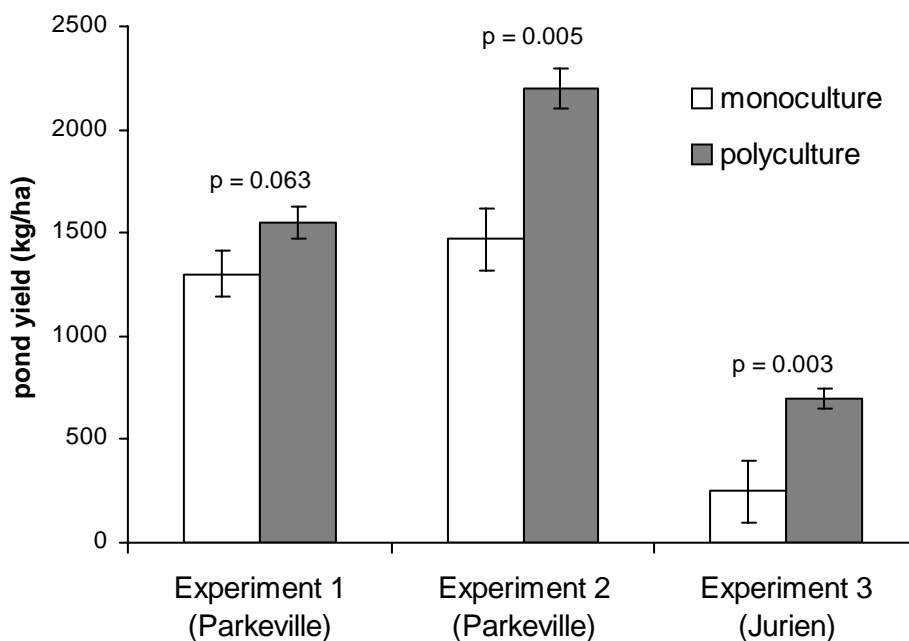
Research into the commercial polyculture of marron and silver perch was pioneered by Dr Glen J. Whisson (1995, 1997, 1999, 2000). These studies, and the studies in this thesis, are the sum knowledge in the area of marron-perch polysystems. In Whisson's PhD thesis (2000) 'Investigations into the commercial polyculture of *Cherax tenuimanus* and *Bidyanus bidyanus*', several conclusions were made relating to specific culture technology, these are discussed below.

#### **2.2.5.1 Interspecific interactions in free-range cultures**

Silver perch have been shown to predate on small and moulting marron, especially in clear-water systems (Whisson 1997, 2000). In one trial, marron pond yields were approximately half that of monoculture systems, attributed mainly to reduced survival (Whisson 1998). However, in this, and other free-range trials, growth rates of marron were favourable and suggested that correct management of niche overlaps between silver perch and marron could still produce commercial benefits (Whisson 2000).

### 2.2.5.2 Managing interactions

Whisson (1998, 2000) trialed silver perch in purpose built floating cages within marron ponds, in an attempt to reduce negative interaction seen in early attempts. Although results were varied (growth and survival), in several systems marron production demonstrated a significant increase over monoculture yields. In three studies, increases in pond yields over monoculture were approximately 125% (Experiment 1), 153% (Exp. 2) and 280% (Exp. 3) (Figure 2.1).



**Figure 2.1** System yields from marron and silver perch production experiments: polyculture versus monoculture (Whisson 2000)

Partial budget analysis indicated that culturing silver perch in floating cages in marron ponds could significantly increase net revenues (Whisson 2000), a result supported by other researchers assessing polyculture economics for other species combinations (Rouse and Stickney 1982, Engle and Brown 1998). Also, the culture of caged silver perch was seen as an effective management tool for a number of other reasons, including ease of stock control, grading, harvesting, and better observation of feeding responses and condition.

### 2.2.5.3 Problems and recommendations

Although polyculture bioeconomics were favourable, many elements were less than desirable. Adult silver perch demonstrated reduced performance (growth and condition) when held in cages, and fry did not appear amenable to cage cultures at all, with low survival reported (Whisson 2000). In order to optimise production, cage culture conditions require improvement, and ideal stocking size of perch to produce marketable sized fish in a short grow-out period (i.e. one season) are needed. Although synergistic benefits to marron were revealed, survival and growth was highly variable (Table 2.2 and 2.3).

**Table 2.2** Marron survival data (%) from polyculture experiments (Whisson 2000)

	marron monoculture	free-range polyculture	Caged polyculture	
			High density	Low density
Experiment 1 Preliminary tank study	77.0 ± 11.4 <sup>a</sup>	89.3 ± 3.2 <sup>a</sup>	n/a	75.0 ± 9.7 <sup>a</sup>
Experiment 2 Preliminary pond study	68.4 ± 9.1 <sup>a</sup>	71.9 ± 5.3 <sup>a</sup>	70.1 ± 9.2 <sup>a</sup>	75.6 ± 2.3 <sup>a</sup>
Experiment 3 Interaction study in tanks	85.0 ± 10.5 <sup>a</sup>	33.0 ± 11.1 <sup>b</sup>	n/a	n/a
Experiment 5 Commercial pond study	13.8 ± 8.7 <sup>ab</sup>	9.8 ± 3.9 <sup>a</sup>	29.0 ± 2.2 <sup>b</sup>	27.5 ± 5.5 <sup>b</sup>

**Table 2.3** Mean initial and final weight of marron and silver perch in free-range polyculture tanks and ponds (Whisson 2000)

	marron		silver perch		Evidence of predation on marron
	initial (g)	final (g)	initial (g)	final (g)	
Experiment 1 Preliminary tank study	3.5	46.0	1.0	13.5	yes
Experiment 2 Preliminary pond study	17.5	122.0	0.65	148.0	no
	17.5	5.0*	0.65	148.0	yes
Experiment 3 Interaction study in tanks	130.0	112.0	515.0	n/a	yes
	n/a	3.5*	515.0	n/a	yes
Experiment 5 Commercial pond study	4.1	62.0	12.3	251.0	yes

\*final weight of 0+ marron harvested in Experiment 2 and 3

The high variability of results suggests influence from system-specific conditions. Several contributing system variables have been examined, and several more identified (Whisson 2000). These included: turbidity, where a positive correlation (0.93 and 1.00  $R^2$  in two experiments) was found between marron survival and Secchi depth; shelter density, where increased shelter was related to increased survival of marron, especially juveniles; and also growth-density relationships, where variations in growth appeared correlated to pond biomass, even with perch in cages. The recommendations stemming from the research into marron-perch polysystems, whether for free-range or cage cultured fish, involved focus on turbidity, supplemental feed, stocking size of crayfish and finfish, crayfish gender, habitat complexity, life stage (including moulting patterns), cage culture dynamics (cage dimensions, materials and mesh size), relative densities, and water quality.

The way each of these factors directly impact on the nature and intensity of interactions between participating species and their environment, and the subsequent effects of interaction responses need to be examined. Therefore, understanding the basis for communication and interaction between component species is paramount.

The success of aquatic polyculture is a function of the biological and economic circumstances of species and environment (Pillay 1993). Optimising polyculture management strategies and technologies relies on research focussed on system and species ecology, with specific attention to niche occupation, species interaction and the role of system specific dynamics. The following section looks at the dynamics of multiple species systems and the impacts of variations in dynamics on production potentials for Western Australian polysystems.

### **2.3 Ecology of aquatic polysystems**

The technology for integrating species within an aquatic biosystem has been developed over more than a thousand years (Pillay 1993, Milstein 1997). A review of literature throughout this period has demonstrated an increasing tendency of researchers to examine the core principles of system ecology and species ethology in order to explain the dynamics of multi-species systems and enable more accurate prediction of management requirements.

The major areas targeted by researchers to explain the ecological processes governing multi-species systems include:

### **Biotic Factors**

- Community structure and trophic dynamics (Moav et al. 1977, Appelberg and Odelstrom 1988, Siddiqui et al. 1996);
- Intraspecific competition (Denno et al. 1994, Diaz et al. 1995a/b, Li et al. 2000, Listerman et al. 2000);
- Predatory relationships (Gilinsky 1984, Boal and Marsh 1998, Brown et al. 2000) - top down effects (Schmitz and Suttle 2001);
- Avoidance responses (Hazlett and McLay 2000, Diaz et al. 2001, Woodley and Peterson 2003);
- Synergistic conditions (Stickney 1986, Jones and Ruscoe 1996, Whisson 1998, 2000); and,
- Foraging efficiency (Charnov 1976, Krebs and Davies 1978, 1991, Kaufman et al. 1996).

### **Abiotic factors**

- Turbidity (Hartnoll, 1982, Benfield and Minello 1996, Chivers et al. 1996b, 2001, Clark et al. 2002, Reynolds 2002);
- Habitat complexity (shelter and substrate) (Quammen 1984, Reinsel and Rittschof 1995, Clark et al. 2002, Gazdewich and Chivers 2002);
- Water flow (Hansen et al. 1991, Hart and Merz 1998, Powers and Kittinger 2002);
- Stocking regime (density, size, timing) (Shepherd and Bromage 1992, Blake and Hart 1993b, Preston et al. 1999, Whisson and Storer 2003, Storer et al. 2004a);
- Species selection (Cohen 1984, Head et al. 2002);
- Specific management devices, such as cage culture (Beem et al. 1988, Beveridge 1996, Whisson 2000).

In nature, organisms have to manage conflicting demands of food gathering, competition, predator avoidance, and finding a favourable abiotic environment in order to maximize their fitness. The following review analyses the decisions made by animals in respect to influences from system-specific factors, and how their decisions

affect production in multi-species systems. This review encompasses examples from both aquaculture and natural systems, including where non-endemic introductions have occurred, which are directly applicable to multi-species culture systems.

### 2.3.1 Trophic dynamics in multi-species systems

Interaction between fish and lower order consumers like macroinvertebrates plays an important role in the trophic ecology of aquatic systems. In an integrated pond system, waste serves as nutrient for phototrophic and detritivorous/heterotrophic conversion by plants, bacteria, and invertebrates (Li 1987, Riise and Roos 1997, Liu and Cai 1998). Invertebrates such as crayfish are generally considered as polytrophic omnivores (Momot et al. 1978, Huner 1994), accepting a range of feed types depending on the present dynamics of the system. Although crayfish are reported to have a predilection for animal protein (Momot 1995) they often target detritus (Morrissy, 1978) and vegetation (Moore 1986, Bird 1995), and these preferences can change depending on age, season and physiological state (Momot et al. 1978, Goddard 1988). Many problems encountered in crayfish-finfish polyculture occur because the majority of cultured fish are higher-order consumers, with crayfish often a principle food item. Examples of commonly aquacultured finfish that predate on marron include, flatfish (Pihl 1985, Wilson 1989), largemouth bass (*Microperus salmoides*, Lambou 1961, Taub 1972, Crowl 1989, Hickley et al. 1994), smallmouth bass (*M. dolomieu*, Rabeni 1992), pike (*Esox lucius*, Elvira et al. 1996), trout (*Salmo trutta* and *S. gairdneri*, Momot 1967, Faragher 1983), white perch (*Morone americana*, Reid 1972), Murray cod (Gunasekera et al. 1998) and European perch (*Perca fluviatilis*, Blake and Hart 1993b, Söderbäck 1994).

Understanding trophic dynamics can aid management strategies in multiple species systems. Macroinvertebrates, such as crayfish, are essential parts of ecosystems, representing integral links between primary production or detritus, and higher trophic levels. Due to their critical link in aquatic ecology, crayfish are often incorporated into fish cultures for the sole purpose of nutrient capture from plant material and waste, and delivery to cultured fish through predation on crayfish (Schneider et al. 2004). The same strategies are employed where bait species are introduced to primary cultured species to both increase nutrition and reduce feed costs, and where live food is



important to stimulate feeding (some species) (Liao et al. 2001); for example, Langdon et al. (2004) combined dulse (red seaweed) and red abalone, where dulse was effective in providing food for abalone and improving water quality by removal of excreted ammonia.

Some species of fish, such as silver perch (*B. bidyanus*), are polytrophic, feeding on aquatic vegetation (Grant 1987, Whisson 1997, FWA 1998) and macroinvertebrates (Barlow et al. 1986, Whisson 2000), including freshwater crayfish (redclaw; Jones and Ruscoe 1996, marron; Whisson 1997, 1998). Furthermore, silver perch have been shown to alter preference for freshwater crayfish depending on life stage and system conditions. Barlow et al. (1986) reported that silver perch avoided *C. destructor* in agricultural farm dams. Barlow (1991) and Lambert (1998) reported that silver perch will accept artificial feeds even in the presence of natural food. Jones and Ruscoe (1996) suggested that marron >5g are less susceptible to perch predation, while Allen (1995) and Hogan (1995) reported that the proportion of algae and other plant material in their diet increases as silver perch grow.

### **2.3.2 Synergistic advantages of multi-species systems**

Synergism is 'the joint action of two or more substances, so that when acting together, their affect is greater than the sum of the parts (Hefferenan 1992). In polyculture, many authors have suggested that an appropriate combination of species could lead to synergism in terms of growth (Sarig, 1988, Milstein, 1992).

The reason polyculture is pursued despite increased management requirements, is both due to the direct economic advantages from risk spreading, and synergistic advantages stemming from increased ecological stability. The potential of polyculture to increase total pond yields (e.g. Rouse and Stickney 1982, Cohen et al. 1983, Scott et al. 1988, Swift 1993, Wahab et al. 1995) has been attributed to a more advanced recycling process (Cohen 1984), where benefits are associated with improved water quality and re-distribution of food (Rouse et al. 1987). Benthic dwellers, such as crayfish, can more easily convert the rich, partially digested faecal pellets from some species of finfish (Yashouv 1971), resulting in higher yields of crayfish. This same relationship has also been suggested to explain increased marron growth in duoculture with silver perch (Whisson 2000).

### 2.3.3 Community structure

In aquaculture the complexity of the aquatic systems, and therefore management requirements, increases with the more species cultured.

In monoculture, community structure is relatively straightforward in that intraspecific relationships are generally a function of a limited number of key factors. One of the core factors driving many responses is competition. Competition between individuals often occurs in response to limited resources, including territory, shelter, feed, or reproductive partners. In many aquatic species a pecking order is established where certain individuals have first access to the best resources. This 'social hierarchy' is dependent on a number of factors, the most common being body size (Peters et al. 1980, Beacham 1987). However, as stable social hierarchies exist even in groups of similar sized animals (Giaquinto and Volpato 1997) other influences are also important. These influences can include: sex (Halperin and Dunham 1994), reproductive status (Francis 1983, Smith 1986), previous hierarchical standing (Zayan 1974, Goncalves 1993) and prior residence in respect to shelter or territory (Zayan 1975, Stacey and Sorensen 1991).

Factors affecting dominance hierarchy form a dynamic multivariate system where the effect of each element can depend on the intensity of the others. For instance, a fish slightly smaller than the opponent may be dominant once inside its territory (Kaufman 1983). The mechanisms involved in such events are poorly understood, but associative learning processes have been proposed (Francis 1983). In fact individual recognition is undoubtedly an important stabilising factor for social hierarchy (Holder et al. 1991) Social hierarchies can have negative outcomes for aquaculture production. For instance, rainbow trout (*Oncorhynchus mykiss*) in monoculture will establish a social hierarchy in which interrenal cell activity, and presumably the stress response is inversely related to position in the pecking order (Grier and Burk 1992). Channel catfish (*I. punctatus*) have been shown to grow and convert food less efficiently when fish of varying sizes are cultured together (Halperin and Dunham 1993, Halperin and Dunham 1994), and in crustaceans, the use of moult inhibiting hormones by dominant individuals is well documented to reduce growth in surrounding conspecifics (Mattson and Spaziani, 1985, Skinner, 1985, Watson et al. 1989, Hazlett 1994a, Webster 1998, Bouwma and Hazlett 2001, Gherardi et al. 2002).

One of the main aims of aquaculturalists is to provide enough resources so competition is unnecessary. This includes provision of enough feed, shelter-territory, optimal water quality throughout all areas of the system and providing for reproduction, i.e. male : female ratios, or removing reproduction from systems by culturing outside of reproductive season or utilising single sex cultures. Competitive interactions will negatively affect production either through increased mortality, or reduced growth of some individuals through exclusion from feed or heightened stress. Physiological and behavioural responses to stress redirect resources used in growth (Appelberg and Odelstrom 1988, Haefner and Spaargaren 1993, Jussila et al. 1997, Patterson and Spanoghue 1997).

Long-term research into monoculture practices has led to increasing optimisation of management techniques. However, these management techniques are greatly complicated in multiple species systems. When two or more animal species use a limited resource, aggressive interactions are often reported as the behavioural mechanism underlying resource distribution (Hazlett et al. 1996). Species stocked in polyculture systems may affect each other if they compete for a limited resource such as food, or exceed the capacity of the culture system causing degradation of the environment (Tomasso 1996). Some polyculture attempts have demonstrated no negative impact (Gherardi 1990), while others exhibit positive interactions between the culture species (Kakinami 1990). How species will interact with each other is difficult to predict without a thorough understanding of all factors involved.

Understandably, predation is one of the most significant determinants of community structure and stability (Gilinsky 1984). In these situations, understanding the dynamics of interspecific interaction (predator-prey) is especially important.

#### **2.3.4 Predator-prey interactions**

Predator-prey relationships can be extremely complex within multi-species systems (Stein 1977, Fischer and Grant 1994), with complexity growing disproportionately with the number of cultured species in the system.

Both predator and prey alter their behaviour in response to interaction (Croze 1970, Stein 1977, Beukema 1968, Schapker et al. 2002) and these alterations in behaviour

can influence production. In crayfish, a common response is to reduce overall activity or choose the most complex shelter available in the presence of fish predators (Stein and Magnusson 1976). Obviously, if the crayfish loses time otherwise dedicated to behaviours such as foraging, a reduction in growth would be expected. Predator avoidance responses that can have other deleterious effects on production also include reproductive interference (Fuelling and Halle 2004), or increasing competition between conspecifics (Werner 1991, Kotler et al. 1994) as densities increase in shelter and food choices in safe areas are more limited. The response of crayfish to potential threats is a multi-faceted decision process based on a range of factors primarily focussed on the degree of threat and necessity for food. The vulnerability of prey (or related success of predation) varies with many conditions - consistent across both freshwater (Peckarsky et al. 1990, De Nicola and McIntire 1991, Sih and Wooster 1994) and marine benthic systems (Palmer 1988). Factors influencing prey vulnerability include:

- Water quality (turbidity; Benfield and Minello 1996, temperature; Achenbach and Lampert 1997, Rincon et al. 2002, dissolved oxygen; Weider and Lampert 1985, Pihl et al. 1991, Breitbart et al. 1994, pH; Arnott and Vanni 1993, or toxicants; Hanazato 1991);
- Water movement (Hansen et al. 1991, Hart and Merz 1998);
- Prey size (Stein and Magnusson 1976, Rincon et al. 2002);
- Life stage (molting; Stein 1977);
- Reproductive stage (Rincon et al. 2002);
- Experience of predator and prey (Chivers and Smith 1995; Mirza et al. 2001, Gazdewich and Chivers 2002);
- The presence of other enemies like parasites (e.g. Burns 1985, Ebert 1995) or competitors (e.g. DeMott 1989, Boersma 1995);
- Prevailing habitat complexity (substrate type; Quammen 1984, Reinsel and Rittschof 1995; shelter type; Rincon et al. 2002);
- Availability of food (e.g. Dawidowicz and Loose 1992, DeMott 1995, Tollrian 1995); or,
- Presence of alternative food sources (Whisson 2000) .

An example of variations in vulnerability exists with cohabitation of crayfish and the predacious finfish, bass and perch. Bass and perch in freshwater lakes in Wisconsin,

USA, have been shown to select *Orconectes propinquus* that have recently moulted over individuals in intermoult (Stein 1977). It was also reported that targeting the recently moulted, softer shelled, crayfish allowed the predatory fish to consume a much larger sized crayfish compared with intermoult prey (Stein 1977). In addition to the ease of capture of moulting or immediate post-moult crayfish, as crayfish greatly reduce activity during ecdysis and claws are soft and ineffective, it is reported that recent moults have twice the amount of digestible material as intermoult (Stein and Magnusson 1976) making them much more attractive to predators (Dehli 1981, Blake and Hart 1993b). In this scenario, as appears true for marron-silver perch combinations (Whisson 2000), vulnerability would increase following ecdysis, therefore provision of suitable habitat in appropriate areas within a polyculture system may greatly reduce stress and mortality of moulting crayfish.

Predation is a strong selective force that shapes many behavioural, life history and morphological traits in prey animals (Sih 1987, Dodson 1989, Lima and Dill 1990, Chivers and Smith 1998). However, in many manufactured polyculture systems, such as with marron and silver perch, species do not have the luxury of evolved specific avoidance tactics as species are generally novel (no previous interaction). Therefore, aquaculturalists need to manipulate systems to provide vulnerable species with a competitive edge. To do this requires an understanding of how system variables affect interaction.

### **2.3.5 Influence of system dynamics**

Major factors influence both positive and negative interactions within multi-species systems. The way these factors influence system ecology can be linked to the energy rewards and losses that come from the activities of the component organisms. This relationship is encompassed by the optimal foraging theory.

#### **2.3.5.1 Optimal foraging**

It is thought that predators will endeavour to maximise their net energy gain when hunting by targeting more vulnerable prey (Stein 1977). Optimal foraging theory predicts that decisions made by predators in searching for food (selection of area, how

much time to stay in area and what food to consume) will evolve under natural selection to enhance fitness (Charnov 1976, Krebs and Davies 1978). Predation is essentially a cost-benefit approach (Mitchell and Hazlett 1996), centring on obtaining the highest caloric reward at the minimal energetic cost. For example, Ware (1972) determined that carnivorous trout would decrease substrate orientated searching if they achieved a reward of less than 0.058 captures per second. Kaufman et al. (1996) demonstrated that large snails and those requiring short handling times were chosen by lizards over small snails and those requiring greater handling times.

Optimal foraging has been studied in many species including amphibians, fish, insects and birds (Krebs and Davies 1978, Jaegar and Barnard 1981, Jaegar and Rubin 1982, Ranta and Nuutinen 1985, Krebs and Davies 1991). Optimal foraging models predict that animals should (Kaufamn et al. 1996):

1. Be more selective when profitable prey are common;
2. Ignore unprofitable prey that are outside the optimal set regardless of how common they are; and,
3. Should concentrate on more profitable prey.

In aquaculture, predator-prey interactions among culture animals can significantly affect production. This can be directly through predation, or via stress responses and reduced foraging in prey due to predation pressure (Milinski and Heller 1978). Appelberg and Odelstrom (1988) reported that the presence of *Perca fluviatilis* reduced activity and foraging of *Pacifastacus leniusculus*, resulting in depressed growth. As predation is related to ease of capture, by increasing the energy required by predators to locate and capture prey farmers should be able to reduce or even prevent predation. There are a number of reported factors capable of manipulation in aquatic environments that can increase the cost of consuming prey. In multi-species systems, correct management of these factors can not only protect and reduce stress of prey, but also force the predatory species to accept a more cost-effective artificial feed. Some of the major factors are turbidity or light intensity, habitat complexity, water flow and aeration, stocking regime, species choice and devices tailored to certain situations - such as cage culture.

### 2.3.5.2 Turbidity and light Intensity

Most fish depend on vision in their search of prey (Guthrie 1986). This is evident in the preferred hunting times of visual predators, where strong diel variations are commonly correlated with time of highest light penetration (Clark et al. 2002). The effect of turbidity, reducing light penetration, on the ecology of aquaculture systems can have profound effects on visual predators (Vinyard and O'Brien 1976, Confer et al. 1978, Gregory and Northcote 1993, Benfield and Minello 1996, Utne-Palm 2004) and thus, on overall production. In clear-water systems, bluegills were shown to remain within habitat, both artificial (Savino and Stein 1982, 1989) and natural (Stein et al. 1988, Werner and Hall 1988), rather than risk predation (Miner and Stein 1996). However, when turbidity was increased, bluegills ventured into open water where predation risk was reduced and as a result, foraging was increased (Miner and Stein 1996).

The relationship between turbidity and predation is essentially a function of cost-reward benefits. Turbidity has been shown to be negatively correlated with reactive distance (maximum detection distance) of aquatic predators (Moore and Moore 1976, Berg and Northcote 1985, Miner and Stein 1996, Utne 1997). With increased reactive distance, predators need to increase search time, therefore increasing cost of locating and capturing prey. Larval striped bass preyed less on copepods in turbid water but continued to consume *Daphnia pulex* independent of turbidity (Breitburg 1988). This suggests that lower energy gain from the copepod was enough to make the cost-benefit of predation unprofitable to bass. The selection of particular size classes of prey by predators was shown not to be influenced by turbidity in the case of bass-daphnia (Breitburg 1988) or bluegill (*Lepomis macrochirus*)-daphnia (Gardner 1981), however overall feeding rate was significantly reduced (Gardner 1981). For a polytrophic predator of crayfish, such as silver perch, this suggests that manipulation of turbidity may greatly influence feed choice. The tendency for omnivorous species to quickly alter feed choice in conditions of rising turbidity is more prevalent than in carnivorous species (Sigler et al. 1984).

In some cases, lower level predators have adapted to feeding in turbid environments. Small planktivorous fish and fish larvae have adapted to low or medium-light foraging (Boehlert and Morgan 1985, Miner and Stein 1993, Bristow and Summerfelt 1994, Bristow et al. 1996, Utne-Palm 1999), where there is a reduced effectiveness of

predators. Rieger and Summerfelt (1997) showed improved performance and viability of larval walleye (*Stizostedion vitreum*) in conditions of low turbidity, and Atlantic herring (*Clupea harengus*) were shown to spawn in the shallow coastal water, where clarity is reduced by freshwater runoffs and algal blooms. The reason why some predators can adapt to high-turbidity feeding relates to search area. Suspended particles between predator and prey scatter light and interfere with detection in the same way that fog affects long-distance vision but has little effect on the detection of close objects (Utne-Palm 2004). Thus, the short reactive distance of planktivorous fish relative to their piscivorous predators means that they benefit more from the positive effects of scattering and absorbance within their relative search volume (Giske et al. 1994, Fiksen et al. 2002). Turbidity has been demonstrated to aid juvenile fish by increasing their feeding rate (Gregory and Northcote 1993), migratory activity (Ginetz and Larkin 1976), and increasing their use of open water (Miner and Stein 1996).

Some predatory species display more dynamic predatory modes in the face of changing turbidity. When macrophytes were eliminated and turbidity increased in ponds containing roach, perch and crayfish, roach were able to switch from visual to tactile foraging at night and were more successful predators of crayfish than perch (Svensson 1993). Turbidity has also been shown to increase predation rates in systems where light intensity and increased turbulence were tested (Chesney 1989). It was hypothesised that the increased turbidity increased the prey contrast (Hinshaw 1985), increasing reactive distance (Utne-Palm 1999). It is thought that the increased prey contrast negates some effects of increased turbulence (MacKenzie et al. 1994, Fiksen and MacKenzie 2002).

An understanding of both general rules and species specific characteristics is important to accurately manage aquatic systems.

### **2.3.5.3 Habitat complexity**

Habitat complexity in aquatic systems including both biotic (i.e. macrophytes) and abiotic shelters (natural and artificial), and substrate, has frequently been shown to be positively correlated with survival in the presence of predators (Quammen 1984, Reinsel and Rittschof 1995, Clarke et al. 2002, Gazdewich and Chivers 2002). In



crayfish culture systems, insufficient or unsuitable shelter has been shown to have a negative affect on both growth (Jones and Ruscoe 2000, Naranjo-Paramo et al. 2004) and survival (Jones and Ruscoe 2000). In Naranjo-Paramo et al. (2004), shelter density supplied at 50% of the initial crayfish population (1 shelter for every 2 crayfish) was insufficient in attenuating the negative affects on growth and survival. The addition of aquatic macrophytes (*Elodea and Carex sp.*) to the culture of perch (*Perca fluviatilis*) and crayfish (*Pacifastacus leniusculus*) reduced foraging efficiency of perch (Blake and Hart 1993b). In contrast, increasing habitat structure has resulted in a large and significant increase in natural enemy abundance, and similarly, decreasing habitat structure significantly diminished natural enemy abundance (Langellotto and Denno 2001). However, this generally does not apply to aquaculture where the relative abundance of predators is stable owing to the confined culture space.

Prey gain more advantage as the structural complexity of habitat increases (Ivlev 1961), so it is important for vulnerable prey to acquire the most complex shelter. This is evident with many crustaceans, where those in life stages more susceptible to predation frequent shelter more than those in other life stages (Stein 1977). In crayfish systems, gravid females are extremely aggressive in response to protection of the eggs they carry (Mason 1975, Stein 1977) and are the most successful life stage at acquiring shelter (Whisson 2000). Juvenile crayfish released from females are often the most susceptible to predation due to increased activity increasing potential interaction with predators (Magnusson 1976, Stein 1977, Doroshenko 1978, Blake and Hart 1993b, Svensson 1993). The lower energy stores, faster use of reserves, less tolerance to starvation (Svensson 1993) and increased moult frequency (Merrick and Lambert 1991, Huner 1994, Timmermans et al. 1995) means that juveniles must venture out of the safety of shelter into higher predation risk areas (Svensson 1993). These factors, combined with a general lack of predator recognition and avoidance tactics, means that farmers breeding crayfish where predators are present must supply a large amount of complex shelter and attempt to spread feed evenly throughout the system.

The availability of refuge in aquatic systems can easily be controlled in aquaculture. Crayfish culture systems utilise a range of shelter materials, from synthetic hides (Fellows 1995, Whisson 1997), roof tiles (Whisson 1995a, 1997), macrophytes (Blake and Hart 1993b, Whisson 2000) and other materials (Hutchings 1988, Merrick and

Lambert 1991). The type of shelter utilised in aquaculture production systems is dependent on not only the benefit to the target species, but also on the ease of management. For example, vegetation has advantages over other artificial forms in that it can also provide a food source, both directly, and indirectly through associated invertebrates. However, in some cases vegetation can be hard to control and can quickly engulf a system (Pillay 1993), making drain harvesting difficult.

The ability of increased habitat complexity to reduce the availability of prey species to predators and force predators to deliberately alter feeding habits has been shown on a number of occasions (Ivlev 1961, Momot 1967). However, shelter also plays an important role in attenuating negative effects of density (Naranjo-Paramo et al. 2004). This is especially evident in crayfish systems, as stocking densities are based on number per m<sup>2</sup>, as opposed to number per m<sup>3</sup> in fish culture. Thus, densities can be increased as shelter effectively increases living space (increased surface area).

One factor that must be considered when manipulating shelter complexity is that the provision of shelter will also increase its use, especially in the presence of predators, and foraging may be reduced. Shelter plays an important role in protection and stress reduction of stock in aquaculture systems, however, where this results in negative effects for production, a combination of management tools may be required, i.e. shelter and turbidity.

#### **2.3.5.4 Water flow and aeration**

Additional factors affecting predator success in aquatic systems include concentration of gases (e.g. dissolved oxygen: Pihl et al. 1991, Breitburg et al. 1994) and water movement (Hansen et al. 1991, Hart and Merz 1998), for freshwater (Peckarsky et al. 1990, De Nicola and McIntire 1991, Sih and Wooster 1994) and marine benthic systems (Palmer 1988). *Daphnia* have been shown to trade off reduced predation mortality in a refuge against disadvantages due to unfavourable oxygen conditions (Lass 2001), demonstrating that environmental conditions may constrain predator avoidance strategies. As previously mentioned, factors such as competition and predation can force animals into smaller microhabitats within systems. In both scenarios, the provision of optimal water quality conditions is important to ensure that

predatory avoidance strategies are not complicated by poor water quality. Increased flow can also decrease predator success due to hydromechanical predator constraints (Weissburg and Zimmer-faust 1993, Powers and Kittinger 2002). However if increased flow can cause dislodgement of meiofauna, for example, predation success is increased (Palmer 1988).

### 2.3.5.5 Stocking regime

Ecological studies of invertebrate predator-prey systems have indicated that body size (Werner and Hall 1974, Stein 1977, Howard 1988, Persson and Greenburg 1990, Wahle and Steneck 1992, Blake and Hart 1993b), predator size (Blaxter and Stains 1970), prey size (Ware 1973), swimming behaviour (Preston et al. 1999, Utne-Palm 1999), population density (Preston et al. 1999) and encounter rate (Utne-Palm 1999) are important components influencing predation risk. The stocking regime (size and density) is especially critical where multiple species inhabit the same ecological structure (Tapaidos et al. 1977, Blakely and Hrusa 1989, Pillay 1993).

#### Stocking size

Where finfish predate on decapod species, small or juvenile prey often attract the highest predation intensity (Howard 1988, Wahle and Steneck 1992, Blake and Hart 1993b). Juvenile (0+) crayfish were reported as the sole life stage selected by trout in a marl lake (Momot 1967). Svensson (1993) commented that moulting behaviour in juvenile crayfish is synchronised, a behaviour quickly capitalised on by adaptive predators. The size of predators is also important in the prey targeted. Huner (1986) demonstrated that minnows and small ornamental finfish species rarely predate on *Procambarus clarkii*, where as large catfish virtually eliminated crayfish from culture ponds. Generally, predator size is positively correlated with prey size; understandably as larger prey should provide the greatest caloric reward to the consumer. Trout (*Oncorhynchus mykiss* and *O. virilis*) in Lake Eucumbene, Eastern Australia, were shown to increase the maximum size of their crayfish prey (*C. destructor*) in relation to their own size (Faragher 1983). This trend was also seen in white perch (*Morone americana*) targeting *Orconectes limosis*, where crayfish size increased disproportionately with perch size. In contrast, Galbraith (1967) reported that perch and trout chose similar size prey independent of their own size. This may reflect an optimal cost-benefit approach for selecting the one size of prey. Similarly, *P. clarkii*

introduced into central Spain were actively predated upon by all size classes of pike (*Esox lucius*) (Elvira et al. 1996). In marron-silver perch polysystems, predation of marron by perch is not believed to be limited by gape size, with survival of both adult and juvenile marron reduced in trials conducted by Whisson (2000). Whisson (2000) found that survival of marron was greatly reduced in periods of mass moulting, such as warm summer conditions where growth rates are highest, it was suggested that perch attack soft post-moult individuals, regardless of size.

Relative size of conspecifics is also a major factor in competition. During antagonistic encounters individuals match their own strength to that of the opponent, thereby guiding their decisions to escalate, retaliate, or retreat (Beecher 1989). Interactions between closely matched individuals typically escalate over time (DiMarco and Hanlon 1997, Guiasu and Dunham 1997), and the risk of injury thereby increases with each step-up in intensity (Cairns and Scholz 1973, Huntingford et al. 1995). In aquaculture, similar sized individuals are generally the ideal, because of the requirement for final harvest sizes to be at a marketable level. This requirement may lead to increased conflict if not managed correctly.

Understanding size selectivity of predators can have remarkable effects on interspecific relationships. Simply stocking similar sized animals in multi-species systems, along with continual grading, may alleviate many problems.

### **Stocking density**

Correct stocking densities are crucial in multi-species systems (Shepherd and Bromage 1992), affecting production parameters, such as growth, survival, and yield (Morrissy 1979, Mills and McCloud 1983, Lutz and Wolters 1986, Villagran 1993). Several authors have studied the effects of stocking density on farming feasibility of crayfish species (Lutz and Wolters 1986, McClain 1995, Geddes et al. 1991, Morrissy et al. 1995a, Whisson 1995a, Verhoef and Austin 1999). In these investigations, an inverse relationship between stocking density and final size has been demonstrated, for example:

- Marron, *C. tenuimanus* (Morrissy 1992b) - Australia;
- Redclaw, *C. quadricarinatus* (Pinto and Rouse 1996) - Alabama (US);
- Redclaw (Jones and Ruscoe 2000) - Australia;

- Freshwater prawns, *M. rosenbergii* (Brody et al. 1980, D'Abramo et al. 1989, Tidwell et al. 1999) - United States;
- Red Swamp Crayfish, *Procambarus clarkii* (Lutz and Wolters 1986, Villagran 1993) - United States;
- Signal crayfish, *Pacifasticus leniusculus* (Savolainen et al 2004) - United States

A consistent observation is that feed conversion rates (FCR) are unaffected by density. Thus, reduced growth must be affected by other undefined processes. Stocking strategies in polyculture obviously need to take into account both density and final size of stock, and how this equates to pond yields. Strategies should be governed by the feeding biology of the participating species, given the availability of natural food within the ecological niches, and the ultimate management objectives (Cohen 1984).

Weighting the relative contributions of predation risk factors, the manner in which they interact, and responses to toxicant exposure requires multi-species predator-prey systems which consider both empirical measures of predator efficiency as well as the behaviour of predator and prey (Preston et al. 1999). For instance, in situations of high turbidity, low relative prey densities compound this relationship by increasing predator search time and energy use when hunting (Breitburg 1988). In order to best choose densities and sizes farmers should understand the biology and behaviour of the species they are culturing.

#### **2.3.5.6 Species selection**

Selection of potential species requires observation of economic variability, government policy, regulatory direction and market opportunity (Spencer 2000). Once appropriate and available candidates are identified, an understanding of ecological processes governing interaction between species is required. Some of the primary components of aquatic environments that can influence species choice in respect to both optimal growing conditions for each species and interaction ecology include: water quality, photoperiod, light intensity, shade, substrate, substrate cover, and depth. These factors can affect animals directly, or can be considered a secondary response due to factors such as competition (Tomasso 1996). Therefore, consideration of population

and community structure (density, size, size variability, monoculture, predators, polyculture, unwanted competitors, pathogens) and even previous interaction history, is also necessary.

In multi-species systems one of the most important factors governing species choice is analysis of feeding behaviour. For instance, given that the biological basis to aquatic polyculture is the utilisation of different ecological niches by species possessing varying feeding preferences (Moav et al. 1977, Siddiqui et al. 1996, Milstein 1997), a scavenging omnivore like silver perch seems a suitable candidate for duoculture with detritivorous crayfish, such as marron.

### **2.3.5.7 Cage culture**

Although factors such as turbidity and shelter can greatly reduce predatory interactions between species, predation can still occur. Even if predators do not actively seek out prey they will often consume them if encountered. In addition, the physical presence of predators, even if not directly attacking prey, can still affect stress levels in prey through perceived threat. In situations where free-range pond culture is not practical, such as when physical interaction of species within a polyculture environment results in competition or predation, cage culture may be applied (Masser 1988).

Many freshwater finfish species have been successfully reared in cages, including catfish, trout, tilapia, striped bass, red drum, bluegill sunfish, crappie and carp (Masser 1997). However, the responses to cage culture are varied. Channel catfish and rainbow trout appeared to benefit from polyculture in cages, producing significantly larger animals compared to monoculture (Beem et al. 1988), whereas silver perch have shown depressed growth when reared in cages (Whisson 2000). Choosing a species suitable for cage culture often requires a trial and error approach, however one of the major characteristics that aid in a species ability to perform well in cages is schooling. A schooling species is generally amenable to high stocking densities associated with cages. In the United States, catfish have been stocked at around 260 fish/m<sup>3</sup> (Masser 1988), and a common average production in cage culture is around 84-135 kg/m<sup>3</sup>, and up to 235 kg/m<sup>3</sup> in small cages (Masser 1997).

The benefits of cage culture are include (Masser 1988, Beveridge 1996):

- In large systems (lakes, reservoirs, rivers and oceans), aquatic species can be cultured which would otherwise be difficult or impossible to harvest;
- Relatively low initial investment in existing bodies of water;
- Easier observation of stock;
- Greater stock control;
- Easy and more efficient grading and harvesting, with less deleterious affects to stock. Drain harvesting can force stock into sediment which can clog and irritate gills, also cages allow removal of gut contents prior to harvest;
- Allows combinations of species which would normally compete or predate on one another.

A fish farmer can utilise cage culture to diversify existing monoculture practices without having to invest large amounts of capital for construction or equipment, and can therefore trial new species without unreasonable risks. However, there are also a number of management concerns with cage culture (Masser 1988), including:

- A requirement for nutritionally complete feed - as caged species are prevented from accessing natural feeds in the system;
- Water quality conditions, especially oxygen, must be maintained more carefully, as caged species cannot move through the system to find better conditions;
- Incidence of disease and injury can be high if not closely observed as fish are more prone to contact with other fish or the cage structure.

Stocking silver perch in cages in marron ponds is an attractive option as interspecific interaction is avoided, bird predation is eliminated and management of stock is more effective than in free-range practices (Whisson 2000). However, growth of silver perch is clearly reduced when stocked in cages (Rowland 1995c, Whisson 1999) with the growth-density relationship requiring further research due to the profound impact of density changes on system yields and profitability (Whisson 2000).

### 2.3.5.8 Intraspecific dynamics in multi-species systems

As previously discussed, higher order consumers can force prey species into confined areas (i.e. shelter), increasing relative densities of conspecifics, and the potential for negative social interactions.

Awareness of the importance of social interactions among crustaceans as a growth-regulating factor has gradually increased over the last three decades, with many studies focussing on fresh and saltwater crayfish (Cobb and Tamm 1974, Nelson and Hedgecock 1983, Ra'anan and Cohen 1985, Karplus et al. 1992a, Karplus and Hulata 1995). Comparisons between the growth patterns of individuals raised at the same density in groups or in individual cells have shown clear evidence of the importance of intraspecific interactions (Malecha et al. 1981, Lee and Fielder 1983, Ra'anan and Cohen 1984, Geddes et al. 1988). Crustaceans raised in isolation were shown to grow significantly more uniformly than those raised in groups, and the growth rates differed between separately and group-reared individuals.

The particular strategies utilised in competitive encounters can provide insight into proper management for aquaculture to reduce negative effects from interactions. Strategies adopted by individuals under conflict are sensitive to absolute values, relative differences, and asymmetries in information of a variety of factors. These include: size and physical superiority (Rutherford et al. 1995, Pavey and Fielder 1996, Barki et al. 1997); moult stage (Tamm and Cobb 1978); gender (Sinclair 1977); prior residence (Peeke et al. 1995, Huntingford and deLeaniz 1997); reproductive condition (Debusse et al. 1999); aggressive state (Huber et al. 1997, Huber and Delago 1998); metabolic state (Sneddon et al. 1998); previous antagonistic experience (Rubenstein and Hazlett 1974, Gössmann et al. 2000); levels of social isolation (Dunham 1972); and assessment of both the opponent (Archer 1988) and the resource at stake (Hazlett et al. 1975, Sneddon et al. 1997, Vye et al. 1997).

In several studies into redclaw cultures in Australia, both in tropical and sub-tropical conditions (Lawrence and Jones 2002), growth was shown to be inhibited with increasing stocking densities. Redclaw readily fight (Karplus et al. 2003) and juveniles compete aggressively for clumped food resources (Barki et al. 1997). Several indications of the involvement of social interactions in size regulation in redclaw have



been suggested (Barki and Karplus 2004), these are: (a) Individuals that are relatively small because of their lower growth rates within their broods exhibited higher growth rates after isolation; (b) Individuals reared in isolation attain sizes comparable to those of individuals in the upper quartile of the same population, suggesting that growth inhibition occurred under conditions of social interactions; (c) Density affected growth and size frequency distribution despite the fact that food was provided *ad libitum*. In a laboratory study conducted by Barki and Karplus (2004), redclaw held at low density, presumably with fewer social interactions, a high proportion of juveniles attained a large size and growth was relatively uniform, whereas at higher density, growth was reduced and size variation increased.

Four mechanisms relating to intraspecific interactions have been suggested to suppress growth in crustaceans:

- Direct competition for food - dominant individuals might actively deprive subordinates (i.e., smaller individuals) of food. (Segal and Roe 1975);
- Appetite suppression - antagonistic interactions can result in the establishment of social hierarchy, where subordinates may grow less rapidly, even with unlimited food, because of lower food intake (Cobb et al. 1982);
- Decreased food conversion efficiency - smaller subordinate individuals may have lower food conversion efficiency due to reduced digestibility and/or a metabolic shift related to their lower social status (Karplus et al. 1992b);
- Increased motor activity - small subordinate individuals may be engaged in continuous evasive manoeuvres to escape from dominant individuals, and the resulting high energy expenditure reduces their growth (Cobb et al. 1982).

The sensory modalities involved in social control of growth have received considerable research attention over the past 20 years (e.g. Howe 1981, Malecha et al. 1981, Cobb et al. 1982, Nelson et al. 1983, Nelson and Hedgecock, 1983, Moore et al. 1985, Juarez et al. 1987). These studies demonstrated the involvement of tactile, visual and chemical cues, separately or in combination, in regulating the growth of conspecifics, illustrating the need for research into the communication and interaction responses within and between species.

### **2.3.6 Behavioural analysis in multi-species systems**

In nature, an organism's daily activities are affected by predation and predation risk, which may have behavioural and physiological costs that negatively affect the individual or translate into long-term population and community consequences. Obviously, in multi-species systems where niche overlap exists the negative interactions need to be understood and mediated in order to maximise aquaculture production. The importance of behavioural analysis in describing and managing interactions has been consistently shown. Behaviour can be conscious or unconscious, overt or covert, voluntary or involuntary (West-Eberhand 1989), and is the most flexible phenotypic feature of animals, being the direct interface between animals and a variable environment (Hazlett 1995). Behaviour can track environmental variation the fastest because the cues guiding the variability are so closely associated with changes in phenotype (West-Eberhand 1989).

Behavioural analysis was used in all laboratory trials in this thesis to examine communication and interaction responses between crayfish-crayfish and crayfish-fish. Behavioural measures of stress are sensitive indicators of the stress response, having an advantage over other methodology as they are readily interpreted within an ecological context, thereby increasing the efficiency for extrapolation of laboratory results to the natural environment (Schreck et al. 1992).

## 2.4 Communication and interaction responses

In monoculture operations, production is fundamentally governed by the ability of the farmer to select an appropriate culture species and optimise growing conditions (water quality, habitat and feed).

In multi-species systems, management is made more complex by the addition of interspecific interactions, which can have both direct and indirect ramifications for production, such as: predation (i.e. Sih 1987, Lima and Dill 1990, Chivers and Smith 1998); interspecific competition (Tomasso 1996); or increased resource competition between conspecifics (Werner 1991, Kotler et al. 1994). Therefore, management of interactions between component species is a key aspect of polyculture production. This is particularly critical in situations where component species display conflicting niche occupation, characteristic of Western Australian polyculture systems (Whisson 2000) - due to paucity of available complementary species (Jones and Ruscoe 1996).

Understanding the ecological basis of interactions, the way in which species communicate and respond, is critical in developing management strategies aimed at reducing negative interactions and maximising synergy (Whisson 2000). For example: increasing turbidity, which increases the time for searching due to increased reactive distances (Miner and Stein 1996, Utne 1997), can reduce predation between species cohabiting the same system (Gradall and Swenson 1982, Benfield and Minello 1996). However, if the predator relied on chemical cues to locate and capture prey, increasing turbidity would be ineffective. For example, *Neoceratodus forsteri* (lungfish) were shown to effectively predate on crayfish using electric fields generated from the bodies of prey when all visual and chemical cues were inhibited (Watt et al. 1999).

The nature and extent of communication between aquatic animals is associated with their ability to detect, interpret and respond to exteroceptive signals. These ecological and ethological cues may have chemical (e.g. Halpin 1986, Hazlett 1994a, Mirza et al. 2001), visual (e.g. Halpin 1986, Mirza et al. 2001, Bouwma and Hazlett 2001), tactile (e.g. Enger et al. 1989, Mirza et al. 2001, Herbaholtz et al. 2004), acoustic-audio (Halpin 1986, Gil-da-costa et al. 2003, Vester et al. 2004), electric (Kalmijn 1971, Mirza et al. 2001, Carlson and Hopkins 2004), magnetic (Rosenthal and Ryan 2000), thermal (Rosenthal and Ryan 2000) or other origins (Batty et al. 2004). The ability to detect and respond to the various information cues available is species dependent

(Krebs and Davies 1993), can be hierarchal (Dawkins 1976, Enquiste et al. 1987, Nelson 1990) or require multiple signals (Bradbury and Vehrencamp 1998, Rekwot et al. 2001), can change over ontogeny (Russock 1990, Stacey and Sorrensen 1991), and can fluctuate temporally and spatially (Dicke 2000).

The following sections examine the various sensory modalities utilised by aquatic organisms. The responses to cues pertaining to interaction between component species in polyculture, and the subsequent affects on routine behaviour (i.e. food acquisition, intraspecific dynamics), is of particular concern and will be focused on in this review. As the aim for Western Australian polysystems is to promote synergy between species that have less than complementary feeding niches, the following review will focus on factors affecting predator-prey dynamics: threat detection; predator avoidance; learning; and abiotic factors affecting interaction.

#### **2.4.1 Visual communication**

The visual system is a major sensory device employed in communication (e.g. Halpin 1986, Culp et al. 1991, Rosenthal and Ryan 2000, Bouwma and Hazlett 2001, Mirza et al. 2001). Visual cues certainly play one of the most important roles among terrestrial or semi-terrestrial species (Vannini and Cannicci 1995), however their use in aquatic environments is varied and often dependent on water conditions (Gregory and Northcote 1993, Benfield and Minello 1996, Utne-Palm 2004). In clear-water systems, such as coral reefs, visual signals are often the main method of communication (Watson 1999), providing early accurate information (Culp et al. 1991, Brown et al. 1997, Brown and Godin 1999, Murray and Jenkins 1999, Hazlett and McLay 2000, Bouwma and Hazlett 2001), however visual cues would be less effective in turbid environments (Vinyard and O'Brien 1976, Confer et al. 1978, Utne 1997). Understandably, vision is the most predominant communication medium utilised by diurnal (Enquiste et al. 1987) and non-cryptic species (Diaz et al. 1999).

##### **2.4.1.1 The role of visual information**

Visual cues in aquatic environments can communicate a variety of information. The various roles of visual signals include:

### Routine behaviour

- Food acquisition (pond snail - Andrew and Savage 2000);
- Shelter (Forward 1988) - i.e. shell transfers in hermit crabs (Kinosita and Okajimi 1968, Hazlett 1996);
- Migration (McKelvey and Forward 1995, Lass 2001).

### Intraspecific interactions

- Social communication (Li et al. 2000, Listerman et al. 2000);
- Conspecific identification (Diaz et al. 1995a/b);
- Perception of motion, shape (Chinese Perch – Liang et al. 1998, Gastropods approach vertical objects - Hamilton 1977, Hamilton and Winter 1984, Watson 1999, Cephalopods detect body patterning - Hanlon and Messenger 1996) or colour (Diaz et al. 1999, Watson 1999);
- Competition and readiness to fight (Watson 1999);
- Male-female interactions (Zalesky et al. 1984, Rekwot et al. 2001);
- Sex detection (Hemptinne et al. 1998, Kodric-Brown and Strecker 2001);
- Mate searching and selection (Diaz and Thiel 2004, Knuttel and Fiedler 2001);
- Courtship and reproduction (Watson 1999; female peacock blenny responds exclusively to male visual features, Goncalves et al. 2002).

### Interspecific interactions - Predator-prey interrelationships

- Threat detection (Brown et al. 1997, Watson 1999);
- Prey recognition (Chinese Perch, Liang et al. 1998; Glowlight tetras, Kaufman et al. 1996, Boal and Marsh 1998, Brown et al. 2000)
- Inspection of novel predators (Dugatkin and Godin 1992, Brown and Chivers 1996; Glowlight tetras, Brown et al. 2000);
- Attack - disturbance pheromones from prey capture (Langdon and Herrnkind 1985; glass shrimp by fish, Clark et al. 2002);
- Anti-predator behaviour (Herrnkind 1968, 1972, 1983; blue crabs, Diaz et al. 1999, Diaz et al. 2001; marine copepods, Bollens et al. 1994, Murray and Jenkins 1999, Woodley and Peterson 2003);
- Predator deterrent (fin-flicking, Heller and Milinsi 1979, Brown et al. 1999, Lass 2001), offering opportunity for escape (Curio 1978, Magurran 1990, Hasson 1991, Godin and Davis 1995a/b);
- Capture – alarm cues (Smith 1989, Brown et al. 1999, Watson 1999).

#### 2.4.1.2 Responses to visual cues

Physiological (Li et al. 2000, Listerman et al. 2000, Smith et al. 2000) and behavioural modifications can occur in response to visual stimuli (Stein and Magnussen 1976, Blake and Hart 1993b, Spanier et al. 1998). Behavioural responses to the detection of interspecific visual cues pertaining to predators or competitors include increased sheltering (Lass 2001), decreased locomotion (Godin 1997), and flight responses (Mathis and Smith 1993b, Hazlett 1999).

In the case of predation risk, responses to visual signals can be alarm signals (Smith and Smith 1989, Godin and Davis 1995a, Mathis et al. 1996). Visual alarm signals can be used to warn conspecifics, sympatrics and heterospecifics of potential danger (Smith and Smith 1989), resulting in increased anti-predator behaviour of those in visual range of the signal sender. Alarm responses have been shown to quickly spread through entire populations in an area (i.e. fathead and European minnows - Magurran and Higham 1988, Mathis et al. 1996). The release of visual alarm signals, such as head bobbing in gobiid species (Magurran and Higham 1988, Mathis et al. 1996) or fin-flicking in tetras, can also function by deterring predators, and result in increased distance from prey, longer time to bite and less bites (Brown et al. 1999). They may also work in confusing predators, with responses including swarming-aggregation-shoaling (Heller and Milinski 1979), which would reduce the chance of being captured for the individual (Godin 1986, Pitcher and Parrish 1993, Lass 2001). Visual alarm signals in response behaviours to visual predator cues may allow the opportunity for escape (Curio 1978, Magurran 1990, Hasson 1991, Godin and Davis 1995a/b), for both the producer and detector (Smith 1992, Chivers and Smith 1998).

Different visual signals can produce varied responses, for instance Megalopae crabs (post larval blue crabs) become motionless or escape by swimming directly away from stimulus when solid shapes are detected, however if vertical stripes are presented (representing sea grass or fish schools) the crabs respond with erratic swimming (Diaz et al. 1999). Many factors may influence responses to visual signals, from sex differences (Hemptinne et al. 1998) to prior learning (Mathis and Smith 1993b, Chivers and Smith 1998, Dicke and Grostal 2001) to ontogenetic differences (Giaquinto and Volpato 1997). Investigators must consider these differences if appropriate management strategies are to be developed.

### **2.4.1.3 Manipulating visual communication in polysystems**

Responses to visual cues can be advantageous in natural systems in preventing predation, however avoidance strategies require energy, which will indirectly affect growth and condition in aquaculture. The responses to predation risk can also disadvantage the detector if they involve movement away from optimal conditions (e.g. daphnia shelter in unfavourable oxygen conditions to avoid predation) (Lass 2001), result in lost resources (increased sheltering - reduced foraging), or if avoidance is carried out when not required (wasted energy) (Lima and Dill 1990). If aquaculturalists can prevent predation along with the associated stress, resources can be focussed on growth. As predation by visual predators is affected by light conditions, when visual interaction is manipulated, such as through increased turbidity, increased growth is observed (Wang et al. 2003).

In many cases visual cues are sufficient in providing all information required for particular events (Boal and Marsh 1998, Goncalves et al. 2002). However, the addition of other cues, in combination with visual stimuli, often results in a more rapid and confident response (Andrew and Savage 2000, Bouwma and Hazlett 2001). In some species visual reception is important only in later life and other sensory modalities such as chemoreception (Giaquinto and Volpato 1997) are required in the first days of life. In some cases, visual stimuli seemingly offers no information (Kiesecker et al. 1996, Kodic-Brown and Strecker 2001). When studying the interrelationships between species, researchers must compare and contrast a range of information cues.

### **2.4.2 Chemical communication**

Chemical communication is a well-known and widespread ecological phenomenon mediating a variety of interactions between organisms (e.g. Dicke and Sabelis 1992, Hazlett 1994a, Burks and Lodge 2002, Gherardi 2002) and between organisms and environment (e.g. Maynard Smith 1993, Andrew and Savage 2000, Grasso and Basil 2002). Historically, the study of chemical ecology has focussed on terrestrial environments (Lass 2001), beginning with insects as early as 1609 (Roitberg 1992). More recently, the importance of chemical ecology in aquatic environments has been recognised (e.g. Beldon et al. 2000, Watson 1999, Rekwot et al. 2001, Burks and Lodge 2002).

The transmission of chemical information is well suited to aquatic environments with many compounds dissolving easily in water (Kleerekoper 1969, Hara 1994) and aquatic animals have evolved highly specialised receptors for detecting these compounds (Kats and Dill 1998, Derby 2000, Wisenden 2000, Mirza et al. 2001).

In aquatic systems, chemical cues may be particularly important where vision is limited, such as: at night; in densely vegetated habitats; or in turbid water (Chivers et al. 1996b). In these situations, the ability to recognise chemical cues from faeces or other metabolic by-products would be an advantage over visual or tactile recognition (Stoddart 1980, Lass 2001). Many animals demonstrate responses to chemical cues but depend little on, or show no change in behaviour, when other cues are presented (Tukey 1977, Kiesecker et al. 1996).

Chemical communication is often viewed as the primary source of information in aquatic environments (Chivers et al. 1996b, Kiesecker et al. 1996, Brown et al. 1997), with responses demonstrated in many species in all major groups of aquatic species (Kats and Dill 1998, Brown et al. 1999, Vet 1999, Hay 2002); for example

- Finfish (Brown et al. 1999, Mirza and Chivers 2002);
- Marine crustaceans (Forward Jr and Rittschof 1994, Welch et al. 1997);
- Freshwater crayfish (Gebauer et al. 2002, Grasso and Basil 2002);
- Molluscs (Morse et al. 1979, Hadfield and Scheuer 1985, Zimmer-Faust and Tamburni 1994, Pechenik et al. 1995, Doroudi and Southgate 2002);
- Barnacles (Crisp and Meadows 1962, Rittschof 1985, Yule and Walker 1985, Claire et al. 1995);
- Amphibians (Lopez and Martin 2001);
- Invertebrates (Black and Dodson 1990, Forward and Rittschof 1999); and,
- Aquatic vegetation (Wolcott and De Vries 1994, Brumbaugh and McConaughy 1995, Forward et al. 1994, 1996, 1997).

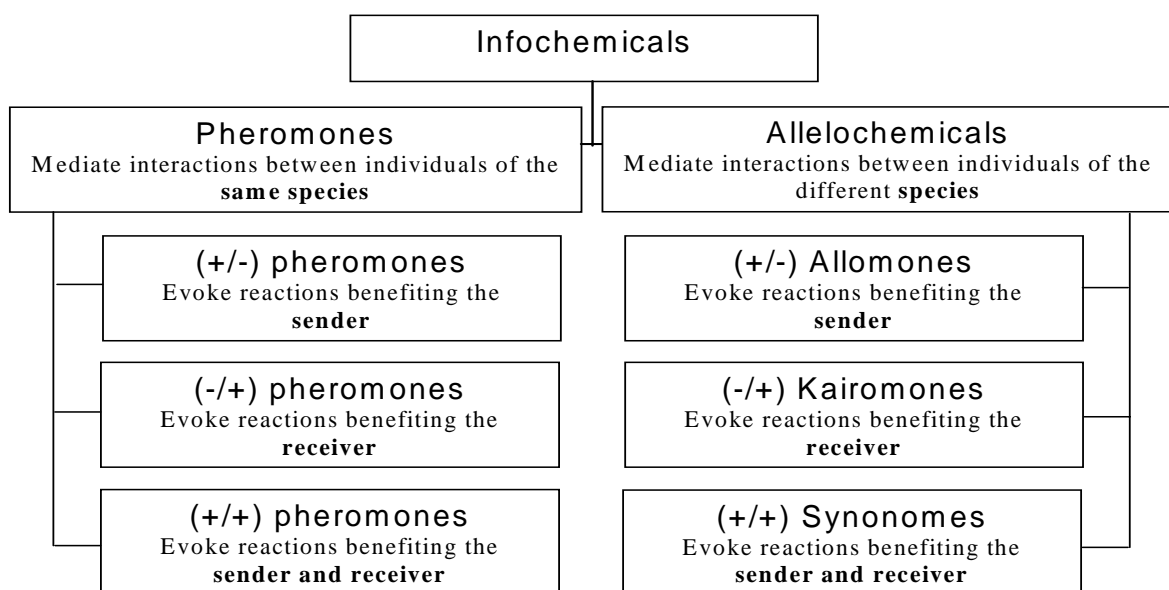


### 2.4.2.1 The role of chemical information

Chemical signals play “important roles in the loves and lives of living organisms” (Vet 1999)

Some chemicals are directly beneficial or detrimental for organisms, such as nutrients and toxins, while others (infochemicals) transmit information and induce a response to the benefit or detriment of the organisms involved (Dicke and Sabelis 1988).

Chemosensory cues are perhaps the most ancestral means of information flow, providing strong, reliable information (Chivers and Smith 1998, Kats and Dill 1998, Sorenson and Caprio 1998, Vet 1999, Wisdenson 2000). Chemicals signals play an important role in countless interactions among organisms and steers many ecological and evolutionary processes (Vet and Dicke 1992, Burks and Lodge 2002). Generally, the term pheromone, coming from the Greek *pherein* (to carry) and *hormon* (to excite), has been used to describe most of the chemical signals produced in aquatic environments, however chemical cues are varied in their nature and roles. A number of terms are used to describe infochemicals, released or detected, in aquatic environments. These signals are defined in Figure 2.2, based on the information they provide and the relative costs and benefits experienced by the interacting organisms.



**Figure 2.2** Infochemical terminology (Dicke and Sabelis 1988, In Lass 2001)

The importance of chemically mediated interactions for population dynamics, for structuring communities and for cohabitation of species is increasingly recognised and investigated (for review see Vet 1999). The roles that infochemicals have, specifically relating to dynamics within polysystems, include:

#### Routine behaviour

- Food differentiation (Hazlett 2003);
- Food acquisition by odour (lobsters, crayfish and crabs - Tierney and Atema 1988, Barnes 1997, Giri and Dunham 1999, Moore and Grills 1999, Hazlett 2000a, Hazlett and McLay 2000, Grasso and Basil 2002, fish - Mirza and Chivers 2002, Ingvarsdottir 2002, molluscs - Audesirk et al. 1982, Andrew and Savage 2000, mammals - Jacquot and Baudoin 2002, reptiles - Kaufman et al. 1996, appetitive learning);
- Sheltering – habitat selection (lobsters, crayfish and crabs - Grasso and Basil 2002), migration and settlement (molluscs - Pechenik et al. 1995, Doroudi and Southgate 2002, crabs - Gebauer et al. 2002);

#### Intraspecific interaction

- Social communication (Yamazaki et al. 1976, Hurst 1987, 1989, 1990a/b, Drickamer and Mikesic 1990, Mucignat-Caretta and Caretta 1998, Penn and Potts 1998);
- Conspecific identification (lobsters, crayfish and crabs - Grasso and Basil 2002, fish – Giaquinto and Volpato 1997, Baker and Montgomery 2001);
- Perception of motion, shape or colour (Hargeby et al. 2004);
- Aggregation (Deneubourg et al. 2002, sessile invertebrates - Burke 1986, Pawlik 1992, reef fish - Sweatman 1988, pelagic fish - Mangel and Clark 1988, lobsters - Ratchford and Eggleston 1999);
- Physical competition (marking territory - Crowcroft and Rowe 1963, Brown 1985, advertise strength - Hurst 1993, suppress competitors - Hay 2002, deter feeding - Agarwala et al. 2003, intrasexual competition - Hurst 1993, Gosling et al. 1996, Drickamer 1997, identifies aggressive state - Breithaupt et al. 1999, Breithaupt and Atema 2000, Dulac 2000, Breithaupt and Eger 2002, Schapker et al. 2002, reduces antagonistic reactions/ decreases aggression – Giaquinto and Volpato 1997);
- Growth inhibition (MIH - inhibit food related responses (Hazlett 1994a, Bouwma and Hazlett 2001, Gherardi 2002);

- Male-female interactions (Zalesky et al. 1984, Rekwot et al. 2001);
- Sex determination (review by Halpin 1980, Asai et al. 2000, Kodric-Brown and Strecker 2001, Olivotto et al. 2002);
- Mate location (Atema and Engstrom, 1971, Gleeson et al. 1987, Yen and Strickler 1996, Vickers, 2000, Diaz and Thiel 2004, crustaceans - Borowsky 1984, 1985, Bushman and Atema 1997, Ratchford and Egglestrom 1998);
- Mate selection (Alcock 1984, Boal and Marsh 1998, Hemptinne et al. 1998, Zanetti et al. 2001, Rantala et al. 2002, Diaz and Thiel 2004);
- Courtship – readiness for mating (Dulac 2000, Frade et al. 2002, Murphy and Stacey 2002, in decapod crustaceans - Review, Dunham 1978, Carr and Derby 1986, amphipods - Dahl et al. 1970, Borowsky 1984, 1985);
- Reproduction (gamete production - Watson 1999, Vermeirssen and Scott 2001, synchronised reproduction - Rekwot et al. 2001, Tankersley et al. 2002, spawning aggregations: fish - Colin 1992, sea cucumber - Watson 1999, crabs - Stone et al. 1993, worms - Caspers 1984).

#### Interspecific interaction

- Sympatric communication (Hemptinne et al. 1998, Kodric-Brown and Strecker 2001);
- Interspecific competition (Burks and Lodge 2002);
- Predator-prey relationships (Larsson and Dodson 1993, Hanazato 1994, Chivers and Smith 1998, Preston et al. 1999, Burks and Lodge 2002);
- Locating prey (Powers and Kittinger 2002);
- Threat detection - predator odours (Mathis and Smith, 1993c, Covich et al. 1994, Chivers et al. 1996b, De Meester and Cousyn 1997, Wisenden 2000, Tomba et al. 2001);
- Risk assessment (Chivers and Smith 1998, Kats and Dill 1998, Head et al. 2002), recognition (Dodson et al. 1994, Chivers and Smith 1995, Chivers et al. 1996b, Lopez and Martin 2001) and inspection of novel predators (Dugatkin and Godin 1992, Brown and Godin 1999, Brown et al. 1999);
- Attack cues - released by predator (Chivers et al. 1996b, Hazlett and Schoolmaster 1998, Wisenden 2000) or disturbance pheromones (Hazlett 1990, Wisenden 2000, Hazlett et al. 2002, Olivotto et al. 2002);
- Anti-predator behaviour (Kiesecker et al. 1996, Kats and Dill 1998, Wisenden and Millard 2001, Diaz et al. 2001, Head et al. 2002), predator

- deterrent (Hay 2002), fight or flights (e.g. Cuadras 1980, Brown et al. 1995, Schapker et al. 2002), aggregation;
- Capture (Hirsch and Bolles 1980, Wisenden 2000), injury-released alarm cues (Howe and Scheikh 1975, Hazlett 1994a, Chivers and Smith 1998, Mirza et al. 2001, Wisenden and Millard 2001, Gherardi et al. 2002), attraction to alarm cues (Wisenden and Thiel 2002);
  - Alarm signals (non-injury) (e.g. Smith 1992, Mathis and Smith 1993a, Brown and Godin 1997);
  - Ingestion (Wisenden 2000) - dietary cues (Howe and Harris 1978, Brown et al. 1995, Chivers et al. 1996b, Beldon et al. 2000, Brown and Godin 1999, Wisenden 2000).

The roles of chemical cues in aquatic environments are wide ranging and varied, and in many cases provide information overriding all other communication cues. The strength of chemical signals is evident in examining mating behaviour in male shore crabs, *Carcinus maenus*. When female shore crabs are ready to mate they release pheromones in their urine which trigger mating behaviour in males. If you dip a male crab, a stone or even a tennis ball into water containing the female urine the male crab will mate with it - overriding all other signals (Watson 1999).

Chemical cues can provide valuable information regarding predator-prey ecology. Anti-predator behaviour is commonly associated with a response by prey animals following direct (i.e. visual or tactile) contact with a predator, however recent research has identified the potential importance of less direct factors, such as predator chemical cues (kairomones) (e.g. Kats 1988, Jedrzejewski et al. 1993, Koskela et al. 1996).

Studying chemical communication between predator and prey is more difficult than other exteroceptive cues because signals are not easily detectable (Breihaupt and Eger 2002). This is made more difficult as the nature of the cue released depends on stage of predation sequence, with cues released during detection, attack, capture and ingestion of prey (Wisenden 2000). Behavioural and sometimes physiological responses are often used to gauge the effects from chemical interaction.

#### **2.4.2.2 Responses to predator derived chemical cues (kairomones)**

Predators are believed to be important agents of selection eliciting a variety of adaptations in their prey (Lynch 1980, Kerfoot and Sih 1987). The responses of prey to kairomones are especially well investigated (Mathis and Smith 1993c, Chivers et al. 1996b, Wisenden 2000, Tomba et al. 2001). Predator-induced responses have been reported for an extensive taxonomic and geographic range of prey organisms including plants, several invertebrate groups and vertebrates (see review by Karban and Baldwin 1997, Tollrian and Harvell 1999). In response to chemicals released from predators, animal prey organisms alter life history characteristics (e.g. Warkentin 1995, Laurilla et al. 1998, De Meester and Weider 1999, Stibor and Navarra 2000), morphology (e.g. Bronmark and Miner 1992, Stibor 1992, Tollrian 1994, McCollum and Leimberger 1997), body mass (Lilliendahl 1997), reproductive condition (Korpimäki et al. 1994) and behaviour (e.g. Krueger and Dodson 1981; De Meester 1993, Flowers and Graves 1997, Persons et al. 2002).

Behaviour modifications in response to perceived threat from predator-derived kairomones will generally affect the fitness of organisms as routine behaviours, such as resource acquisition, is impeded. Anti-predator behaviour that can influence production in polysystems include general physiological stress in readiness for fight or flight (Cuadras 1979, 1980, Frost 1999, Li et al. 2000, Listerman et al. 2000, Schapker et al. 2002), increased 'alertness' (De Meester and Pijanowska 1996, Boersma et al. 1998, Brewer et al. 1999), inhibited food-related responses (Hazlett 1994a, Brown et al. 1999, Hazlett and McLay 2000, Bouwma and Hazlett 2001), diapause/decreased activity (Hairston 1987, Pijanowska and Stolpe 1996, Slusarczyk 1999, Haney et al. 2001), reduced locomotion or other movements (Hazlett and Schoolmaster 1998, Persons et al. 2002, Hazlett 2000a, Mirza et al. 2001), movement from preferred water quality conditions (Strand and Hammer 1990) or preferring shelter in least preferred areas which offer more protection (e.g. Boudeau et al. 1993, Rittschof 1993, Welch et al. 1997, Baumgartner et al. 2003), increased shelter (Appelberg et al. 1993, Baker and Montgomery 2001) or avoidance of risk areas (Brown et al. 1995, Persons et al. 2002). Responses to predation pressure can result in reduced growth (Hazlett 1994a, Bouwma and Hazlett 2001, Gherardi 2002) reduced reproductive condition - egg reabsorption, starvation of offspring (Stibor and Navarra 2000), or changes in maturation time of animals (Lass 2001), and eventually mortality (Hazlett 1994a).

### 2.4.2.3 Alarm cues

Chemical alarm cues are produced by prey on imminent danger or capture (Brown et al. 1995, Chivers and Smith 1998, Mirza and Chivers 2002), through chemicals released from flesh damage during capture of conspecifics (Pfieffer 1977, Smith 1992, Brown and Godin 1999, Stabell et al. 2003) or sympatric species (Smith 1992), or in signatures in faeces of predators after consuming prey (Stabell et al. 2003). Alarm substances are produced to enact predator avoidance in conspecific or other species (Hazlett 1994a, Chivers and Smith 1998), providing escape opportunity (Chivers and Smith 1995, Wisenden and Thiel 2002). Evidence also suggests that the anti-predator function of alarm signals exists for both signal senders and receivers (Smith 1992, Chivers and Smith 1998) and opportunistic predators can take advantage of alarm cues to locate easy prey opportunities (Wisenden and Thiel 2002). A wide diversity of aquatic organisms release chemical alarm cues (Murray and Jenkins 1999): including gastropods (Crowl and Covich 1990), aquatic insects (Chivers et al. 1996a, Wisenden et al. 1997), fish (e.g. Keefe 1992, Mathis and Hoback 1997, Stabell and Lwin 1997, Chivers and Smith 1998, Mirza et al. 2001), aquatic invertebrates (Chivers and Smith 1998) and aquatic amphibians (Wilson and Lefcort 1993).

Alarm odours are not generalised (Bryer et al. 2001), as only conspecifics and sometimes close sympatric species, appear capable of detecting information from the odours produced. Swordtail skin extract was not shown to elicit a response in minnows (Chivers and Smith 1994b, Chivers et al. 1995), salmonids (Brown and Smith 1997, Berejikian et al. 1999, Mirza and Chivers 2000), sticklebacks (Mathis and Smith 1993c, Brown and Godin 1997) and sculpins (Bryer et al. 2001). However, the extract will produce a response in swordtails (Mirza et al. 2001). In contrast, some species do not possess alarm pheromones (Smith 1976, Mathis and Smith 1993b, Brown et al. 1995).

### 2.4.2.4 Crayfish responses to kairomones

Behavioural responses to predatory odours alone have been documented for many species of freshwater crayfish (Listerman et al. 2000, Li et al. 2000), including *Cherax albidus* (Gherardi et al. 2002), *C. tenuimanus* (Gherardi et al. 2002), *Astacus astacus*, *Orconectes propinquus*, *O. rusticus*, *O. virilis* and *Pacifastacus leniusculus* (Appelberg et al. 1993, Blake and Hart 1993a, Willman et al. 1994, Hazlett and Schoolmaster

1998). Reactions to predator-derived chemical cues in freshwater crustaceans can include direct avoidance (*Heterozius rotundifrons*, Hazlett and McLay 2000), decreased foraging (*Orconectes propinquus*, Hazlett 1994a, Bouwma and Hazlett 2001, *C. albidus*, Gherardi et al. 2002), decreased locomotion and posture (*Orconectes virilis* - Hazlett and Schoolmaster 1998) and increased sheltering (Baumgartner et al. 2003).

Physiological differences have also been recorded where no change in behaviour was seen (e.g. increased heart rate - Listeman et al. 2000, Li et al. 2000). In these cases researchers have suggested an increased alert status, or readiness for flight or fight where crayfish remain motionless until action is necessary (Hazlett 1994a).

#### **2.4.2.5 Factors affecting chemical communication**

The anti-predator responses displayed by animals to kairomones may be dependent on many factors, such as the degree of predation risk, requirement for resources (e.g. food), abiotic factors, and the age/sex and size of interacting species. Responses also depend on the predator avoidance strategies of different species, for example; animals such as zooplankton are restricted in their ability to escape due to slow swimming speed (Allaby 1994). In this case, natural selection may favour increased body protection, camouflage or early detection of predator risk (Allaby 1994). Responses also depend on the hunting techniques of predators (Brett 1992, Stibor and Luning 1994), i.e. some species aggregate to confuse predators (Hay 2002), whereas others, such as Antarctic krill, disperse in order to reduce target size to aerial predators, and to not provide predators with cost effective feeding source (Strand and Hamner 1990)

The factors affecting chemical communication that have attracted the greatest research focus, predominantly due to ease of manipulation in aquaculture, are abiotic system conditions and population dynamics - size, age and sex of stock.

#### **Abiotic factors**

Chemical communication compounds are primarily steroidal in nature and are generally, if not always, hydrophobic or amphiphilic. The degree to which odours dissolve in suspended or deposited organic matter may affect their signalling function (Mesquita et al. 2003).

Once released into the aquatic environment chemical signals dissipate with time (Lass 2001). This can be a result of turbulent mixing, molecular diffusion, adsorption, photolysis, chemical transformation, unidirectional flow in lotic habitats and bacterial uptake or breakdown (Atema 1995, Moore et al. 2000). Such spatio-temporal patterns are important as they determine signal strength and direction, and enable the receiver to respond appropriately. Animals detecting chemical cues would need to consider (consciously or subconsciously) the abiotic effects on signals in aquatic systems.

Factors that can influence chemical communication, and thus vulnerability to predation, include: water flow (Hay 1996, Powers and Kittinger 2002) with results dependent on whether flow benefits predator or prey; toxicant exposure (Preston et al. 1999); impediment of cues in weakly acidic conditions (pH 6.0 - fathead minnows, *Pimephales promelas*, finescale dace, Leduc et al. 2004, *Phoxinus neogaeus*; rainbow trout, *Oncorhynchus mykiss*; brook charr, *Salvelinus fontinalis*, Leduc et al. 2004); low temperature reducing concentration (Lass 2001); and disruption by humic acid (Hubbard et al. 2002), metals (Webber and Haines 2003), UV radiation (Hay 1996) and nutrient levels (Hay 1996). Anthropogenic substances can also either mimic the effects of predator kairomones, or inhibit induction of defences (Barry 1999, Hanazato 1999). Some heavy metals and synthetic chemicals, such as insecticides and pesticides, have been found to induce responses in zooplankton similar to those produced by predator kairomones (Hanazato and Dodson 1992, 1993, Barry 1998, Michels et al. 2000).

### **Response differences between size/age/sex**

The variation in anti-predator responses to kairomones between sexes, age or size of prey may be a result of selective predation. Pike cichlids, *Crenicichla alta*, selectively attack females in mixed sex pairs of guppies (Pocklington and Dill 1995), alarm cues from crushed conspecifics result in male swordfish inhabiting the top of tanks, whereas females seek shelter in benthic areas (Mirza et al. 2001) and many predators target smaller, more vulnerable prey - as with silver perch-marron polysystems (Whisson 2000). Conspecifics have also been shown to react differently to alarm cues depending on the size/age class of the signal source (Mirza and Chivers 2002). How animals differentiate between size or age of source is unknown, whether chemical signatures in cues vary or whether there is a direct relationship between volume or concentration (Courtenay et al. 2001) of signals released. In contrast, some studies suggest that kairomones are unspecific chemical cues (Loose et al. 1993, von Elert and Loose 1996).



Ontogenetic changes in behaviour have also been recorded, where fish showed varied alarm status depending on age of fish producing the alarm cue, i.e. small fish reacted more strongly to alarm cues from small fish. Results suggest that chemicals that act as the alarm cue for fish of different age/size classes may be: (1) identical and that there may be other chemicals that allow the test fish to distinguish between cues from fish of different ages/sizes, or (2) the cues are not identical, but similar enough to be recognised (Mirza and Chivers 2002).

#### **2.4.2.6 Chemical communication in polysystems**

The widespread role of chemicals in mediating intraspecific and interspecific interactions has been recognised for many years (Dicke and Sabelis 1988), with kairomones and inducible defences regulating energy flow through systems (Ringleberg et al. 1991, Ringleberg 1997), shaping entire food webs. In aquatic polyculture, negative interactions between species could potentially be mediated by interference of chemolocation abilities of predators, thereby increasing the cost of acquiring prey. One of the main concerns in polysystems is increased intraspecific conflict, as predatory stress can result in responses such as increased sheltering, which can increase conflict amongst conspecifics due to higher relative densities within shelter. Few studies have tried to understand how chemically-mediated defence reactions influence spatial and temporal dynamics of prey populations (e.g. De Meester et al. 1995, Spaak and Boersma 1997, Burks and Lodge 2002), and the subsequent effects on intraspecific dynamics. Understanding chemical ecology of polysystems can provide valuable information for developing mechanisms to avoid or counterbalance predation risk within polyculture management strategies.

#### **2.4.3 Tactile communication**

Tactile cues (mechanoreception), or physical interaction, play an obvious role in the relationships between conspecifics and heterospecifics. Generally, the most evidence for successful use of mechanoreception is at night where other sensory modalities are less effective (Bouwma and Hazlett 2001). Many successful nocturnal foragers rely on tactile cues, including one of the largest group of organisms, arthropods (Grostal and

Dicke 1990, Hoffmeister and Roitberg 1997, Persons et al. 2001). The use of tactile information has been shown with:

- Male-female interaction (Zalesky et al. 1984);
- Predator detection (Gilbert 1980, Wurdak et al. 1983, Bollens and Frost 1989, Herbaholtz et al. 2004);
- Prey detection (Enger et al. 1989) and location (Persons et al. 2001);
- Conditioned feeding (Kemenes and Benjamin 1989, Kojima et al. 1997);
- Reproduction (Bouwma and Hazlett 2001, Herbaholtz et al. 2004)
- Habitat selection (Scully 1983, Elwood and Stewart 1985, Hazlett 1996).

A number of species have been identified as requiring tactile information for various daily, seasonal and reproductive activities (crayfish, Herbaholtz et al. 2004; *O. propinquus*, Bouwma and Hazlett 2001; brachyuran crab, *Heterozius rotundifrons*, Hazlett and McLay 2000). In arthropods, such as freshwater crayfish, tactile cues are often detected through antennae (Panksepp and Huber 2004).

Tactile cues reflect confident information pertaining to a range of events, however in the case of predator-prey relationships, tactile cues may often be too late to aid escape. The responses to tactile cues pertaining to threat are often obvious and strong. Reactions include defence (Field 1990, Hazlett and McLay 2000), aggression (fight) or evasion (flight) (Webb 1979, Herbaholtz et al. 2004). For example, when *H. rotundifrons* receives a strong tactile input from a predator, it displays an aggressive behaviour by spreading its chelipeds and stopping all movement (Field 1990, Hazlett and McLay 2000). Branchyuran crabs may respond with a catatonic body posture in response to being grasped (Hazlett and McLay 2000). In the latter, the crab becomes rigid and appendages extended for several minutes, which has been shown as an effective predator defence mechanism, making the crab hard to handle and consume (Hazlett and McLay 2000). Freshwater crayfish have been shown to respond to tactile stimuli relating to threat by tail-flipping (Wiersma 1961), a common observation with all *Cherax* species of freshwater crayfish (Storer pers. obs.).

Reactions to other forms of exteroceptive cues are often heightened, initiated faster or prolonged by the coupling with tactile cues (Rekwot et al. 2001, Bouwma and Hazlett 2001, Hazlett 1971)

#### 2.4.4 Other methods of communication

In addition to visual, chemical and tactile communication, a number of other sensory modalities exist, including audio (Rosenthal and Ryan 2000), electrical (Himstedt et al. 1982, Scheich et al. 1986, Gould et al. 1993), magnetic and thermo-communication. These information media, especially the latter two examples, are often more specialised, rare and therefore less studied in aquatic environments. A brief description of audio and electrical communication cues is provided.

##### 2.4.4.1 Audio

The auditory system is likely to play a direct role in a number of ecological situations, including male-female interactions (Zalesky et al. 1984; mating calls - Bradbury and Vehrencamp 1998), alarm or predator startle response (Richardson et al. 1996; cod producing clicking sounds, Vester et al. 2004), predator detection and identification (Gilda-costa et al. 2003), feeding - communicating feed source to conspecifics (Lagardere et al. 2004), or a cumulative role with other external information cues, such as with signalling or priming pheromones (Rekwot et al. 2001). Acoustic signals have some advantages over other information signals, for example they disperse faster than chemical cues (Lass 2001).

In invertebrates, audio signals are believed to be received via hair vibrations (Bahar and Moss 2004). In crayfish, hairs on the tail have been shown to pick up sound from both prey and predators (Bahar and Moss 2004). Teleost fishes, the largest group of living vertebrates, include both vocal and non-vocal species that exploit a wide range of acoustic niches. Behavioural studies demonstrate that temporal features within a call, including pulse duration, rate and number, can all be important to its communication value (Bass and McKibben 2003). Audio communication has been investigated in catfish *Platydoras costatus* and *Pimelodus pictus*, loach *Botia modesta* and labyrinth fish *Trichopsis vittata* (Wysocki and Ladich 2003), all of which are hearing specialists. Results from these species indicate that besides temporal patterns, amplitude fluctuations and the frequency context of sounds can be information for acoustic communication (Wysocki and Ladich 2003)

#### 2.4.4.2 Electrical

Electroreception is a specialised sensory modality, utilised by a diverse range of organisms (Watt et al. 1999), dominated by elasmobranches (Kalmijn 1971) and including numerous non-teleosts (Northcutt 1986), teleost species (Szabo 1974) and even primitive animals such as the platypus (Scheich et al. 1986) and star nosed mole (Gould et al. 1993). The importance of electrical signals for communication has been described in a number of species (Carlson and Hopkins 2004). The competitive advantage of electrical cues over more direct signals (visual, tactile and audio) is the ability to locate submerged or hidden prey (Kalmijn 1971, Himstedt et al. 1982, Scheich et al. 1986, Gould et al. 1993). Watt et al. (1999) demonstrated the ability of lungfish, *N. forsteri*, to detect weak electric fields surrounding crayfish when held in adjacent compartments with visual and chemical cues inhibited.

#### 2.4.5 Multiple component signals

Previous sections have examined the roles and ramifications of the most commonly studied sensory modalities employed by aquatic organisms. However, ecological events are rarely governed solely by a single source of information. In fact, the structure of behaviour is often referred to as the nature of interaction between multiple sources of information (Hazlett 1996).

Multiple cues are detected and utilised by many animals (e.g. Hazlett 1996, Kaufman et al. 1996, Bouwma and Hazlett 2001, Diaz et al. 2001), with information interpreted and memorised more efficiently than with simple signals (Goncalves et al. 2002). The advantage of detecting multiple cues pertaining to one ecological event is that they afford the organisms more security through increased confidence in information (Rowe 1999, Goncalves et al. 2002), which results in an ecological advantage to the receiver (Rowe 1999). For example, some predators have developed the ability to deceive prey by mimicking non-threatening signals (Brown and Godin 1999), whereas prey that can detect a combination of cues are less likely to be misled.

The advantages of utilising multiple sensory channels are demonstrated for a range of species and situations. The use of chemical signals, and other sensory modalities, by diurnal species, which traditionally rely on visual communication (Enquiste et al. 1987)

has been suggested to increase the range and length of signals used in maintaining social hierarchy (Grier and Burk 1992). Similarly, anti-predator behaviour in the freshwater crayfish *O. propinquus* responding to visual indicators of predation threat is increased by the addition of an alarm cue, in that the crayfish will respond at a greater distance and retreat further than with visual cues alone (Bouwma and Hazlett 2001). Glowlight tetras have been shown to inspect the combined chemical and visual cues originating from novel predators, and to modify their inspection behaviour (time to initiate inspection, size of inspection group and inspection distance) based on additional information sources, such as whether the predator recently consumed conspecifics (Brown et al. 2000). Giaquinto and Volpato (1997) demonstrated that in developing social hierarchy in tilapia, if only visual cues were present then antagonistic behaviour continued significantly longer than with a combination of cues.

Generally the rule is that sensory modalities complement each other (Giaquinto and Volpato 1997), however, some cues appear ineffective unless coupled. Anti-predator behaviour displayed by *H. rotundifrons* (branchyuran crab) in response to tactile input (Field 1990, Hazlett and McLay 2000) is prolonged by the addition of chemical or visual cues, although if the latter are detected alone no reaction is evident. This suggests, that although insufficient to elicit a response alone, some stimuli can increase the potency of other information media.

In some cases multi-component signals are essential for communication (Bradbury and Vehrencamp 1998, Rekwot et al. 2001). This is seen especially in interaction between conspecifics. For example, courtship behaviour in many species often requires the coupling of vocal, tactile and/or visual displays (Bradbury and Vehrencamp 1998), often in combination with olfactory cues (Rekwot et al. 2001). Dependency on multiple signals for one event would be a disadvantage in some situations, and perhaps only applicable in events where speed of reaction is less essential.

The final situation is where a number of signals are each capable of producing the same response, regardless of coupling. For example, bluegill sunfish naturally predate using mechanical and visual cues, although when lateral lines and eyes are blocked they are still effective predators, using tactile cues, with a 58% success after touching prey (Enger et al. 1989). This may be the epitome of ecological fitness, as responses do not rely on single information streams, which individually may be impeded.

In multi-species systems, the factors governing responses to simple tasks, such as locating feed, are much more complex than just being able to detect a range of exteroceptive cues. One of the most important abilities an organism has is to accurately and efficiently make decisions involving situations where information pertains to contrasting simultaneous events. A common example of this is the trade off between foraging and predation risk. Where simultaneous and conflicting signals exist, poor decision-making may result in fitness loss (Dawkins 1976). To maximise fitness in multi-species systems, an organism must weigh responses against risks.

#### 2.4.6 Hierarchical and graded responses

Generally, the structure of behavioural responses is said to be hierarchical (Dawkins 1976, Enquist et al. 1987, Nelson 1990), with some elements having higher priority over others (Hazlett 1996, Hazlett and McLay 2000). In the relationship between predator avoidance and foraging, the hierarchical dominance logically lies with predation risk over food acquisition (Houston et al. 1993, Werner and Anholt 1993, Ydenberg 1998) - living to feed another day. Combinations of snail odour (indicating the presence of an available shell) and predator odour in the hermit crab, *Diogenes avarus*, yield an all or none, hierarchical response. Predator odour completely overrides the affects on behaviour by snail odour in *D. avarus* unless the predator odour is very weak (Hazlett 1997). However, the structure of behaviour must also be taken in context, as obtaining food would gain increasing priority over anti-predator behaviour as necessity increases (Anholt and Werner 1998). Some models of behaviour assume a graded response, where increasing desire to feed overrides increasing levels of risk (Jackson and Edwood 1989). The crayfish *Orconectes virilis* shows feeding behaviour in proportion to the relative strengths of food and alarm odours (Hazlett 1999). A combined hierarchical and graded response structure appears to be the most appropriate system. Crustaceans display both graded and hierarchical responses, where behaviours appropriate to one input dominate over those appropriate to another (Hazlett 1994a, 1999). However, in many situations maximum fitness comes from experience, where responses are mediated by learning.

### 2.4.7 Learned behaviour

*"It is not the strongest of species that survive, or the most intelligent, but the ones most responsive to change"* - Charles Darwin

Altering behaviour in response to a predator can be costly concerning factors such as foraging success and reproduction (Gilliam and Fraser 1987, Travers and Sih 1991, Hedrick and Dill 1993, Godin 1995). The ability to acquire information about potential risks, assess and modulate responses appropriately, and retain information for future similar events is an important ecological tool for all organisms (Pfeiffer 1977, Brown and Godin 1999). Not reacting to potential threats, or failure to recognise signals, can increase the probability of predation (Hirsch and Bolles 1980), whereas overreaction or misguided responses can mean lost resources (Lima and Dill 1990, Lima 1998).

In many cases predator recognition is innate (Sih and Moore 1993, Storfer and Sih 1998), however for some species recognition requires experience (Hazlett 1971, Mathis and Smith 1993b, Chivers and Smith 1998, Dicke and Grostal 2001). That is, prey individuals must experience a predator cue and a danger cue simultaneously before the predator cue is treated as a danger signal (Chivers et al. 1996b, Hazlett and Schoolmaster 1998, Grostal and Dicke 1999, Wisenden and Millard 2001). Even a non-predator such as the herbivorous goldfish *Carassius auratus* will be treated as a predator following simultaneous detection by prey individuals of conspecific alarm odour and goldfish odour (Chivers and Smith 1994b).

The ecological advantages for species capable of successfully acquiring information pertaining to predators is well reported. Delgado et al. (2002) demonstrated that predator conditioned conch move significantly less and buried themselves more frequently than naïve conch - resulting in significantly higher survival in conditioned conch. Kats et al. (1988) found that several larval amphibians collected as eggs from ponds containing predatory fish showed an increased shelter use when exposed to chemical cues from green sunfish, even in the absence of experience. In the case of hermit crabs, experience will decrease delay for shell changes, entry time and mistakes (Hazlett 1971, Gilchrist 1985) - reducing chance of predation or competition by other crabs, thus experience increases crab survivorship and fitness (Hazlett and Provenzano 1965, Hazlett 1995). Wild caught fathead minnows, *Pimephales promelas*, reacted to chemical stimuli from predatory northern pike, *Esox lucius*, while

predator naïve fathead minnows of the same size and age did not respond. Wild young-of-the-year minnows react equally compared with adult fish - demonstrating that the ability to recognise predators is learned within the first year. After holding wild minnows in a predator free environment for one year - no difference was seen in reaction to predators - suggesting that reinforcement is not required. Furthermore, clones from habitats with fish predators proved more responsive to fish kairomones than clones from fishless locations (De Meester 1996, Boersma et al. 1999).

Experience also favours predators. It is assumed that predators with experience feeding on certain species will be a greater risk to that prey, as the predator would have an improved search image (Tinbergen 1960), reduced feeding neophobia (Dutoit et al. 1991, Greenberg 1992) increased handling efficiency or general preference for that prey (Persons et al. 2002). The differences between closely related species may best demonstrate the influence of learning and experience on genetic adaptations. Hazlett (1994) found that *O. virilis* displays anti-predator behaviour when faced with predatory odours, however *O. propinquus* does not alter its behaviour in response to chemical stimuli alone. Phylogenetically (Fitzpatrick 1987) and ecologically (Hazlett 1994a) these two sympatric congeneric species are very similar, coexisting widely and displaying only slight differences in habitat preference. It is assumed that both species are faced with similar predation risks (Hobbs 1993), so it is unclear why sensitivity to chemical cues has only evolved in *O. virilis*. Hazlett and Schoolmaster (1998) suggested that differences may relate to the nocturnal nature of *O. virilis* (Hazlett and Schoolmaster 1998) whereas *O. propinquus* is more diurnal (Hazlett 1994a). As previously examined, in low light intensity chemical cues are favoured, and vision in clear-water systems (Brown et al. 1997). Also, *O. propinquus* possesses an alternative predator avoidance mechanism, a tail-flip response (Webb 1979), which can be displayed upon the detection of a strong visual or tactile predator stimulus (Hazlett 1999). This may reduce need for early detection. Another example of differences between species can be seen with catfish, where chemical communication is widespread in all species, depending little on vision (Tukey 1977). However, in some examples chemoreception is important only in the first days of life and vision is predominant later (Giaquinto and Volpato 1997). The great variation between species relates to both evolutionary traits held by populations and also modulatory change developed through life experiences - learned behaviour.



The influence of learning on behavioural modifications in animals, as opposed to genotypic characteristics, can be seen in our ability to artificially alter their responses. In an early study, Mikhailoff (1923) trained *Dardanus arrosor* (hermit crab) to withdraw from light that they were originally attracted to, and associate a particular colour with food.

Most studies suggest that previous experience, and not genetic factors, is the major factor in recognition of predatory cues (Semlitch and Ryer 1992, Chivers et al. 1999, Wildy et al. 1999, Mirza et al. 2001), as many species display the ability to acquire predator avoidance behaviour after short periods of interaction (Chivers and Smith 1995, Diaz et al. 2001). Several mechanisms for acquiring predator recognition have been demonstrated (Chivers and Smith 1995). These can be the association of certain cues with a potential threat following observation of alarm behaviour from conspecifics or heterospecifics reacting to danger, or pairing of alarm cues from crushed conspecifics with a novel threat. Predator recognition can also require direct learning, such as through an encounter between predator and prey. In all situations inspection is an important aspect of predator recognition.

#### **2.4.8 Predator recognition**

One mechanism utilised to gather information about potential threats is inspection. Inspection can result in learning, producing benefits through more effective responses (Pfeiffer 1977, Brown and Godin 1999). Inspection behaviour has been recorded in most animals, e.g. Ostariophysi species (almost 64% of all fish) (Mathis and Smith 1993a, Chivers and Smith 1995, Smith 1997, Brown and Godin 1999).

Inspection generally includes approach of novel cues in a salutatory or tentative behaviour (Dugatkin and Godin 1992, Pitcher 1992), either individually or in groups (Brown et al. 1999). The high risk associated with inspection is mediated by species fitness, i.e. following a predation event where a large number of bacteria were consumed, the remaining bacteria demonstrated increased predator avoidance success in subsequent encounters (Shemesh and Jurkevich 2004). Variation in inspection behaviour can also occur, dependent on factors such as dietary cues (Brown et al. 1999). European minnows, *Phoxinus phoxinus*, modify their behaviour after inspecting a potential predator depending on its behaviour (Murphy and Pitcher 1997). Inspection is

also an inherently risky behaviour (Pitcher et al. 1986, Dugatkin and Godin 1992, Milinski et al. 1997) with learned recognition of novel stimuli being recognised as dangerous for several species (Chivers and Smith 1998). Individuals that do not alter visual inspection behaviour of predators have a greater probability of not surviving the encounter (Godin and Davis 1995a/b, Brown et al. 1999). Individuals that dare approach predators (predator inspection behaviour) may benefit by acquiring information regarding the potential threat of predation (Brown and Godin 1999).

The behaviour of conspecifics, sympatrics or heterospecifics is another source of information regarding potential threat (Brown et al. 1999). Mathis et al. (1996) have shown that fathead minnows and brook sticklebacks are able to acquire the recognition of novel predators simply by observing the anti-predator responses of an experienced individual. Prey has been shown to produce anti-predator responses to distantly related heterospecifics, especially in diet; this is most likely a result of experience (Chivers and Smith 1994a, Chivers et al. 1995).

Learning can also occur through pairing of predatory signals, such as predator cues with stimuli from injured conspecifics (Magurran 1989, Chivers and Smith 1994b/c, Chivers et al. 1995, Hazlett et al. 2002). Chemosensory recognition of predators by naïve prey may be facilitated if the predators diet chemically 'labels' the predator (Chivers et al. 1996b). Pike-naïve damselflies may initially respond to chemical stimuli from pike based on stimuli of conspecifics or familiar heterospecifics in the pikes diet, and can learn to recognise chemical stimuli of pike irrespective of the pikes recent feeding regime based on the initial association with damselflies or minnows in the pikes diet (Chivers et al. 1996b). Diet-related chemical labelling of a predator has been demonstrated in several studies (Crowl and Covich 1990, Mathis and Smith 1993a/b). Chivers and Smith (1995) demonstrated that snails (*Physella virgata*) can discriminate between crayfish based on diet-related cues. Predation risk is reduced in aquatic flatworms through avoidance behaviour in conspecifics recognising alarm cues following a predation event (Hews 1988, Mathis and Smith 1993, Wisenden et al. 1999). In four species of freshwater crayfish, exposure for just two hours was sufficient to establish an association between novel odour and elevated predation risk (Hazlett et al. 2002). Fish trained with alarm signals to recognise predators gain a survival benefit during staged encounters (Gazdewich and Chivers 2002). An obvious advantage of this type of learning is seen with guppies (*Poecilia reticulata*), which are

able to differentiate between hungry and satiated predators (Licht 1989). Naïve prey often show no response when first presented with predator odour. However if presented with a novel stimulus simultaneously with a conspecifics alarm cue they learn to associate risk with novel stimuli. After a single exposure to both cues a novel cue alone elicits a full suite of anti-predator behaviour (e.g. Magurran 1989, Chivers and Smith 1994a). A fright stimulus was also elicited when chemical cues from pike combined with minnow alarm odour – this suggests that minnows can acquire predator recognition through releaser induced recognition learning (Chivers and Smith 1994b). For a more detailed review of diet-related anti-predator responses see Chivers et al. (1996a).

The ability to differentiate between different cues has been demonstrated on many occasions (e.g. Black and Dodson 1990, Stibor and Lüning 1994, Wisenden and Smith 1998). Examples include: minnows avoiding areas of a tank containing the faeces from pike on diets of minnows or sticklebacks but not on pike fed swordtails (Brown et al. 1995); juvenile *A. astacus* increasing shelter use following exposure to chemical stimuli from four different fish predator species, but not to stimuli from a non-predatory fish (Appelberg et al. 1993); and, juvenile toads shown to avoid chemical cue from snakes fed juvenile toads, but not from snakes fed larval toads (or food or conspecifics) (Beldon et al. 2000).

The behaviour of the predator may be a significant source of information (Murphy and Pitcher 1997), however visual cues such as behaviour and posture may prove unreliable as they could be manipulated by the predator (Brown and Godin 1999). The ability to detect multiple sources of information through inspection is critical.

#### **2.4.9 Behavioural plasticity**

The relationship between evolution and experience is obviously critical in responses displayed by organisms. Although experience is well supported as a major factor governing fitness (Magurran 1989, Chivers and Smith 1994a/b, Chivers and Smith 1995), evolution obviously influences the ability to take advantage of experiences.

The three major advantages an organism can have regarding predator avoidance are:

1. Ability to detect signals pertaining to factors such as predation risk
2. The tools to avoid predation - capacity for flight or fight
3. Capacity to remember vital information for future encounters - learning

The role of evolution in respect to predator avoidance affects the organisms capacity for each of these qualities, and perhaps most important is their capacity to learn as this will influence both detection and avoidance strategies.

Avoidance and escape behaviour is often highly developed and species specific (Gellar 1982, Marko and Palmer 1991, Dix and Hamilton 1993). Avoidance tactics are commonly triggered by detection of cues associated with previous predator encounters (learned behaviour), however once an association is formed it will generally tend to decay unless reinforced (Hazlett 1995). The rate of decay has been suggested to be linked with the duration of learned associations (Hazlett 1995). In some species the memory of certain cues pertaining to an event can be retained for several months without reinforcement (Courtenay et al. 2001), in other cases reinforcement is not required at all (Tukey 1977). More impressive than this is the ability of some prey species to avoid novel threats, affording them time for learning to acquire appropriate responses. Animals that possess innate abilities to react to multiple situations, or learn quickly in response to novel situations, would have the greatest advantage. These animals often possess adaptive or plastic behaviours.

**Plasticity** - the capacity of a given genotype to develop one of several phenotypic states depending on the environment (Lee 2002).

**Plastic response** - a response of a given genotype that can vary depending on external conditions (Lee 2002).

DeWitt et al. (1998) stated that "Adaptive phenotypic plasticity seems like the pinnacle of evolution". The ability for an organism to adapt its phenotype to changing environments allows a species to exploit a broader range of environmental conditions. The magnitude in variation ranges from relatively small changes to extreme shifts in morphology (Hughes and Elner, 1979, Bertness and Cunningham 1981, Johansson 1986, Stabell and Lwin 1997) and life history, such as inducible defences (Lass 2001). Inducible defences are striking examples of phenotypic plasticity.

When variability in other phenotypic features is added to a consideration of the variability in behaviour, it emphasizes the great advantage of plasticity (Gabriel and Lynch 1992). Behaviour of almost all categories has been shown to be variable depending upon conditions and species (Lott 1991). Animals displaying plastic behaviour are also often successful invaders, being 'super-competitors'. Invasive species display the best examples of advanced or heightened learning, with differences also existing in the memory capabilities of invasive and native species. Invasive species and populations pose major threats to biodiversity, ecosystem integrity, agriculture, fisheries and public health (Lee 2002). Results from an impact study of mosquito fish suggest that introduction of mosquito fish into naturally fishless wetlands may lead to a loss of diversity of their highly specialised aquatic fauna (Leyse et al. 2004). The negative impacts from invaders can even go to the extent of environmental changes. Some species, affectionately called invasive engineers, will alter their environment to suit themselves - often at the detriment to native inhabitants, a common example being beavers (Cuddington and Hastings 2004). Among species that are introduced, only a very small proportion become established and then invasive (Lee 2002). Invasive species often possess permanent defences, which will protect them in novel environments. Individuals of invasive species showed evidence of retention of the learned association longer than did individuals of the native species. The results are consistent with the hypothesis that invasive species have a greater capacity for behavioural plasticity (Hazlett et al. 2002)

The freshwater crayfish marron has also been exposed to a typical invader, the yabby. A rapid colonisation of yabbies throughout the south-west of Western Australia, in areas previously inhabited by marron (Lynas et al. 2004), suggests that in many cases marron have been displaced. The ecological threat from the invasive yabby on marron is explained on the basis of its plastic behaviour, hardiness, and burrowing (Gherardi et al. 2002, Lynas et al. 2004). In addition, the yabby may out compete marron due to factors such as sex differences and body size, described in other native *versus* invader species encounters (Nakata and Goshima 2003). Although marron obtain a larger final size compared to yabbies, juvenile yabbies grow at greater initial rate and breed in their first year, unlike marron (Wingfield 2000), and yabbies are known to be aggressively dominant over marron of smaller size (Lynas 2002). Researchers have hypothesised that invasive species out-compete native species through higher plasticity in the use of information (Hazlett 2000a, Gherardi et

al. 2002, Hazlett et al. 2002). It is widely accepted that invasive crayfish species are better equipped to process information about impending threats than native species, resulting in more protective modifications to their behaviour in the presence of predators (Gherardi et al. 2002, Hazlett et al. 2002). Of importance is efficient learning about cues associated with elevated predation risk (Hazlett et al. 2002). As marron are also exposed to introduced predatory fish species, primarily redfin perch, within their natural habitat, this may provide more evidence towards the ecological advantage held by yabbies. The efficient use of a wider range of ecological information is the basis of behavioural plasticity - promoting rapid adaptation to the surrounding environment and thus displacement of competitors.

## **2.5 Anti-predator behaviour of crayfish within multi-species systems**

Where niche overlaps exist in multi-species systems the negative interactions between species need to be understood and mediated in order to maximise aquaculture production. The importance of behavioural observations in analysing these interactions has been a consistent theme throughout this review. With a few species-specific exceptions, the predator-induced behaviours of crayfish fall into the following categories: reduced foraging, increased sheltering, defensive and aggressive postures, changes in movement or locomotion, area avoidance, no response, and the use of sensory systems. The typical predator avoidance responses of crayfish are discussed.

### **2.5.1 Reduced foraging**

Reduced foraging is predominantly an indirect result of predator, or competitor, avoidance behaviours (Rahel and Stein 1988, Brown et al. 1999, Hazlett and McLay 2000, Bouwma and Hazlett 2001). How prey balances potentially risky activities, such as feeding, against anti-predator demands has been a major issue in modern behavioural ecology (Sih 1980, 1992, Houston et al. 1993, Werner and Anholt 1993, Houston and McNamara 1999). In many studies, prey respond to predators by

reducing their activity and by increasing their use of safer microhabitats (e.g. Metcalfe et al. 1987, Sih 1987, Lima and Dill 1990, Kats and Dill 1998, Lima 1998, Woodley and Peterson 2003), with both responses resulting in reduced foraging time. In interactions between crayfish and predators, crayfish have been shown to completely shutdown food-related responses upon detection of the predation related cues (Rahel and Stein 1988, Hazlett et al. 2002). In contrast, Hazlett (1999, 2000b) showed that feeding responses were intermediate but did not shutdown. It is apparent through most studies that animals will select less feed in more secure areas, than greater feed in areas where predators have more chance of acting (Stokes et al. 2003).

### **2.5.2 Increased sheltering**

Seeking cover is one of the most prevalent danger response mechanisms, used by most organisms to minimise detection (Stein and Magnuson 1976, Appelberg and Odelstrom 1988, Blake and Hart 1993b) or utilise a safer microhabitat (Sih 1987, Lima and Dill 1990, Kats and Dill 1998, Lima 1998, Woodley and Peterson 2003). Sheltering is often used as the immediate fright response to potential danger (Heczko and Seghers 1981, Lawrence and Smith 1989, Mathis and Smith 1993b), providing time for assessment of the situation. Increased shelter use may be particularly effective against predators that locate their prey through movement (Kiesecker et al. 1996).

Shifts in microhabitat use obviously influence predations rates, but they can also have important impacts on species interactions, including competition among prey (Werner 1991, Kotler et al. 1994), interactions among predators (Soluk and Collins 1988, Sih et al. 1998) and trophic cascades (Schmitz et al. 1997). A number of authors have reported that competition among prey is greatly increased due to predatory pressure (Werner 1991, and Kotler et al. 1994), as prey species are forced into smaller areas to escape danger, thus increasing the relative density. This can influence production in aquatic polysystems through cannibalism (Denno et al. 1994), resource competition (Denno et al. 1994) and increased stress (Schapker et al. 2002). Stress responses come from increased social interactions. During antagonistic encounters between two crayfish, heart and ventilatory rate correlates with the intensity of the interaction (Schapker et al. 2002). Prolonged exposure to high densities results in physiological costs, which need to be maintained through reserves otherwise be used in areas such as weight gain, foraging, and reproduction - thus, aquaculture production suffers.

### 2.5.3 Defensive and aggressive postures

In crayfish, posture is a major signal - with raised postures displayed by aggressive or dominant individuals. Defensive stances in crayfish often include raised and open chelipeds with a low posture, often with tail curled under body (Hazlett 1994a). Responses to predator cues have been documented in crayfish and other crustaceans. Upon detection of predator odour the crayfish *O. virilis* switches to a lowered posture while decreasing non-locomotory movements (Hazlett and Schoolmaster 1998). In responses to conspecific cues crayfish ceases all movements while assuming an intermediate watchful posture (Hazlett 1994a). A response to tactile stimulation (grasping of prey by predator) is often a catatonic posture - rigid, appendage extended posture for several minutes. This has been shown to be an effective predator defence mechanism (Hazlett and McLay 2000), assumed to be either 'playing possum' or making the animal more difficult to handle and consume - increasing cost of acquisition.

### 2.5.4 Changes in locomotion or movement

One of the most documented responses to potential risk, or predatory stress, is decreased movement (Sih 1987, Blake and Hart 1993b, Hazlett and Schoolmaster 1998, Kats and Dill 1998, Lima 1998, Hazlett 1999, Woodley and Peterson 2003). A reduction in activity, even cessation of activity, has been observed as an antipredator behaviour in many species (Heczko and Seghers 1981, Lima and Dill 1990, Godin 1997, Smith 1997), including crayfish and other crustaceans (Hazlett 1997, 2000).

Rapid escape is another common avoidance response to potential or imminent risk. Dashing (fast sharp bursts in varied direction) is reported in many fish species (Lawrence and Smith 1989, Mathis and Smith 1993b) or escape can be a direct burst of speed in the opposite direction to danger. Early behavioural studies noted the existence of rapid defence reactions in crayfish (Bethe 1897, Huxley 1880, Wiersma 1961), where powerful tails are utilised to quickly retreat backwards. Herbaholtz et al. (2004) reported the following results from interactions between dragonfly nymphs and hatchling crayfish. During attacks, dragonfly nymphs rapidly extend their labium, equipped with short, sharp palps, to capture small crayfish. Crayfish respond to the tactile stimulus by activating neural escape circuits, generating tail-flips directed away



from the predator. Crayfish were reported to use all three known types of escape tail-flips during the interactions with the dragonfly nymphs. Tail-flips generated by activity in the giant neurons were predominantly observed to trigger the initial escape response to an attack, but non-giant mediated tail-flips were often generated to attempt escape after capture. Attacks to the front of the crayfish triggered tail-flips mediated either by the medial giant neuron or by non-giant circuitry, whereas attacks to the rear always elicited tail-flips mediated by the lateral giant neuron. Tail-flips were the sole defence mechanism observed in response to attack, and were found to be a successful behaviour in preventing capture, with only a small percentage of crayfish consumed (Herbaholtz et al. 2004).

The use of tail-flipping in crayfish species may be a cost-effective response to imminent threat, where crayfish can maintain normal behaviour until avoidance is absolutely necessary. Tail-flipping has been used as a measure of responsiveness in a number of studies (Lang et al. 1977, Copp 1986, Fricke 1986, Bruski and Dunham 1987, Pavey and Fielder 1996, Guiasu and Dunham 1997, Kellie et al. 2001).

### **2.5.5 Area avoidance**

A common response to danger is avoidance of risk areas (Brown et al. 1995). This response often lasts longer than acute reactions to predator risk. For example, following exposure to predatory cues, minnows were shown to relax from behaviours indicating fright after some time, however still avoided source areas (Brown et al. 1995). The avoidance of certain areas in itself is not a problem, however if this also means movement away from more optimal conditions (i.e. better water quality or feed resources) this can have adverse effects on growth and survival. As the dominant species usually inhabits the most optimal areas of the system this is often the case. Lass (2001) demonstrated that daphnia traded off reduced predation mortality in a refuge against disadvantages due to unfavourable oxygen conditions. These results indicate that environmental conditions might constrain predator avoidance strategies, which can have flow-on effects in aquaculture.

### **2.5.6 No response**

In many behavioural studies, when test animals do not make significant changes, as measured by bodily movement, the animal is characterised as unresponsive to the given stimulus. This assessment may often be accurate, however, in some cases where no behavioural responses are recorded there are still physiological responses associated with heightened alertness, or readiness for flight or fight. "Alertness" is defined as the capability to escape the attack of a predator through an increased sensitivity to mechanical and light disturbance (De Meester and Pijanowska 1996). Schapker et al. (2002) showed that although behavioural movements of crayfish may not be observed, physiological measures of heart rate and ventilatory rate show dramatic changes in response to defined sensory stimuli. Autonomic control of the cardiovascular and ventilatory systems can regulate the availability of potential oxygen and nutrient needs of the tissue, while at the same time not appearing to cause an external behaviour change that could be assessed by others around it. In certain circumstances it is not beneficial for an animal to relay, by behavioural means, how agitated it may really be, but instead to be ready to deal physiologically with whatever quick demands are put on it for fighting or fleeing (Schapker et al. 2002). Unfortunately, this makes it hard for behavioural biologists to assess an animals' internal state by direct bodily observations (Schapker et al. 2002). Freshwater crayfish, such as marron, may be a prime candidate for increasing alert status or readiness for flight, due to its use of a tail-flip to effectively escape imminent danger. Not overreacting to potential threat may afford these animals a competitive edge, where foraging time and other activities are not as affected.

### **2.5.7 Sensory system behaviour**

A number of sensory devices are employed to detect a range of cues pertaining to predatory threat. In crayfish, the capability to detect environmental signals has been seen in the antennules (Tierney and Atema 1988, Hazlett 1990, Grasso and Basil 2002), antennae (Panksepp and Huber 2004), and in hairs on claws (Takahata 1981) and ambulatory dactyls (Hazlett 1971). Where 'no behavioural response' is observed in response to predatory stimuli (as discussed in 2.5.8), closer observation of sensory activity may be especially important. The use of sensory devices by crayfish are described.

### 2.5.7.1 Antennules

The primary olfactory sampling structures that have been observed in crayfish, lobsters and crabs are antennules (Grasso and Basil 2002). Hydrodynamic receptors located within the antennules of crayfish (Hazlett et al. 2002) provide information on the direction of water flow and the presence/movements of other organisms (Vogt 2002). Through morphological, behavioural and electro-physiological studies, antennules for a number of decapods have been shown to be the main distance chemosensory organs used to detect food odours (Hazlett 1971, Tierney and Atema 1988, exceptions in Ameyaw-Akumfi 1977) and disturbance chemicals (Hazlett 1990). Although the number of cells in the lobsters' olfactory system is much lower than in a vertebrate olfactory system, it is a highly complex system (Derby 2000).

### 2.5.7.2 Antennae

Evidence demonstrates the use of antennae for various mechanosensory tasks, such as movement, foraging, identifying obstacles and other organisms (Panksepp and Huber 2004). In freshwater crayfish, antennae has been described as touch sensors (Withnall 2000), and observation of antennae movements within behavioural analysis in laboratory trials has shown usage for investigating novel system structures (Panksepp and Huber 2004).

### 2.5.7.3 Chelipeds and ambulatory dactyls

The sensory abilities of the chelipeds and ambulatory dactyls (legs) of crayfish are poorly represented in literature, however a number of studies have identified similar functions as the antennules. Hazlett (1971) reported that when various concentrations of fish juice were introduced to hermit crabs *Petrochirus diogenes* the following observations were made: 1). The threshold concentration for chemical elicitation of feeding behaviour was over ten times as high for the ambulatory dactyls as for the antennules; 2). Combining tactile input with chemical input decreased the behavioural threshold of the dactyl responses ten-fold; and 3). Ablation of the antennules was followed by a 100-fold increase in the behavioural sensitivity to dactyl stimulation. Sensory hairs on crayfish claws have been identified, and these hairs appear to be functionally different (Takahata 1981) suggesting a more complex role than credited.

## **2.6 Factors affecting behaviour in multi-species systems**

The standard interaction responses of organisms within multiple species systems, based on a diverse range of biotic and abiotic conditions, have been reviewed in this thesis. However, several factors can influence these standard responses, including health and stress levels (injury-nutrition), life stage and reproductive status. In addition, the relative risk levels faced by prey organisms at different times will affect the way they react (i.e. diel variations in predator feeding). These factors can have significant effects on decisions made by organisms.

### **2.6.1 Health status**

The condition of an animal may affect responses to stimuli based on consequences. Periodic changes in conditions have been associated with moult cycle, breeding (Barnes et al. 1963, Du Preez and McLachlan 1983, Fernandes et al. 1994), food availability (Clark and Holmes 1986) and nutritional state (Stocker and Huber 2001). Any physical or physiological response will have a direct cost to the organism or follow-on effects through reducing the time for beneficial behaviours. These costs can affect the way organisms react to subsequent events, for example, unhealthy animals may not have the reserves to avoid predators (Godbout et al. 2002). In multi species systems, physiological costs associated with interaction come from social interactions (Listerman et al. 2000, Li et al. 2000), direct conflict (Cuadras 1979, 1980, Schapker et al. 2002), and perceived predatory pressure. Woodley and Peterson (2003) found that long-nose killifish respond to visual cues from predators by exhibiting an elevated plasma cortisol consumption and mass-specific oxygen consumption rate, resulting in decreased growth. Alterations in behaviour induced by stress may significantly affect activities essential for survival, including the acquisition of food, predator avoidance and habitat selection (Schreck et al. 1992). In crayfish, condition was shown to affect the tail-flip response (Page and Cooper 2004), where loss of chelipeds rapidly alter tail-flip frequency (Kellie et al. 2001) and stressed crayfish reacted differently to non-stressed crayfish (Basso 2001).

### 2.6.2 Nutritional state

Nutritional state has been demonstrated as a strong determinate in responses displayed in crayfish (Stocker and Huber 2001). During antagonistic encounters hungry crayfish appear to escalate reactions more rapidly, taking greater risks, while the presence of a food source reduced the rates at which fighting increased in intensity (Stocker and Huber 2001). Many studies have focused on the existence of the ecological trade-off between foraging and predation risk (see review by Lima 1998). Where resources are limiting, and thus perceived value of a resource is high, animals should be more persistent and willing to take greater risks (Enquist and Leimar 1987, McNamara and Houston 1989). As foraging becomes more and more critical, with extended starvation, animals will employ a risk-prone foraging strategy (McNamara and Houston 1986, Godin and Crossman 1994). Similarly, satiated animals will usually display a much more relaxed motivation towards antagonistic encounters (Wilcox and Ruckdeschel 1982, Lawton 1987, Griffiths 1992), especially facing heightened motivation of nutritionally deprived individuals where an actual food source is present (DiMarco and Hanlon 1997, Sirot 2000). Hungry individuals engage in more fights compared to satiated animals (Hazlett et al. 1975), with 'less to lose' because food deprivation reduces chances for survival (McNamara and Houston 1989), and thus adopt more dangerous fight strategies. Alternatively, hungry crayfish may place increased value on time spent fighting because this takes away from opportunities to forage (Griffiths 1992). Page and Cooper (2004) supported these findings, concluding that sensory stimuli can produce varied responses depending on the physiological condition of an animal.

### 2.6.3 Life stage

Life stage differences in interaction responses are commonly associated with changes in size (Peters et al. 1980, Beacham 1987, Svensson 1993), experience (Tinbergen 1960, Dutoit et al. 1991, Greenberg 1992, Persons et al. 2002), or development of defensive structures (Lass 2001) and sensory systems (Skajaa et al. 2004). The lower energy stores, faster use of reserves, less tolerance to starvation (Svensson 1993) and increased moult frequency (Merrick and Lambert 1991, Huner 1994, Timmermans et al. 1995) of juveniles means they must venture out of the safety of shelter into higher predation risk areas (Svensson 1993). In contrast, the decreased energy

requirements and greater experience of older individuals may result in them giving up searching earlier (Svensson 1993, Persons et al. 2002). Other authors have reported more efficient use of time and energy resources of predators due to experience (Tinbergen 1960, Dutoit et al. 1991, Greenberg 1992, Persons et al. 2002). Ontogenetic related effects on the effectiveness of predator avoidance were demonstrated by Skajaa et al. (2004) investigating herring larvae, *Clupea harengus*. Starved larvae showed lower responsiveness than fed, however older starved larvae showed higher responsiveness than younger fed larvae. The higher responsiveness in older individuals was explained by differences in sensory development.

#### **2.6.4 Reproductive stage**

The reproductive state of an animal can also affect interaction responses. Status changes associated with reproduction reflect an altered biochemical status that affects the responsiveness of an animal to hormones and neuromodulators, which control animal behavioural responses to sensory stimuli (Page and Cooper 2004). In crayfish, tail-flipping was reduced in stressed males, and not utilised by gravid females (Page and Cooper 2004). Gravid females and females with young commonly display increased aggressiveness (Mayer and Rosenblatt 1987, Albert et al. 1993, Mello et al. 1999). Some behaviours of gravid females are said to be bluffing responses, *versus* true aggression in seeking out to attack an opponent (Listerman et al. 2000).

These findings emphasise the importance of taking into account age and condition of animals when assessing stocking, shelter, feeding regimes and grading requirements of multi-species systems.

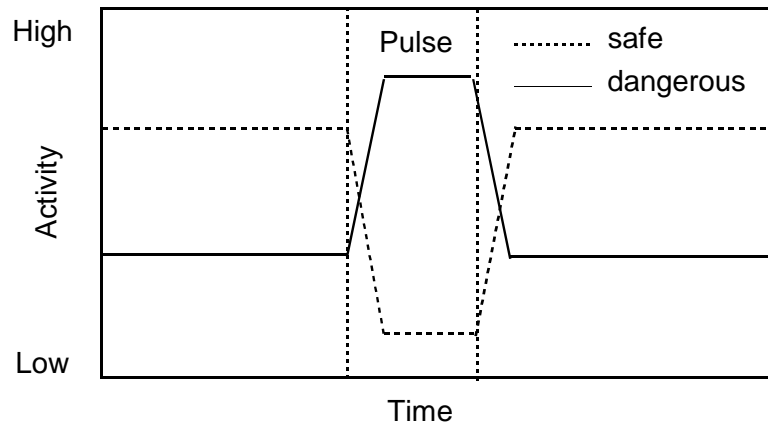
#### **2.6.5 Pulses of risk and safety**

The level of predation risk faced by prey species is largely a function of spatial variations (between different microhabitats such as between benthic and pelagic zones) or temporal changes (diurnal or seasonal) in the number and species of predators. Learning effective cost-benefit responses requires consideration of these spatial and temporal variations in risk in order to maximise resource utilisation with predator avoidance.

The risk allocation hypothesis predicts that prey responses to predation risk should depend on the pattern of risk (Lima and Bednekoff 1999, Sih et al. 2000). To fully understand optimal prey responses, a consideration of both the variations in the magnitude of risk, and the proportion of time that prey spend in each risk level is required (Sih and McCarthy 2002). In nature, prey probably experience a broad range of temporal patterns of risk. If predators are abundant and usually nearby, then prey might face sustained periods of risk with only occasional periods of safety. In contrast if predators are sparse and wide ranging then prey might experience low risk with only occasional pulses of danger when predators appear. Responses to risk should depend on whether prey experience only occasional pulses of risk in an otherwise safe environment, as opposed to brief periods of safety in an environment that is usually dangerous.

If prey live with only occasional pulses of safety, then during these safe periods they should be very active, displaying high feeding rates. Snails held in continual risk had very low activity levels but showed an immediate, large increase in activity during a period of safety (Sih and McCarthy 2002). During the extended periods of danger, to meet minimum energy demands prey must still maintain low to moderate activity and feeding rates (Sih and McCarthy 2002).

During extended periods of safety, assuming some costs of activity or a threshold maximum benefit of feeding, prey should show moderate feeding activity. If prey experience only rare pulses of risk, then during these pulses they should drastically reduce their activity and feeding rates (Figure 2.3) (Sih and McCarthy 2002). In contrast, snails held in continual safety showed moderate levels of activity, but surprisingly only a weak reduction in activity when exposed to a pulse of danger (Sih and McCarthy 2002).



**Figure 2.3** Basic predictions of the risk allocation hypothesis (Lima and Bednekoff 1999).

The temporal patterns of risk might depend on variations in external factors. In the case of nocturnal prey, the proportion of risk throughout a night changes over a lunar cycle (Rosenzweig 1974, Kotler 1984). Prey behaviour reflects not only the immediate level of risk, but also with the temporal pattern of risk. For example, Daly et al. (1992) showed that kangaroo rats compensate for longer periods of risk during a full-moon by increasing their activity at dusk and dawn (Sih and McCarthy 2002). Anecdotal evidence suggests that the same trend is apparent in marron (Storer pers. obs.). This has ramifications for experimental design - with most investigations into behaviour focussing on prey responses to sudden increases in predator intensity as they are introduced to systems.



## 2.7 Project rationale

It is generally assumed that animals react based on an analysis of costs and benefits and therefore, that the costs of response can be measured as a function of fitness. Given this, assessments of the interactions between organisms in multi-species systems (natural or artificial) is a complex task. Researchers need to consider the species involved, individual variations within species (including health status, life stage and genetic variation), predator ecology, temporal and spatial variations, geographic differences, information cues available and the impact of biotic and abiotic system variables.

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The advantages of multi-species systems include multiple revenue sources, income spreading and improved system ecology. Even where species exhibit some degree of niche overlap resulting in competition or predation, there can still be economic advantages to their combined culture. Obviously, in multi-species systems where niche overlaps exist, the negative interactions need to be understood and mediated in order to maximise aquaculture production.

Management practices have a major impact on crayfish yields in polyculture ponds. Many factors have been identified through this review that can influence the ecological dynamics of crayfish-finfish polyculture. These factors include the relative size of component species, the species involved, shelter regime, turbidity, intraspecific dynamics as a function of predation pressure, and cage culture techniques.

Trials reported in this thesis were aimed at developing appropriate management strategies that can be used in optimising marron-silver perch polysystems. Trials focus on developing an understanding of communication between these two species, the nature and intensity of responses and the system-specific ecological processes governing them. Interaction responses were primarily examined through behavioural analysis, as behavioural traits have been shown to influence a key trade-off between resource acquisition and vulnerability to predation, and understanding trait differences between species can provide critical insight into their interactions. Such an approach should enhance our understanding of the criteria for coexistence between species that can interact through both competition and predation.

## ***Chapter three***

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### ***Experimental Systems and Species***

*This chapter explains the system dynamics used in laboratory and field trials and explains rationale for selection of species.*

### 3.1 Experimental systems

Four aquaria-based experiments and three field trials were conducted. Facilities utilised for each of these investigations are described. Note: animal weights were determined using a KERN 430-33 electronic balance ( $\pm 0.01$ ) and water quality was measured using a TPS AQUA - Cond / pH (T1661) for temperature ( $^{\circ}\text{C}$ ), salinity (ppt), conductivity (mS) and pH, and dissolved oxygen (mg/L) measured using a Winlab data line oxygen meter (Windaus - 1115015).

#### 3.1.1 Laboratory experiments

All aquaria-based experiments (Chapters 4, 5 and the first trial in Chapter 6) were conducted at the South-West Aquaculture and Environment Centre (SWAEC), a research facility in Collie, Western Australia ( $33.361^{\circ}\text{S}$ ,  $116.157^{\circ}\text{E}$ ). Collie is approximately 200 km south of Perth and is located 25 km from the coast in the Darling Scarp. Air temperatures range from an average daily minimum of approx.  $16^{\circ}\text{C}$  in winter (Jun-Aug) to  $30^{\circ}\text{C}$  in summer (Dec-Feb) (Australian Bureau of Meteorology).

Glass aquaria (54L and 250L) were utilised for experiments (Plate 3.1). With system designs varying across trials, system specifics will be discussed in applicable chapters. The water source for all investigations was a spring fed dam adjacent to the SWAEC facility. Water is pumped from this system to a 10 tonne holding tank at SWAEC where it is screened to  $100\mu\text{m}$  before entering the facility.



**Plate 3.1** Aquaria based system used in experimental work at the South-West Aquaculture and Environment Centre

Marron and fish were placed in holding tanks prior to use in experimental systems (Plate 3.2 and 3.3).



**Plate 3.2** Crayfish holding systems at SWAEC, 5 tonne flat-bottom fiberglass tanks



**Plate 3.3** Fish holding systems at SWAEC, 4.5 tonne conical fiberglass tanks

### **3.1.2 Field investigations**

The three field investigations (Chapter 6 - 2<sup>nd</sup> trial, and Chapter 7) were carried out at the Collie Aquafarm, 15 km east of Collie townsite. This facility was designed to examine aquaculture as a beneficial end use for acidified mine lakes. A brief background of the mine lake project is provided below.

#### **3.1.2.1 Background: acid mine lakes in Collie**

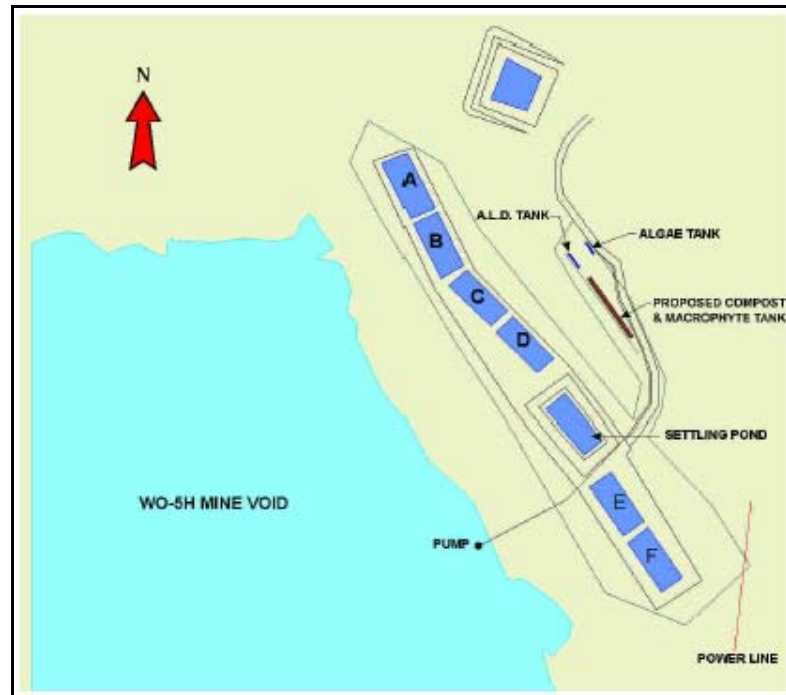
Mining companies employing open pit techniques are often faced with relinquishment responsibilities following cessation of mining activities. Besides the usually cost-prohibitive option of land-filling the void, a relinquishment programme could involve site rehabilitation that results in beneficial end-usage for local communities, including recreational pursuits or commercial aquaculture (ACARP 2000, Whisson and Storer 2003). A number of water-filled coal mining voids exist in the Collie Coal Basin in the south-west of Western Australia. The majority of these voids are affected by acidification to some degree, displaying pH levels as low as 3.0 (Evans et al. 2000, Storer et al. 2002a). At these levels of pH, the growth, reproduction and survival of many aquatic organisms is severely affected, and often negated (Chiras 1994, Harries 1997, Storer et al. 2002a).

To combat this, a recent initiative has considered water remediation of these sites (Storer and Evans 2003, Whisson and Storer 2003). In 2000, a demonstration facility (the Collie Aquafarm) was constructed to investigate remediation options for a typical disused coal mine in the Collie Coal Basin. The site incorporated an aquaculture farm designed to utilise remediated mine-water for fish and crustacean farming.

#### **3.1.2.2 The Collie Aquafarm**

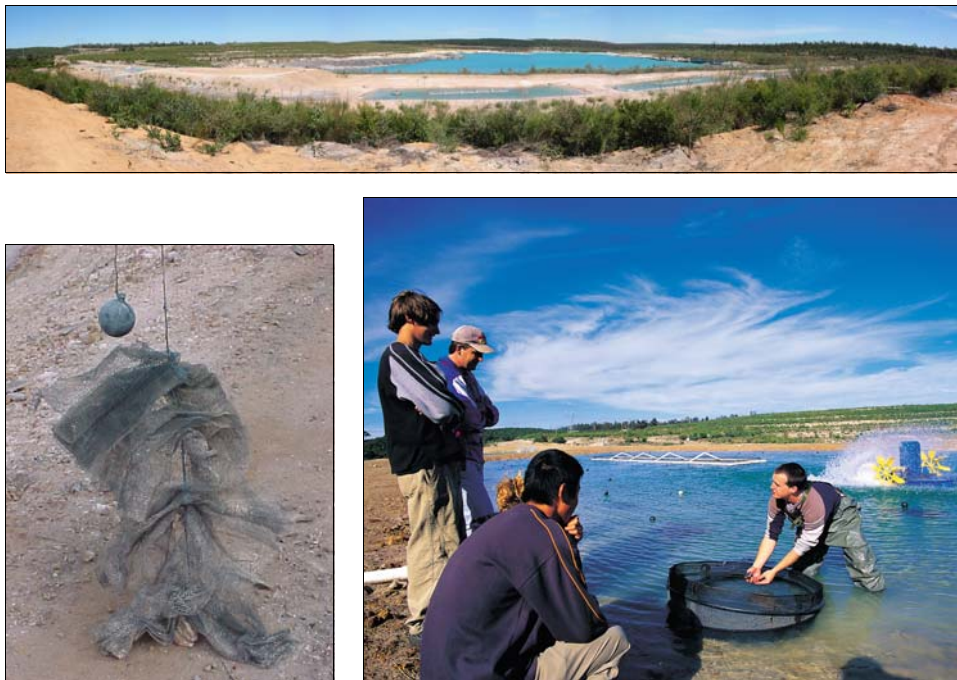
The Aquafarm is a semi-intensive aquaculture facility, comprising six rectangular purpose-built earthen ponds, each 0.072 ha (40m x 18m x 1.8m depth). Ponds are located adjacent to an acidified water-filled mine void (Plate 3.4). As mentioned in the previous section, the farm was developed to demonstrate the viability of aquaculture

using remediated mine water, and the field trials presented in this thesis are the first studies carried out using this facility.



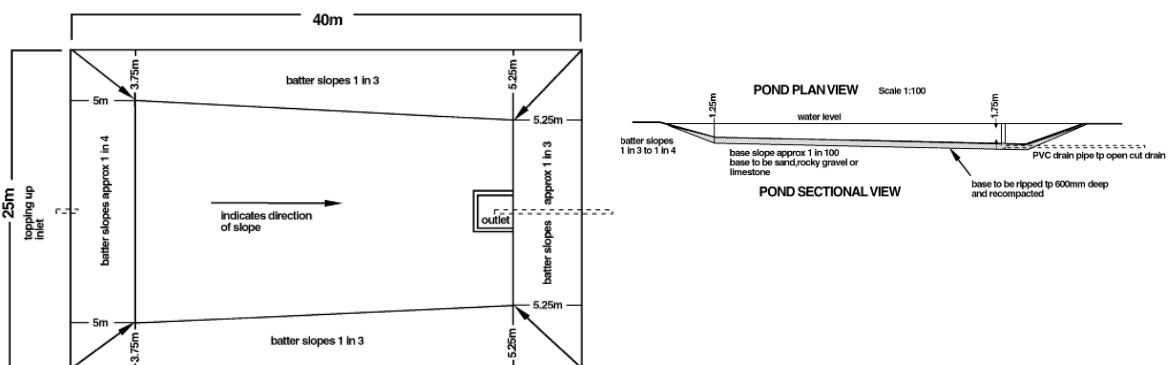
**Plate 3.4** Top view of the Collie Aquafarm, showing the main system components including remediation system, aquaculture ponds (A to F), settling pond, and WO5h void

Acidic void water (pH 3.3) is pumped to a treatment system (120L/min.) using a submersible pump mounted 3m below the water surface on a tethered float. Within the treatment system, water is passed through an experimental fluidised limestone bed reactor - raising pH to around 6.5, and through a macrophytes pond and compost pond before being stored in a settling pond above the aquaculture ponds. The role of the macrophyte and compost systems is to increase organic load and raise pH to its final level, around pH 7.3. Water is taken from just below the surface of the settling pond system and gravity fed through separate water intakes into each of the six aquaculture ponds (Plate 3.5), at a flow rate of 20L/min./pond. Excess water is removed from the bottom of ponds using a standpipe in the deepest section with a sheath pipe containing holes at the base. Out-flowing water is fed back to the mine lake via a common drain.



**Plate 3.5** Top: showing location of ponds adjacent to mine lake. Bottom left: loose-mesh marron hide used in ponds. Bottom right: aquaculture pond with paddlewheel aerator and floating fish cage

Ponds were built based on size and slope specification for commercial marron production (Figure 3.1). Width of Aquafarm ponds was 18m, as opposed to 25m in Figure 3.1.



**Figure 3.1** Commercial marron grow-out pond design (FWA 1999)

Each pond was fitted with a single 1 hp Nan Rong paddlewheel for circulation of water, operated for 1 hr between 0700 and 0800 throughout trial, and for 1 hr between 1500 and 1600 in warmer conditions as required. Loose mesh marron hides (Plate 3.5) were used for shelter at varying densities depending on requirements of the experiment (see methodology sections in Chapters 6 and 7). Large-scale floating cages (15m x 1.5m x 0.75 depth) were utilised in each pond to hold fish. The number of cages/pond depended on requirements of each investigation. Cages were designed for commercial scale polyculture experiments in field trials carried out by Whisson (1998) (Plate 3.6), and replicated in this study due to previous use and success with species being cultured, and to allow direct comparison of results.



**Plate 3.6** Left: fish cage design. Right: TAFE students preparing for fish harvest

Cages were constructed from extruded polypropylene, UV stabilised, general purpose mesh (Nylex corporation Pty Ltd). Mesh was 12mm x 12mm on sides and base, with a 3m section of 6mm x 6mm oyster mesh attached to the center of the base of each cage to act as a feeding platform and prevent fish pellets from falling through. Cages were attached with 5mm rope to a 90mm stormwater grade pipe floatation system, coated with 100% water-based acrylic gloss paint to assist with UV protection. Each pipe structure had four evenly spaced triangular arches protruding above the cage to hold the bird netting and provide stability of structure. UV stable 25 cm<sup>2</sup> bird netting



covered all cages (Plate 3.6). A freeboard of 10 cm above water surface was included to prevent fish escaping over the top and to reduce the effects of wave action. With the freeboard excluded, cage volumes were 14.63 m<sup>3</sup>. Cages were held in the center of each pond using guy ropes anchored to the pond embankment. All design and set-up aspects of cages were from Whisson (2000).

Experimental aquaculture ponds were drainable, where water level could be rapidly dropped to a minimum height of 400 mm, and completely drained when required to enable controlled harvesting of crayfish. All ponds were emptied and left to dry for 2-3 weeks prior to filling immediately before each trial. 1 tonne of coarse lime rock was spread throughout each pond before filled to increase alkalinity and calcium levels.

## 3.2 Test species

Research work within this thesis included investigations into a number of fish and crayfish species. Field trials incorporated marron, *C. tenuimanus*, and silver perch, *B. bidyanus*. Laboratory trials focused on marron, silver perch, Murray cod, *Maccullochella peelii peelii* and yabbies, *Cherax albidus*. A brief overview of the selection rationale for each of these species follows.

### 3.2.1 Marron and silver perch

Marron (Plate 3.7) were chosen as the base species for polyculture investigation as existing infrastructure (ponds, aeration, fencing...) in the established monoculture industry would mean that large capital outlay was not required to incorporate additional species. In addition, marron farming is generally a single crop/yr industry, which is at economic risk from fluctuating market prices. The addition of a second species to current monoculture practices will not only diversify risk, but preliminary polyculture data with silver perch has shown a synergistic advantage to marron, with growth rates increasing between 7-50% (Whisson 2000). Whisson (2000) also suggested that marron grown in polyculture with silver perch also demonstrate a more uniform growth. This would be a significant market advantage as less proportion of the harvested stock would fall below minimum size requirements for sale. This would also mean that less

animals would require on-growth to achieve market size, therefore freeing up farm resources. Silver perch (Plate 3.7) were selected as the main candidate for polyculture with marron due to existing translocation policy allowing their import into certain areas in Western Australia. More importantly, silver perch possess a number of characteristics conducive to successful culture with marron. These include schooling behaviour (amenable to high densities), accepting a wide range of water quality conditions, and a generally favorable feeding biology. Although predation of marron by silver perch has been recorded, management strategies targeting turbidity, habitat complexity and utilising cage culture have shown encouraging results.



**Plate 3.7** Marron, *C. tenuimanus*, and silver perch, *B. bidyanus* (juvenile)

Recommendations from the preliminary work into the combination of marron and silver perch (Whisson 1995a, Jones and Ruscoe 1998, Whisson 1998, 2000) outlined the following target areas: stocking regime (density and size), effect of system variables (turbidity, habitat complexity) and understanding of interaction biology (Whisson 2000). See section 1.11 for a more detailed overview of general biology and aquaculture attributes of these species.

### 3.2.2 Murray cod

Murray cod (*Maccullochella peelii peelii*) (Mitchell, 1839) (Plate 3.8) are native to the Murray-Darling Basin and are the largest freshwater fish in Australia, growing to 1.8 m and weighing 83 kg (Whitley, 1955). A fish of 113.6 kg has been recorded but not

confirmed (Noble 1955). Due to its high aquaculture and recreational potential, Murray cod were previously introduced and stocked into Western Australia's inland Wheat-belt area in the 1890's (Morrissy 1970, Lawson 2002), and are currently the focus of translocation approval for tank-based aquaculture. This species was chosen for study in this thesis due to an alternate predator feeding strategy to silver perch, and literature suggests avoidance responses are affected by the hunting techniques of predators (Brett 1992, Stibor and Luning 1994). Unlike the pelagic silver perch, Murray cod are generally referred to as benthopelagic ambush predators (Chivers et al. 1996b), and are known predators of freshwater crayfish. Finally, Murray cod are a strict carnivore, as opposed to the polytrophic silver perch.

Although cod are not a current candidate for introduction into pond systems containing marron, due to translocation implications and low evidence of suitability to cage culture, examination of marron responses to varying predator strategies is important in understanding their decision processes, threat detection and avoidance strategies.



**Plate 3.8** Murray cod, *Maccullochella peelii peelii*.

### 3.2.3 Yabbies

'Escape' of yabbies from man-made impoundments has resulted in their widespread distribution in the south-west of Western Australia. The resulting impact on marron stocks is currently under debate, however it is known that yabbies will compete with

indigenous crayfish for resources (Morrissy and Cassells 1992, Pen and Potter 1992). Yabbies (Plate 3.9) were chosen for study in this thesis to compare responses to novel finfish with that of marron. Yabbies were also utilised to determine how behaviour is influenced by competition between the two species. The comparison between marron and yabbies was made for contrast between a species evolving in a predator rich environment and capable of surviving and thriving in foreign systems – and marron, evolving in a predator free environment (Morrissy 1997, Allen et al 2002) and not shown to actively or successfully invade other areas.



**Plate 3.9** Yabby, *C. albidus*

Previous studies of the relationship between marron and yabbies have suggested reasons for yabbies dominance in some systems – these have included higher breeding frequency and dislodgement from preferred habitat. However, recent studies have shown yabbies to be out competed by marron under certain conditions (Whisson 2003). Previous behavioural studies into the response of yabbies to potential threat (Gherardi et al. 2002, Height and Whisson 2004) will allow direct comparison to investigations in this thesis.

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The common name, yabby, is used in reference to *C. destructor*, *C. albidus*, and *C. rotundus*. For ease of discussion, making no assumptions of lineage, yabbies used in trials in this thesis are referred to as *C. albidus*, as this is more commonly used when referring to Western Australia stock (C. Lawrence pers. comm. 2005).



### **Chemical communication by marron**

*This chapter covers one laboratory investigation (T4:1) aimed at elucidating the ability of freshwater crayfish to detect and differentiate between chemical cues from food and potential kairomones from fish, and determining whether detection ability is affected by size or sex of crayfish.*

## CHAPTER FOUR

### Chemical communication by marron

To understand the complex relationships between marron and silver perch, an examination of the nature and extent of communication between the two species, and in particular any predatory or competitive interactions, is required in order to manage antagonism and maximise synergism with the goal of optimising system yields.

The focus of this preliminary experiment was chemical communication, one of the major information media controlling interactions in aquatic environments (e.g. Chivers et al. 1996b, Kiesecker et al. 1996, Brown et al. 1997). Chemical signals have a number of features that make them particularly suited to communication in aquatic systems; they are water soluble, quickly released into the medium, non-volatile and stable over a wide range of temperature (Loose et al. 1993). The use of chemical cues in interspecific interactions, where signals from one species produces a reaction in another (allelochemicals), is well documented (e.g. Kats and Dill 1998, Brown et al. 1999, Vet 1999, Hay 2002).

The effect of food cues on reactions to predatory signals is another element requiring elucidation. Animals encountering both a risk cue and an alternative stimulus (i.e. food) often cannot simultaneously respond to each stimulus (e.g. Hazlett and McLay 2000, Hazlett and Rittschof 2000). When animals are presented with multiple cues, a trade-off must often be made in response to those cues (Lima and Dill 1990, Pecor and Hazlett 2003). Due to this, tritrophic investigations have gained growing consideration for their importance in understanding the dynamics of adaptive antipredator behaviour (Sih 1980, Werner and Mittelbach 1981, Sih 1982, Abrams 1982, 1984, Werner and Peacor 2003, Bolker et al. 2003).

The aim of this experiment was to determine whether marron could detect chemical cues from the novel silver perch, and what responses, if any, they would employ. Differences between size classes and sex of marron in their abilities to detect and respond to cues was also tested, and this was done in the presence of food to determine if feeding responses were inhibited, promoted or unaffected by the fish cues.

The null hypothesis for this experiment was:

**H<sub>0</sub>:** Marron, being a non-invasive species (Gherardi et al. 2002), will not react to silver perch odour (being a non-native species), regardless of size or sex of crayfish.

## 4.1 Materials and methods

### 4.1.1 Site and culture system

This experiment (T4:1) was conducted in the aquarium system at the South-West Aquaculture and Environment Centre (SWAEC) located in Collie, Western Australia. Twenty-four glass aquaria (300 mm x 300 mm x 600 mm) were used (Plate 4.1), described in Section 3.1.1.



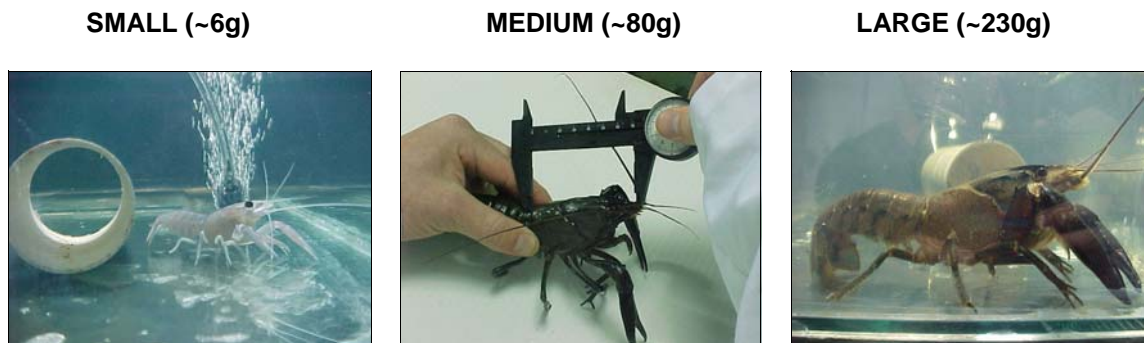
**Plate 4.1** Experimental systems, 54L glass aquaria - filled to 25L

### 4.1.2 Experimental stock

Marron (Plate 4.2), reared in monoculture ponds in Pemberton (34.449°S, 116.039°E), were transferred to holding tanks at SWAEC in January 2003. Silver perch were sourced from ponds at Parkerville, Western Australia (32°S, 116°E) and kept in holding tanks at SWAEC for two weeks prior to the trial. Holding systems are detailed in Section 3.1.1.

### 4.1.3 Experimental design

Eight marron (1:1 sex ratio) in three size-classes (Plate 4.2): small ( $5.6 \pm 0.79\text{g}$ ); medium ( $78.6 \pm 2.97\text{g}$ ); and large ( $230.8 \pm 4.2\text{g}$ ), were distributed using an 8x3 random block design into the twenty four aquaria, each with 25L of water ( $19.8 \pm 0.05^\circ\text{C}$ ). Individual aquariums were visually isolated from other aquaria, and contained a piece of polyvinyl chloride tube (length 150 mm, diameter 50 mm) for shelter. Constant aeration was supplied using a single air stone in each aquarium. As with all studies examining response to chemical cues, chlorinated water was added and subsequently cured using hypochlorite for use in experimental systems to prevent introduction of external chemical information.



**Plate 4.2** marron size classes used in experiment - small, medium and large

Following acclimatisation to individual aquariums (24h), behavioural records were taken every 15s for 5 min. during two time periods; (A) a 5 min. control period following injection of 10 ml of distilled water (control water), and immediately afterward, (B) a 5 min. period following the injection of test solution, according to Hazlett (1999) and Gherardi et al. (2000). Thus, each experiment lasted 10 min., the injection of control water always preceding the injection of test water. All tests were carried out between 1200 and 1700h.

### 4.1.4 Preparation of test solutions

Test solutions were (1) 10 ml of food odour (FOOD), or (2) 10 ml of food odour plus 5 ml of silver perch culture water (F+PCW). The FOOD solution was prepared by macerating 75g of commercial crayfish pellets (Glen Forrest Stockfeeders Pty Ltd, Appendix D) in 600 ml of distilled water and filtering with coarse filter paper. The F+PCW solution



incorporated 10 ml of food solution combined with 2.5 ml of water from a holding tank containing silver perch with an average weight of  $419.8 \pm 38\text{g}$  at a density of  $20 \text{ kg/m}^3$ , and 2.5 ml from a tank containing silver perch, with an average weight of  $102.8 \pm 5.2\text{g}$ , also at a density of  $20 \text{ kg/m}^3$ . Silver perch were held in these two size classes to exclude any variation in crayfish response due to fish size. The use of silver perch culture water was to attempt to capture natural chemical cues (allelochemicals) released by the fish.

Control water and test solutions were added via syringes to the corner of the aquarium furthest from the crayfish. All test solutions were prepared immediately before testing (Hazlett 1994a/b). Test solutions (1) and (2) were tested in each aquarium over the two-day trial period. The order of delivery was randomly determined within the three size classes. That is, four marron of each size received test solution (1) on the first day, and test solution (2) on the second day. The situation was reversed for remaining tanks in each size-class.

To determine the speed of dispersion of test solutions throughout systems a replicated test using food dye was trialed prior to all experiments (Appendix E). The dye test demonstrated that the added solution would reach all areas of the experimental systems within 20 s of injection.

#### **4.1.5 Behavioural responses**

Behaviour analysis was used to gauge responses of crayfish to test solutions using recording protocols previously developed to document observations. The fundamental recording protocol used for tank-based experiments in this chapter, and in Chapter 5, was developed by Hazlett (1994a), and has been previously used in a number of crayfish behavioural studies (Hazlett and Schoolmaster 1998, Hazlett 1999, Hazlett 2000a, Gherardi et al. 2002, Hazlett et al. 2002). The protocol involved; reaction time and time spent in a range of behaviours (%) and posture (%), recorded for every 15s period. The reaction time being the time lapsed following injection of control water or test solutions before a change in behaviour or posture, if any, was recorded. When no obvious modification of behaviour was observed throughout the 5 min. period a reaction time of 315 s was assigned to allow statistical analysis and draw direct comparison with previous trials using the same methodology (Gherardi et al. 2002).

Behavioural observations were:

- (a) in shelter
- (b) locomotion
- (c) general feeding movements
- (d) flicking of antennules
- (e) movement of antennae
- (f) climbing
- (g) cleaning

Posture was also recorded as 'lowered', 'intermediate' and 'raised', defined by Hazlett (1994a) as follows: 'Lowered': the body is in contact with the substratum, the chelipeds drawn in towards the body, and the tail fan curled under the abdomen; 'Intermediate': the body is held just off the substratum, the tips of the chelae lightly touching the substratum and the tail fan nearly perpendicular to the substratum; and, 'Raised': the body is elevated off the substratum, the chelipeds held off the substratum and parallel to it or higher, and the abdomen or tail fan extended.

This protocol was adapted from Hazlett (1994a) in two ways for use in this investigation. Locomotion was recorded where a change in location was observed, as opposed to 'movement of ambulatory legs', previously described. In initial observations, marron displayed a 'leg sway' where individuals lay to one side and move legs back and forwards, which could be described as movement. The leg sway displayed by marron could also be interpreted as a scraping feeding response, however neither explanation appeared applicable on close observation. The second alteration pertained to feeding movements, which were previously broken up into searching of chelae, searching of ambulatory legs and sham feeding - where legs are taken to mouth. In this trial the three feeding types were combined as one observation. Variations in responses of crayfish to interspecific cues have been described by many authors (Hazlett and Schoolmaster 1988, Willman et al. 1994, Mitchell and Hazlett 1996) and this demonstrates that behavioural protocols must be flexible, especially when dealing with new species.

#### 4.1.6 Feeding

While in holding systems, silver perch were fed commercial pellets (Glen Forrest Stockfeeders Pty Ltd, Appendix C). To reduce effects from general metabolites such as ammonia, silver perch were starved for three days prior to experimentation. Marron were fed on commercial crayfish pellets (Wesfeeds Pty Ltd, Appendix D) until 24 h prior to trial. This was done to ensure marron would recognise food solution and secondly to ensure responses to food odour weren't exaggerated by starvation, whilst not feeding during the trial to prevent ammonia build-up.

#### 4.1.7 Statistical analysis

Reaction time, behaviour and posture for individuals during control periods were compared using t-tests (Selvanathan et al. 2000) to evaluate background differences between the size-classes and sex of marron. For comparison between control water and test solutions for each size-class of marron, reaction time, behaviour and posture were analysed using paired t-tests (Selvanathan et al. 2000). For comparison between test solutions within each size class for the same test, the magnitude of change (difference in absolute values) in the reaction time (s) and in behaviours and postures (%) between the control water and test solutions was determined for each individual. This was necessary as background differences were displayed within size-classes of marron. Responses within each size-class to the test solutions were compared with a Kruskal-Wallis one-way analysis of variance (Selvanathan et al. 2000). Wilcoxon Signed Ranks test was used to compare differences between size classes (Selvanathan et al. 2000). All percentage data were subject to arcsine transformation prior to analysis (Zar 1984).

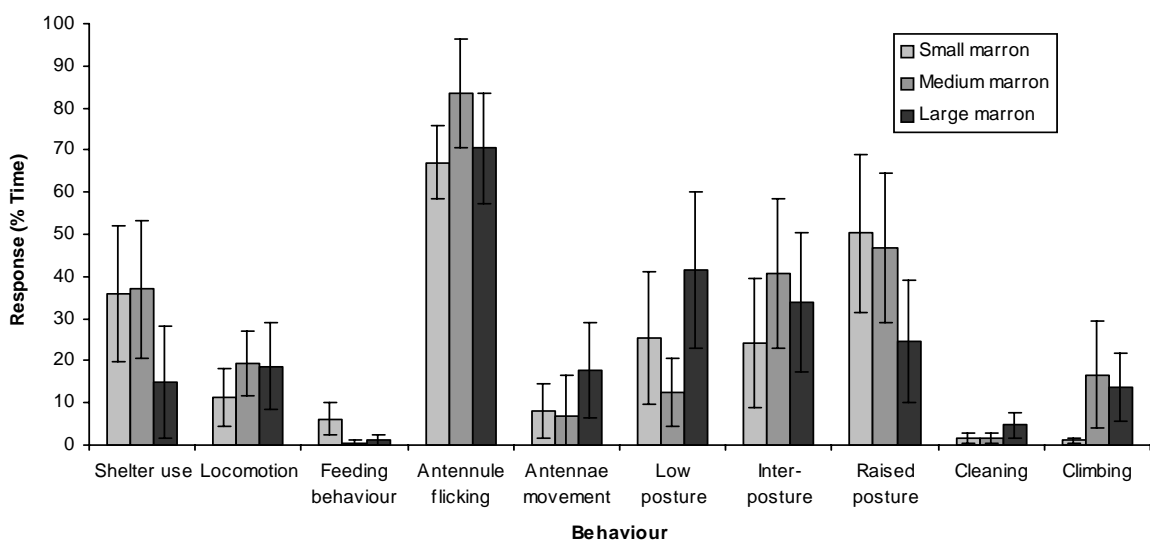
Paired t-tests were carried out between responses recorded in day 1 *versus* day 2 to determine if differences existed for reasons such as learning or potentially increased responses to food as requirement increased. No statistical variations were found,  $P > 0.1$ .

## 4.2 Results

### 4.2.1 Size class differences in response to control water

No significant differences were recorded in reaction time, behaviour or posture between small, medium and large marron in response to 10 ml distilled water during the control periods ( $P > 0.01$ ) (Figure 4.1, Appendix B - Table I).

Although no statistical differences were reported in general behaviour of the different size classes of marron, a number of trends were apparent (Figure 4.1). Shelter was preferred by small and medium marron ( $35.7 \pm 12.4\%$  and  $36.9 \pm 11.8\%$ ) compared with larger marron ( $14.6 \pm 9\%$ ). Climbing was most common in medium ( $16.7 \pm 8.7\%$ ) and larger marron ( $12.9 \pm 5.9\%$ ), with little climbing observed in the small size class ( $1.0 \pm 0.5\%$ ).



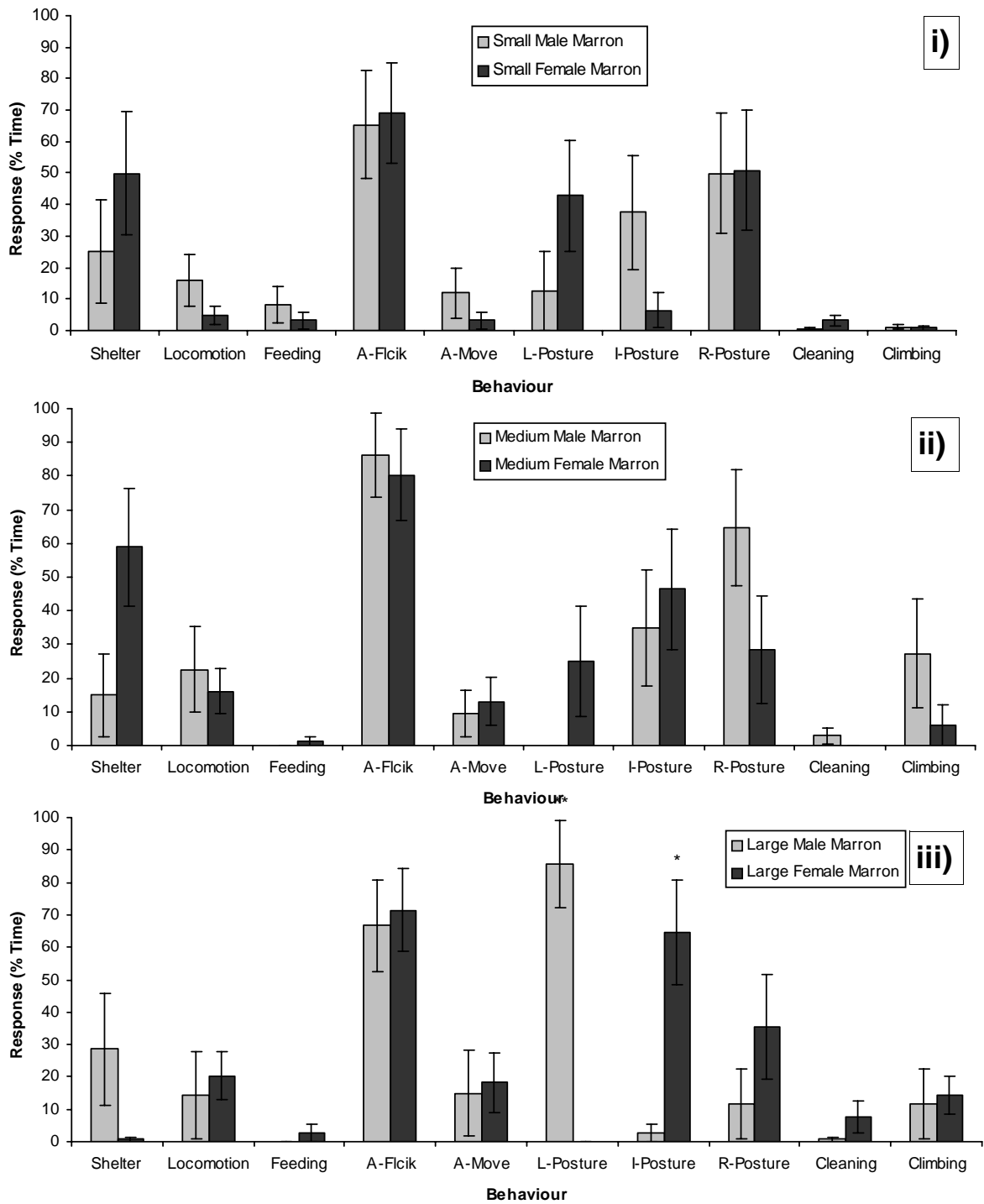
**Figure 4.1** Intraspecific size-class differences in marron response to control water

Values are control means  $\pm$  standard error.

### 4.2.2 Sex differences in response to control water

Apart from large male marron preferring low posture ( $85.2 \pm 13.4\%$ ,  $P < 0.001$ ) compared with large females (with no individuals recorded in this posture) (Figure 4.2), and large females found significantly more in intermediate posture ( $P < 0.05$ ), no

differences ( $P>0.05$ ) between sex were recorded in reaction time, behaviour and posture in response to 10 ml of control water during the control periods (Figure 4.2, Appendix B - Table I).

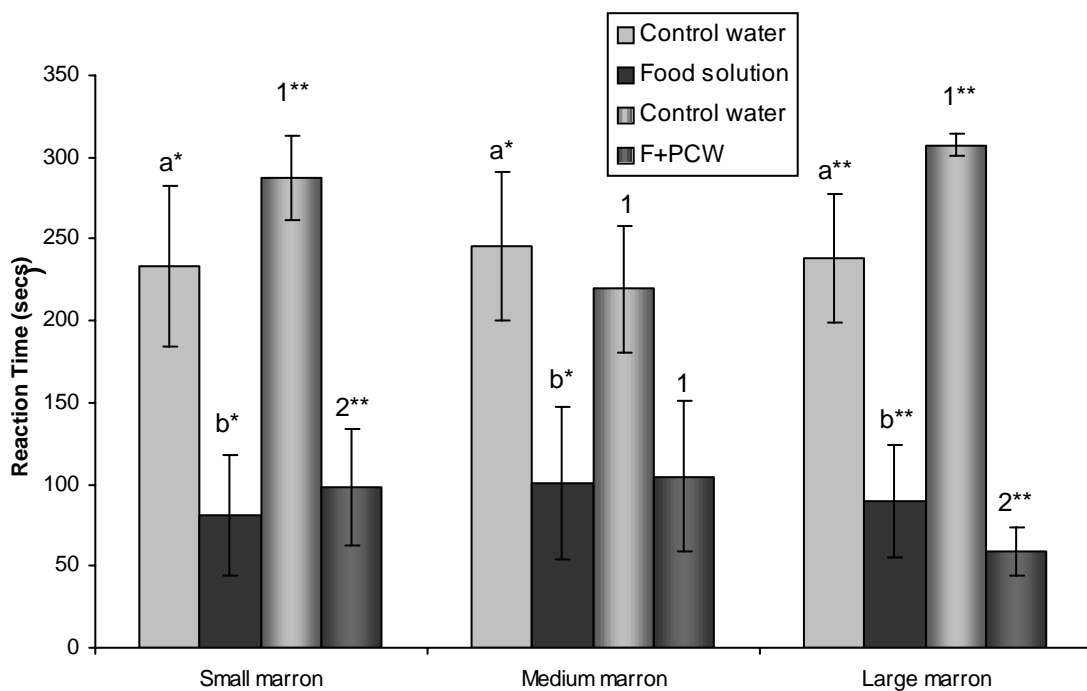


**Figure 4.2** Male-female crayfish responses to control water: i) small marron, ii) medium marron, iii) large marron

Values are the mean ( $\pm$  SE) of the two control periods. Significant differences between sexes for the same behaviour are indicated by \* $P<0.05$ , \*\* $P<0.01$ .

### 4.2.3 Control water versus test solutions

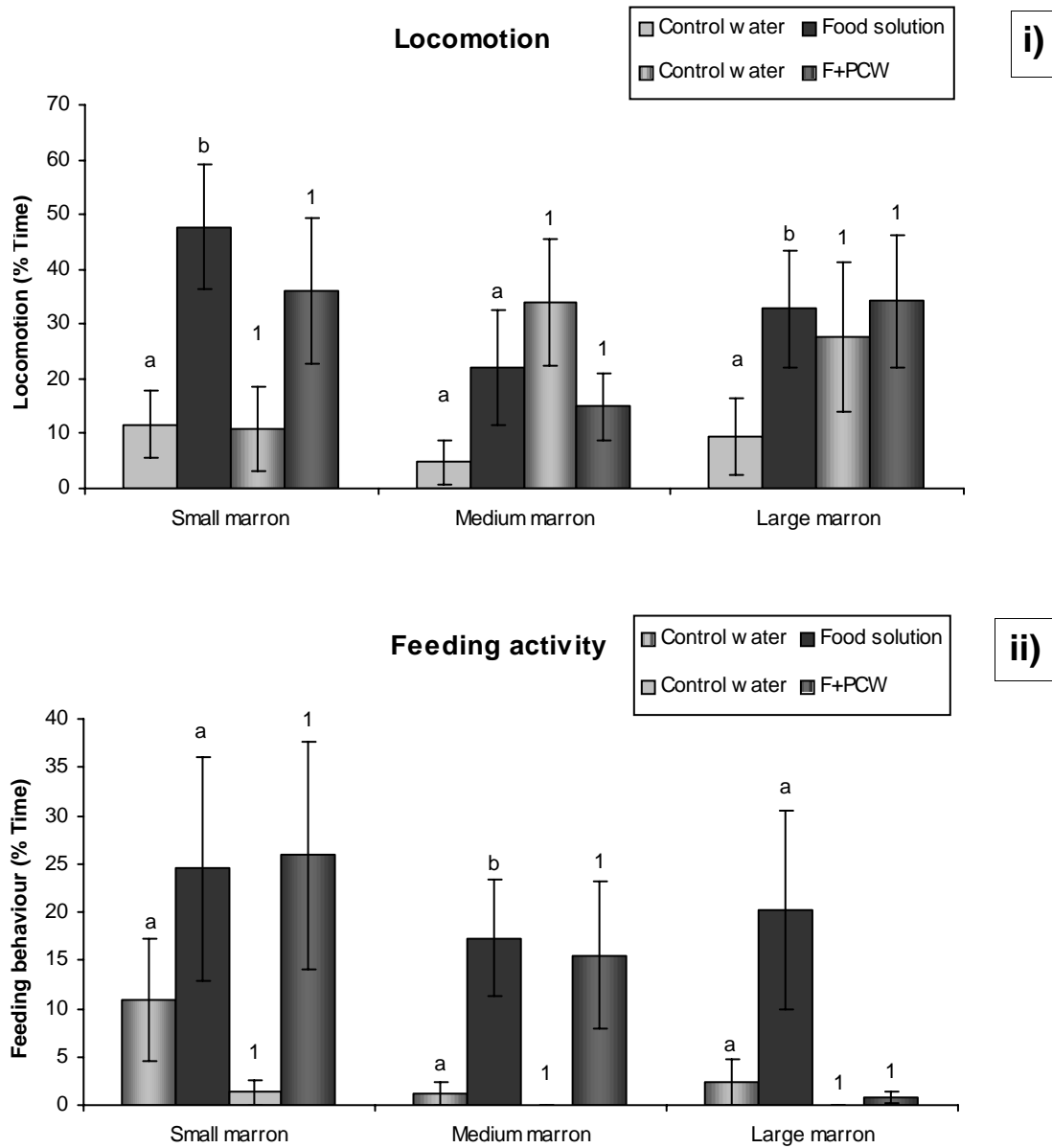
Reaction time to test solutions was faster compared with control water for all crayfish size-classes, with the only non-significant finding in medium marron responding to the combined food and perch culture water solution ( $P = 0.196$ ) (Figure 4.3, Appendix B - Table I).



**Figure 4.3** Reaction times of marron (small, medium and large) to control and test solutions. Data is the average response  $\pm$  SE, with significant variations compared between control water and test solution. Where letters (control vs. food solution) or numbers (control vs. perch conditioned water-PCW) are different within each marron size class a significant difference was found. \* $P < 0.05$ , \*\* $P < 0.01$ .

Compared with control water, locomotion increased in response to food for small ( $P = 0.027$ ), medium ( $P = 0.075$ ) and large marron ( $P = 0.038$ ) (Figure 4.4). Locomotion also increased following injection of F+PCW in small ( $+ 34.7 \pm 11.9\%$ ), and large marron ( $+ 12.7 \pm 5.2\%$ ), however no significant variations were demonstrated ( $P > 0.05$ ) (Figure 4.4, Appendix B Table I).

General feeding activity increased with test solutions for all size classes, although only statistically significantly to  $P < 0.05$  for medium marron and food solution (Figure 4.4).



**Figure 4.4** Responses of marron (small, medium and large) to test solutions: i) Locomotion  
ii) Feeding behaviour

Data is the average response  $\pm$  SE, with significant variations compared between control water and test solution. Where letters (control vs. food solution) or numbers (control vs. food and perch conditioned water - PCW) are different within each marron size class a significant difference was found ( $P < 0.05$ ).

#### 4.2.4 Comparison between test solutions

Analysis of the magnitude of change between test solutions (Table 4.1) showed two significant results: Large marron reacted significantly faster in response to food solution compared to the food solution combined with perch conditioned water (PCW) ( $P < 0.05$ ), and locomotion recorded in medium marron was significantly less ( $P < 0.05$ ) in the presence of food + perch-conditioned water than food alone. However analysis of data showed results to be more a function of variations in control behaviour (Figure 4.4).

**Table 4.1** Magnitude of change between control water and test solutions in reaction time (s), behaviour and body posture (%)

Observation	Small Marron	Medium Marron	Large Marron
Reaction Time	0.4200	0.2540	1.992*PCW>F
In Shelter	1.3420	0.6740	1.0000
Locomotion	0.3390	2.032*PCW>F	1.2610
General feeding movement	1.0540	0.1050	1.6250
Antennule flicking	0.6740	0.6740	0.4050
Antennae movement	0.6310	1.0230	0.5520
Lowered posture	0.5350	1.0000	1.0000
Intermediate posture	0.4050	0.3140	1.6040
Raised posture	0.7300	0.3140	1.0690
Cleaning	0.2720	0.0000	0.8160
Climbing	1.0690	0.3650	0.9210

Comparisons among test odours (F = food, PCW = food + perch culture water) within groups used Wilcoxon Signed Ranks Test ( $X^2$ , df 2). Tests ranked in decreasing order of magnitude of change. \* $P < 0.05$

Feeding activity in large marron also appeared inhibited by perch-conditioned water, although only significant to  $P < 0.1$ , with large standard errors.

#### 4.2.5 Comparison between size classes

No significant differences ( $P > 0.05$ ) were found between marron size class in response to test solutions (Table 4.2), with one exception: Small and medium marron utilised shelter significantly more than large marron when responding to F+PCW ( $P < 0.05$ ). As large marron were rarely recorded in shelter in response to either control or test conditions, this difference is related to increased sheltering by small marron when F+PCW was added, and a higher use of shelter by medium marron throughout the trial.



**Table 4.2** Magnitude of change between size-classes of marron responding to test solutions in reaction time (s), behaviour and body posture (%)

Observation	FOOD	FOOD + PCW
Reaction Time	0.1870	2.6770
In Shelter	0.0000	6.2620*S=M>L
Locomotion	1.9930	3.1840
General feeding movement	1.4640	4.8590
Antennule flicking	1.2420	5.2260
Antennae movement	4.0860	1.0810
Lowered posture	2.8100	4.3290
Intermediate posture	0.1610	2.8320
Raised posture	0.2520	3.0790
Cleaning	0.7380	1.0690
Climbing	4.5810	1.5540

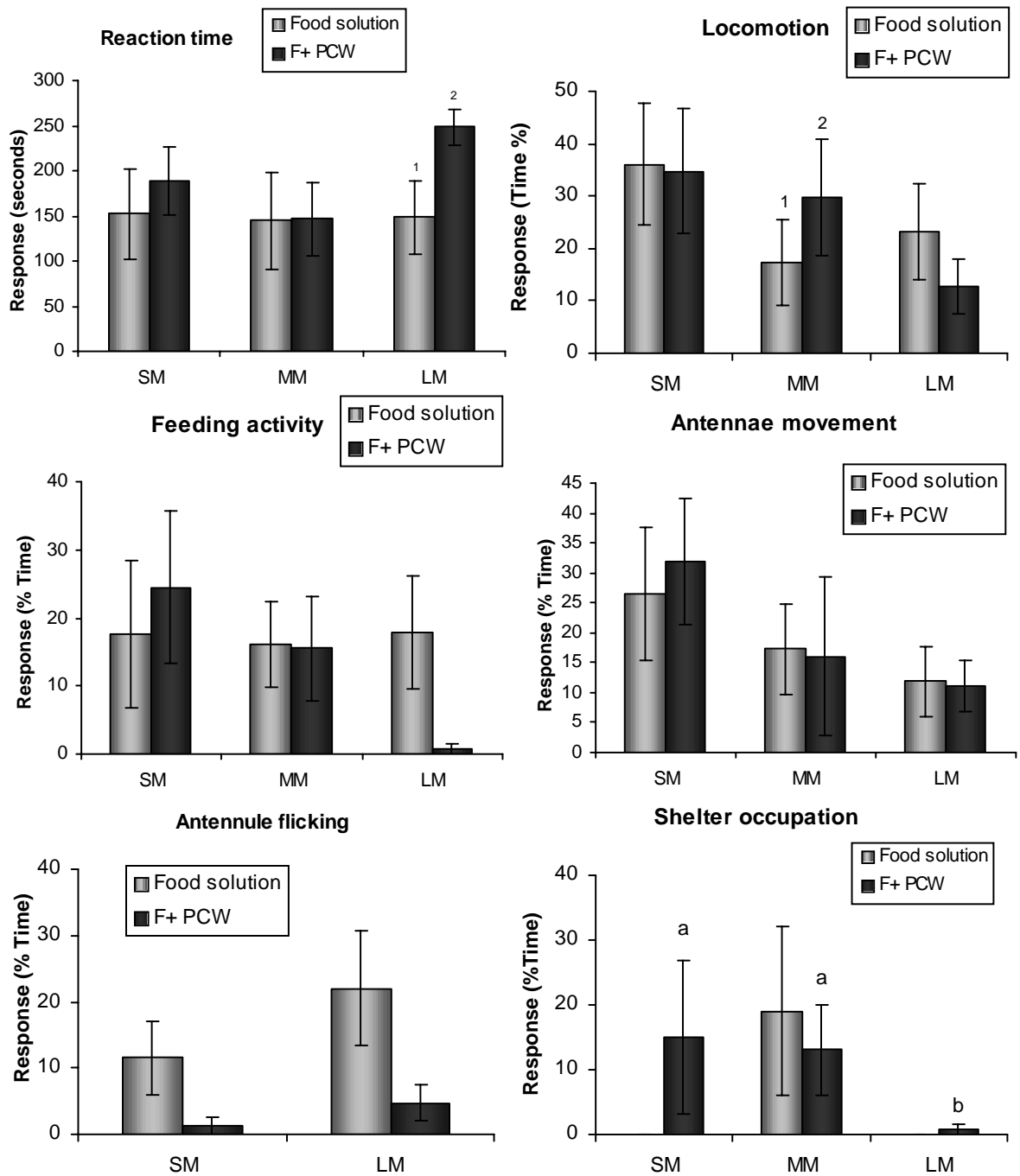
Comparisons between marron sizes (S = small, M = medium, L = large) for each test odour (FOOD, FOOD+PCW = food + silver perch culture water), used Kruskal-Wallis test. Marron sizes ranked in decreasing order of magnitude of changes. \* P<0.05, \*\*P<0.01

Although not significant when examined individually, a number of trends were apparent when responses across all behaviours were examined together (Table 4.3). The duration of average responses to test solutions for many behaviours were prolonged in small marron.

**Table 4.3** Magnitude of change between control water and test solutions between size classes of marron. Negative values represent reduced activity compared to control.

	small	medium	large
locomotion	+35.4 ± 11.7	-6.3 ± 9.7	+18.0 ± 7.1
Feeding behaviour	+21.1 ± 11.7	+15.8 ± 7.0	+9.3 ± 4.5
Antennule flicking	+6.5 ± 3.4	-12.8 ± 9.1	-8.6 ± 6.5
Antennae movements	+29.3 ± 10.9	+0.6 ± 10.5	+11.5 ± 5.1
Raised posture	+26.5 ± 13.9	-20.2 ± 9.5	+14.6 ± 8.7

Secondly, the magnitude of behavioural change across a range of behaviours displayed an overall difference in the responses of large marron to the different test solutions (Figure 4.5), where as reaction differences were less pronounced in other groups.



**Figure 4.5** Magnitude of change in behavioural responses (reaction time, locomotion, feeding activity, antennae movement, antennule flicking and shelter occupation) of three marron size groups to the two test solutions (food and food + perch conditioned water).

Where significant differences exist between size groups different letters are provided, and different numbers provided where differences exist between test solutions ( $P < 0.05$ ). SM - small marron, MM - medium marron, LM - large marron

In response to perch-conditioned water, large marron displayed a greater change in reaction time (indicative of faster reaction), and reduced changes in locomotion, feeding activity and antennule flicking, than compared with response to food alone. Similarly, comparison of responses between small and large marron reacting to fish conditioned water showed smaller marron were feeding, sheltering and using antennae more than larger individuals, as well as displaying higher overall activity. The high standard errors displayed in results, due to relatively large variations in background behaviour of marron across populations, resulted in mostly insignificant relationships between groups, and as such the relationships described in this paragraph were significant to only  $P < 0.1$ .

A summary of results for this trial is provided in Appendix B, Table II.

### **4.3 Discussion**

In order to optimise polyculture management strategies, the factors that influence the occurrence of predation events and predation stress within a specific multi-species system require elucidation. In respect to the polyculture of marron and silver perch, where perch can be held within cages - preventing physical interaction - the most important questions relate to stress associated with perception of risk. That is, whether marron production can be affected by cues from perch held in cages. This was the first attempt to examine the ability of marron to recognise novel chemical cues from a non-indigenous fish species, silver perch. Behavioural responses of marron to the chemical signatures of the silver perch, found in their culture water, are discussed on the basis of whether interaction responses were positive or negative in respect to polyculture production. A number of outcomes were apparent relating to chemosensory perception in marron, size-dependent responses to cues and the ability of marron to detect and accurately respond to fish odour.

#### **4.3.1 Chemosensory perception in marron**

Decapod crustaceans, such as lobsters, crayfish and crabs rely heavily on their sense of olfaction for locating food, shelter, conspecifics and heterospecifics (Grasso and Basil 2000, Diaz et al. 2001, Derby 2000). The behavioural responses of marron to chemical stimuli examined in this trial support these investigations, where reactions to test solutions were significantly faster compared to controls, as well as high overall usage of antennules (the major chemosensory organ in crayfish) in response to test solutions ( $72.7 \pm 20.4\%$  of time). In addition, locomotion and feeding behaviour increased significantly in all size classes in response to test solutions, suggesting recognition of food-derived cues. These results are evidence of chemosensory perception in marron, as previously described in other freshwater crayfish species (Head et al. 2002, Jacquot and Baudoin 2002, Stabell et al. 2003).

#### **4.3.2 Size-dependent responses to chemical cues**

Size-dependent responses to chemical cues in decapod species have not been widely investigated. However, knowledge of size-dependent responses involving freshwater

crayfish could underpin polyculture management strategies. The incorporation of life stage or size in stocking regimes could aid in maximising productivity with manipulation of system variables to accommodate biological changes over the culture period. For example, if smaller marron are more prone to exhibit stress related responses associated with detection of cues from fish held in cages, management may require stocking after a certain growth period.

Results in this study showed no significant differences ( $P < 0.05$ ) between size classes of marron in their behavioural responses to solutions containing perch odour, with one exception. Small and medium marron were found to shelter significantly more than large marron when PCW was added to aquaria. The lack of sheltering by large marron, combined with more frequent climbing, may be a function of stock size versus shelter rather than actual differences in responses to odours between size classes of marron. Although shelters were capable of holding large marron, as seen with the few records taken, the use of larger shelters, along with larger aquaria, is recommended in future studies.

Although individual behavioural responses were not significant, smaller marron demonstrated a more positive and sustained reaction to odours when all behavioural responses were examined holistically. Smaller marron displayed a longer duration of locomotion, feeding, antennule flicking, antennal movement and increased use of raised posture. One likely explanation is the increased energy requirements in younger crayfish (Svensson 1993), where they forage longer in search of food associated with cues. In contrast, the decreased energy requirements, and potentially increased experience, of older individuals may result in them giving up searching earlier (Svensson 1993, Persons et al. 2002) if unsuccessful in locating the food source in a small amount of time. Other authors have reported more efficient use of time and energy resources of predators due to experience (Tinbergen 1960, Dutoit et al. 1991, Greenberg 1992, Persons et al. 2002). This trend was not attributed to higher general activity in smaller marron, as control responses were similar between size classes.

### **4.3.3 Chemosensory detection of fish odours**

Previous studies state that detection of chemical stimuli from a predator or competitor species often results in a behavioural change normally characteristic of either flight or

fight (Hazlett 1999, Schapker et al. 2002). A 'decrease' in locomotion (Blake and Hart 1993a, Hazlett and Schoolmaster 1998, Hazlett 1999) and feeding behaviour (Ivlev 1961, Momot 1967) is often indicative of a response to scents from a predator. Many animals initially respond to a cue associated with elevated predation risk, such as predator odour, with an almost complete cessation of feeding activities (the hierarchical model of the structure of behaviour) (Hazlett 1999). Crayfish, in contrast, usually show a significant reduction in feeding activity in the presence of predatory cues, but do not completely stop feeding (the alternation model) (Hazlett 1999). The theory explaining why crayfish can maintain a certain level of feeding in the face of danger is based on the possession of a rapid escape mechanism, the 'tail-flip'. Tail-flipping is a behaviour elicited by tactile stimuli, offering an alternative to ceasing motion - rapid escape (Hazlett 1999, Bouwma and Hazlett 2001). These reactions to 'predator stress' were in contrast to the findings of this trial, as marron increased duration of feeding and locomotion in response to F+PCW, compared with control responses. Similarly, the use of shelter as a predator avoidance strategy (Stein 1977, Appelberg and Odelstrom 1988, Blake and Hart 1993b) was not observed in this trial in response to F+PCW. These findings suggest that marron did not detect or were not reacting to chemical cues found in silver perch tank water. One explanation is that species evolving in areas of particularly high and diverse predation pressure should be more sensitive to predation-risk cues, than those evolving in relatively risk-free environments, such as marron, as they may not have developed effective response strategies.

Although few significant differences were found between responses to food and responses to F+PCW, a trend was seen when results of large marron were compared holistically. In response to F+PCW (compared to food alone), large marron exhibited a faster reaction time ( $P < 0.05$ ), reduced feeding ( $P < 0.1$ ), reduced locomotion (significant increase with food, but not to PCW) and increased antennule flicking. This may suggest that large marron reduce activity when exposed to fish cues, which is a common threat response to potential risk (Ivlev 1961, Momot 1967, Hazlett and Schoolmaster 1998, Hazlett 1999, Schapker et al. 2002). This conclusion would support other studies where larger, more mature individuals display greater avoidance responses due to experience (Hazlett 1995, Mathis et al. 1996, Mirza et al. 2001). If marron, especially larger individuals, indeed detected fish odours, a number of factors may explain the lack of significant variations in behaviour.

Firstly, marron did not perceive the cues as related to predation risk. As silver perch are not a native predator and test animals had no previous experience with this fish species, it can be hypothesised that experience is required for recognition of threat. The existence of recognition and learned responses is well supported by literature (e.g. Mathis and Smith 1993b, Delgado et al. 2002, Donaldson et al. 2002, Gazdewich and Chivers 2002), in particular, a lack of response to unfamiliar fish odours has been demonstrated in a number of crayfish species (Hazlett et al. 2002). Many investigations also outline the need for alarm odours (crushed conspecifics or sympatrics) in order to produce an avoidance response (Hazlett and Schoolmaster 1998), especially if cues are novel (Chivers et al. 1995, Chivers and Smith 1994b). This explanation can be further justified by the low level of behavioural plasticity exhibited by marron (a non-invader), reported by Height and Whisson (2003) and Gherardi et al. (2002). A low behavioural plasticity is understandable for this species, as marron have evolved in an environment in which they are the dominant macro-invertebrate with almost no natural aquatic predators (Morrissy 1997, FWA 1999, Allen et al 2002), thus utilisation of chemical cues to assess predation risk was probably not warranted. The yabby, *Cherax albidus*, a close relative of marron, evolved under conditions of high aquatic diversity with many natural fish predators. Recognition of predator odours (familiar and novel) in yabbies is well supported (Height and Whisson 2003, Gherardi et al. 2002).

A second reason for the lack of avoidance response in marron was that the possibility of predation was outweighed by a requirement to feed. *C. tenuimanus* were not fed for 1 day prior to experimentation, and the nature of feeding ecology suggests that if nutrition becomes critical, predator avoidance may become less of a priority (Svensson 1993). The period of starvation before the trial was to prevent deterioration of water quality from wastes expelled by marron once placed in experimental systems, and was believed an insufficient time to warrant exaggerated feeding responses in marron, however this should be investigated further.

Thirdly, marron were aware of the threat but only increased alarm status - not altering behaviour immediately. Studies have shown physiological responses to predatory stress, which were not detected through behavioural observation (Schapker et al. 2002). An increased 'alert' status in marron may increase readiness for flight or fight, whilst not wasting excessive resources until situations become critical. The

possession of a strong predator avoidance strategy, the 'tail-flip response', which can be utilised for rapid escape from danger (Bethe 1897, Huxley 1880, Wiersma 1961, Webb 1979, Bouwma and Hazlett 2001) could allow species, such as the marron, to maintain normal activity until a strong visual or tactile stimulus is apparent. Other studies have shown similar results as those reported in this trial, where although chemical cues are detected, avoidance responses were only detected behaviourally following visual or tactile predator cues (Hazlett and McLay 2000, Karplus and Barki 2004).

#### 4.4 Conclusions

The use of chemosensory perception by marron was demonstrated through responses to food odour, although it is unclear whether marron detected cues from silver perch. Further research is warranted to determine the major factors governing predator detection and/or avoidance in marron. Several areas should be addressed, these include the use of kairomones familiar to the test subject - as threat detection may require 'recognition', the use of alarm odours (crushed conspecifics or predators fed on a diet of conspecifics), and the role of other exteroceptive cues, independent and in combination with kairomones. All future trials should be tested in the context of predator-prey ecology.

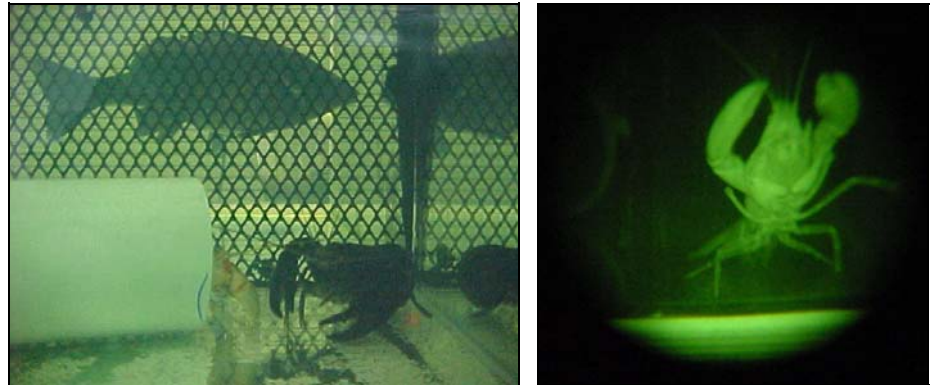
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**The null hypothesis *H<sub>0</sub>*** (4.1) was accepted, with silver perch odour not producing a behavioural reaction in marron, regardless of size or sex.



## Chapter five

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### **Visual and chemical cues**

*This chapter covers two laboratory trials examining the behavioural responses of marron to chemical and/or visual signals from a potential predator.*

*Responses of individual marron to predatory cues (T5:1) is compared with responses under cohabitation with a congeneric crayfish, the yabby (T5:2), to determine any effects from factors such as competition*

## CHAPTER FIVE

### Visual and chemical communication in marron

Understanding the triggers for predator avoidance in marron has obvious ramifications for management strategies in polyculture. In the previous chapter, marron demonstrated responses to chemical cues in food, however, results did not confirm detection of cues in fish conditioned water, with no significant predatory avoidance strategies observed. This lack of apparent predator recognition may be attributed to an evolution void of natural predators (Morrissy 1997, FWA 1999, Allen et al 2002), where cues were not perceived as threatening, or simply that marron make use of other information sources. In this chapter, the role of visual predatory stimuli is examined, both alone and in combination with chemical cues.

The use of visual signals has previously been demonstrated in decapod crustaceans (e.g. Mathis and Smith 1993b, Godin 1997, Hazlett 1999, Hazlett and McLay 2000) and in clear-water systems visual signals are most often the main method of communication (Watson 1999), providing early accurate information (Culp et al. 1991, Brown et al. 1997, Brown and Godin 1999, Murray and Jenkins 1999, Hazlett and McLay 2000, Bouwma and Hazlett 2001). As marron have evolved in clear-water rivers and streams (Morrissy 1997, Allen et al 2002), visual information regarding predation could understandably be the major sensory device used by marron, and may explain lack of responses in the first trial (T4:1). In many cases visual cues are sufficient in providing all information required for particular events (Goncalves et al. 2002), however, the use of compound information, or multiple cues (i.e. visual and chemical) pertaining to the same event, has been shown to elicit faster, more confident responses (Goncalves et al. 2002). Multiple cues are detected and utilised by many animals (e.g. Hazlett 1996, Kaufman et al. 1996, Bouwma and Hazlett 2001, Diaz et al. 2001), with information interpreted and memorised more efficiently than with simple signals (Goncalves et al. 2002). The advantage of detecting multiple cues pertaining to one ecological event is that they afford the organisms more security through increased confidence in information (Rowe 1999, Goncalves et al. 2002), resulting in an ecological advantage to the receiver (Rowe 1999). Anti-predator behaviour in the freshwater crayfish *O. propinquus* responding to visual indicators of predation threat was increased by the addition of a chemical alarm cue, in that the crayfish responded at a greater distance and retreated further than with visual cues

alone (Bouwma and Hazlett 2001). Some species of crabs (Hazlett and McLay 2000, Bouwma and Hazlett 2001) do not appear to alter their behaviour in response to chemical cues that indicate an increased risk of predation. However, anti-predator behaviour displayed by *H. rotundifrons* (branchyuran crab) in response to tactile input was prolonged by the addition of chemical or visual cues (Field 1990, Hazlett and McLay 2000). This suggests that although some info-cues are insufficient to elicit a response when presented alone, they may increase the potency of other information media. Therefore, although marron did not appear to respond to chemical cues from fish, the combination with visual cues may produce a response.

The aim of the first trial in this chapter (T5:1) was to examine the responses of marron to visual and/or chemical cues from silver perch.

The second trial in this chapter (T5:2) investigates responses of marron to visual and/or chemical cues from silver perch, under cohabitation with a congeneric crayfish, the yabby. In Chapter 4, it was hypothesised that lack of behavioural changes in marron to potential predator cues may be associated with increased alert status, where marron physiologically prepare themselves for flight or fight, and would only react when risk becomes imminent. To investigate this, shelter was limited to determine whether marron may be forced to prematurely react to predator cues due to the need to acquire shelter earlier as a result of competition with yabbies. Yabbies have been previously shown to react to a range of predatory cues (Gherardi et al. 2002).

The null hypotheses for the first trial in this chapter (T5:1) were:

**$H_0$ :** Marron will show no alteration in behaviours associated with detection of visual cues from silver perch held in bags, or chemical cues from culture water 5.1

**$H_0$ :** Marron will not demonstrate avoidance responses to either visual and/or chemical cues from silver perch 5.2

## 5.1 Responses of marron to visual and chemical cues from silver perch

### 5.1.1 Site and culture system

This experiment (T5:1) was conducted at the South-West Aquaculture and Environment Centre (SWAEC), located in Collie, Western Australia. Twenty four glass aquaria (300 mm x 300 mm x 600 mm) were used. All standard experimental conditions were replicated from Chapter 4.

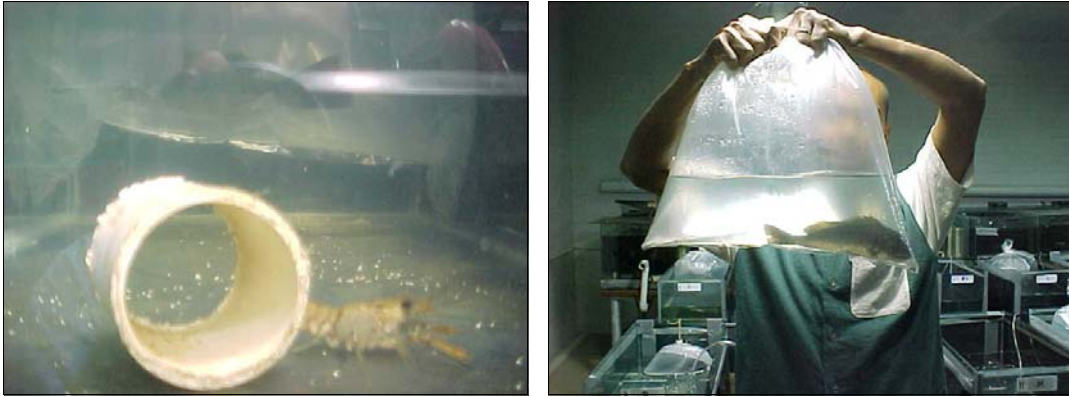


**Plate 5.1** Experimental glass aquaria (54L, filled to 25L), showing fish bags.

### 5.1.2 Experimental animals

Juvenile marron were chosen for this study as results from Chapter 4 demonstrated no differences in size related responses (Figure 4.1). Smaller marron were also thought to be the most vulnerable to predation and least inhibited in small aquariums. Marron, reared in monoculture ponds in Pemberton (34°S, 116°E), were collected and transferred to holding tanks at SWAEC in April 2003. Marron were fed commercial marron pellets (Wesfeeds Pty Ltd, Appendix D). Silver perch were sourced from ponds at Parkerville, Western Australia (32°S, 116°E). All fish were held in holding tanks at SWAEC and fed commercial fish pellets (Glen Forrest Stockfeeders Pty Ltd, Appendix C). The size of silver perch was  $115.3 \pm 6.2\text{g}$ . Fish of comparable size were shown to

predate on juvenile marron in investigations carried out by Whisson (2000). Fish size was limited to reduce stress, as larger fish were observed to be more anxious in bags.



**Plate 5.2** Left: marron in aquarium next to shelter, background - fish in bag. Right: silver perch held in bags.

As with all studies examining response to chemical cues, chlorinated water was cured for use in experimental systems to prevent introduction of external chemical information.

### 5.1.3 Experimental design

Twenty four marron (1:1 sex ratio) ( $6.5 \pm 0.65\text{g}$ ) were randomly distributed into the twenty four aquaria, each filled with 25L of water (water temperature -  $19.86 \pm 0.9^\circ\text{C}$ ). Individual aquariums were visually isolated, and contained a piece of polyvinyl chloride tube (length 100 mm, diameter 50 mm) for shelter. Constant aeration was supplied. Tanks were assigned to one of three treatments using a randomised block design. Treatments were:

1. marron monoculture
2. marron with a bag containing one silver perch
3. marron with an empty bag.

The latter treatment was included to determine any effects on marron behaviour in response to bags *per se*. Bags were commercial clear plastic fish transport bags

(Aquasonic Pty Ltd). Each silver perch was double-bagged and bags were leak-tested (1 minute visual observation) before and after the trial to ensure no chemical cues were released from bags into experimental systems.

Following acclimatisation to individual aquaria (24h), behavioural records were taken every 15 s during two time periods; (A) a 5 min. control period following injection of 10 ml of distilled water (control water); and, immediately afterward, (B) a 5 min. period following the injection of test solution according to Hazlett (1999). Thus, each experiment lasted 10 min., the injection of control water always preceding the injection of test water. All tests were carried out between 1200 and 1700h. Test solutions were (1) 10 ml of food odour (FOOD), or (2) 10 ml of food odour plus 5 ml of silver perch culture water (F+PCW). Preparation of food solution followed methods outlines in Section 4.1.4. The PCW incorporated 2.5 ml of water from a holding tank containing silver perch with an average weight of  $433.6 \pm 45\text{g}$  at a density of  $20 \text{ kg/m}^3$ , and 2.5 ml from a tank containing silver perch, with an average weight of  $131.1 \pm 5.9\text{g}$ , also at a density of  $20 \text{ kg/m}^3$ . The culture water from silver perch held in two size classes was combined in this way to exclude any variation in crayfish response due to fish size.

Silver perch culture water was utilised in an attempt to capture allelochemicals, as in Experiment 1. To reduce effects from general metabolites such as ammonia, fish were starved for three days prior to experimentation. Marron were fed until 24 h prior to trial. This was done to ensure marron would recognise food solution, and secondly to ensure responses to food odour weren't exaggerated by starvation, whilst not feeding during the trial to prevent any effects from nitrogenous wastes.

Control water and test solutions were added via syringes to the corner of aquaria furthest from the crayfish. All test solutions were prepared immediately before testing (Hazlett 1994a/b). Each test solution was randomly delivered to four of the eight replicate tanks in each treatment, including two tanks containing male marron and two with female marron. A dye test (Appendix E) confirmed diffusion of injected solutions throughout systems within 20 s. The experiment was repeated on the following day, with all conditions and stock identical to previous day, except the test solution used on day 1 was reversed on day 2. That is, test solutions (1) and (2) were tested in each aquarium over the two-day trial period.

Behaviour analysis was used to gauge responses of crayfish to test solutions. The same behavioural observations and recording protocols utilised in Section 4.1.5 were followed.

#### **5.1.4 Water quality**

Total ammonia (ppm), salinity (ppt), conductivity (mS), pH, nitrite (ppm), nitrate (ppm) and temperature (°C) were recorded daily. All levels remained within optimum ranges for all test animals and no significant variation between experimental systems was recorded. Temperature in this trial was  $19.86 \pm 0.07^\circ\text{C}$ .

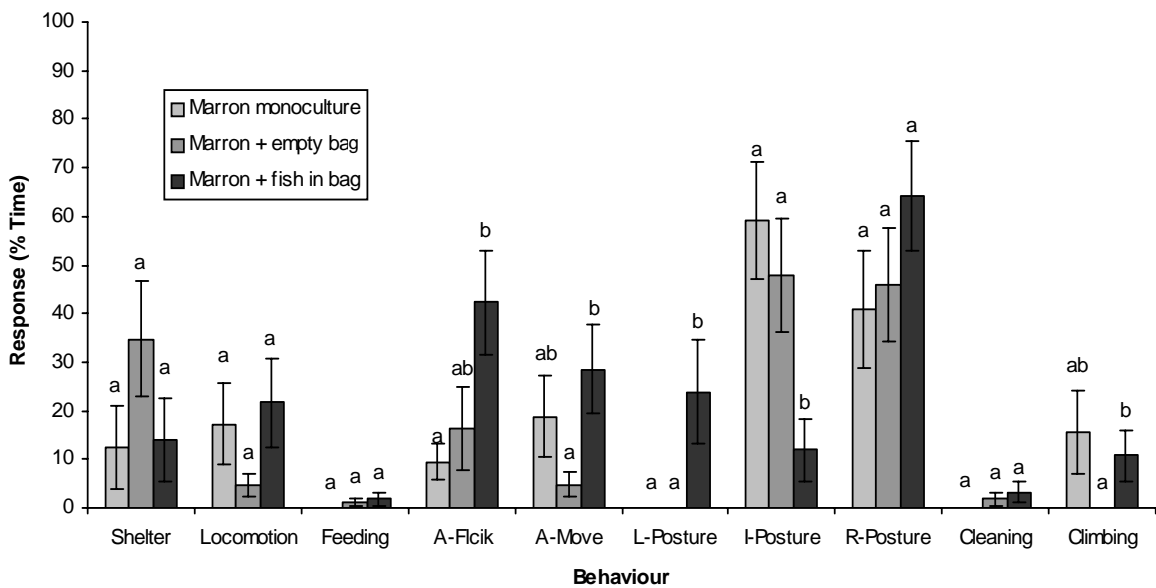
#### **5.1.5 Statistical analysis**

Reaction time, behaviour and posture for individuals during control periods was compared using t-tests (Selvanathan et al. 2000) to evaluate background differences between the monoculture, marron+bag and marron+fish treatments. For comparison between control water and test solutions for each treatment, reaction time, behaviour and posture were analysed using paired t-tests (Selvanathan et al. 2000). For comparison between tests solution within each treatment, for the same test, the magnitude of change (difference in absolute values) in the reaction time (s) and in behaviours and postures (%) for each individual between control water and test solutions, was calculated. Responses within treatment groups to the test solutions were compared with a Kruskal-Wallis one-way analysis of variance (Selvanathan et al. 2000). Wilcoxon Signed Ranks test was used to compare differences in response to each test solutions between the monoculture, fish in bag, and fish with no bag treatment groups (Selvanathan et al. 2000). All percentage data were subject to arcsine transformation prior to analysis (Zar 1984).

## 5.1.6 Results

### 5.1.6.1 Behaviour of marron in monoculture, empty bag and fish in bag treatments in response to control water

Marron in aquariums containing bagged silver perch displayed increased antennule flicking compared to monoculture treatment ( $P < 0.01$ ) and increased antennae movement compared to empty bag treatment ( $P < 0.05$ ) (Figure 5.1). Marron with fish chose lower posture significantly more than other groups ( $P < 0.05$ ), intermediate posture significantly less ( $P < 0.05$ ), and climbed more ( $P < 0.05$ ) than marron with only an empty bag in the aquarium.



**Figure 5.1** Behaviours displayed by marron in each treatment block, recorded following addition of control water.

Significant variations between treatments within each behaviour are identified by different letters ( $P < 0.05$ ).

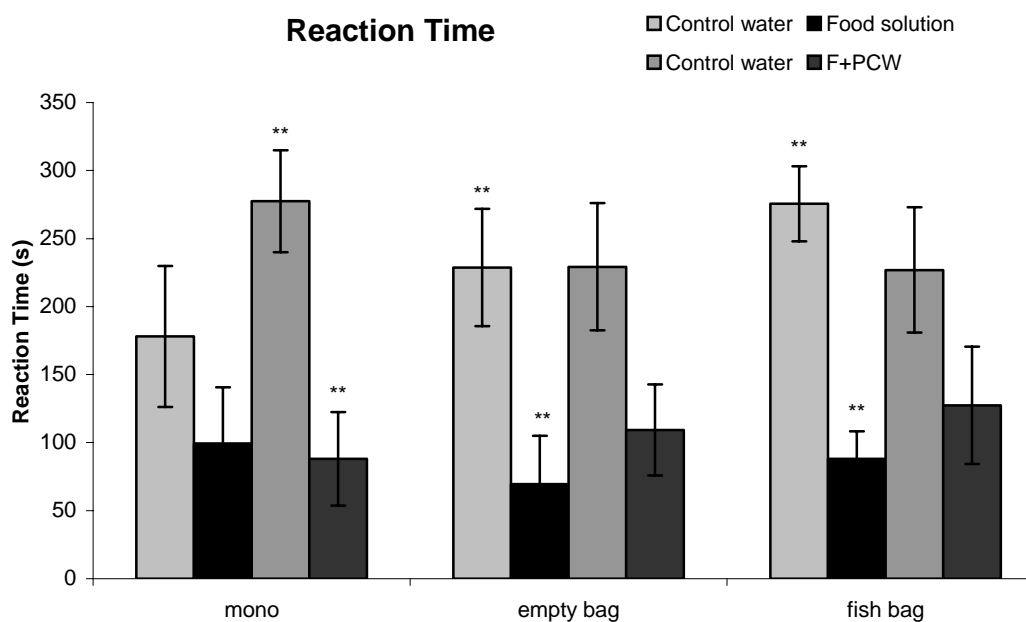
### 5.1.6.2 Gender differences in response to control and test solutions

No significant differences ( $P > 0.1$ ) between sexes were recorded in reaction time, behaviour and posture in response to 10 ml of distilled water during the two control periods.



### 5.1.6.3 Control water versus food and F+PCW solutions

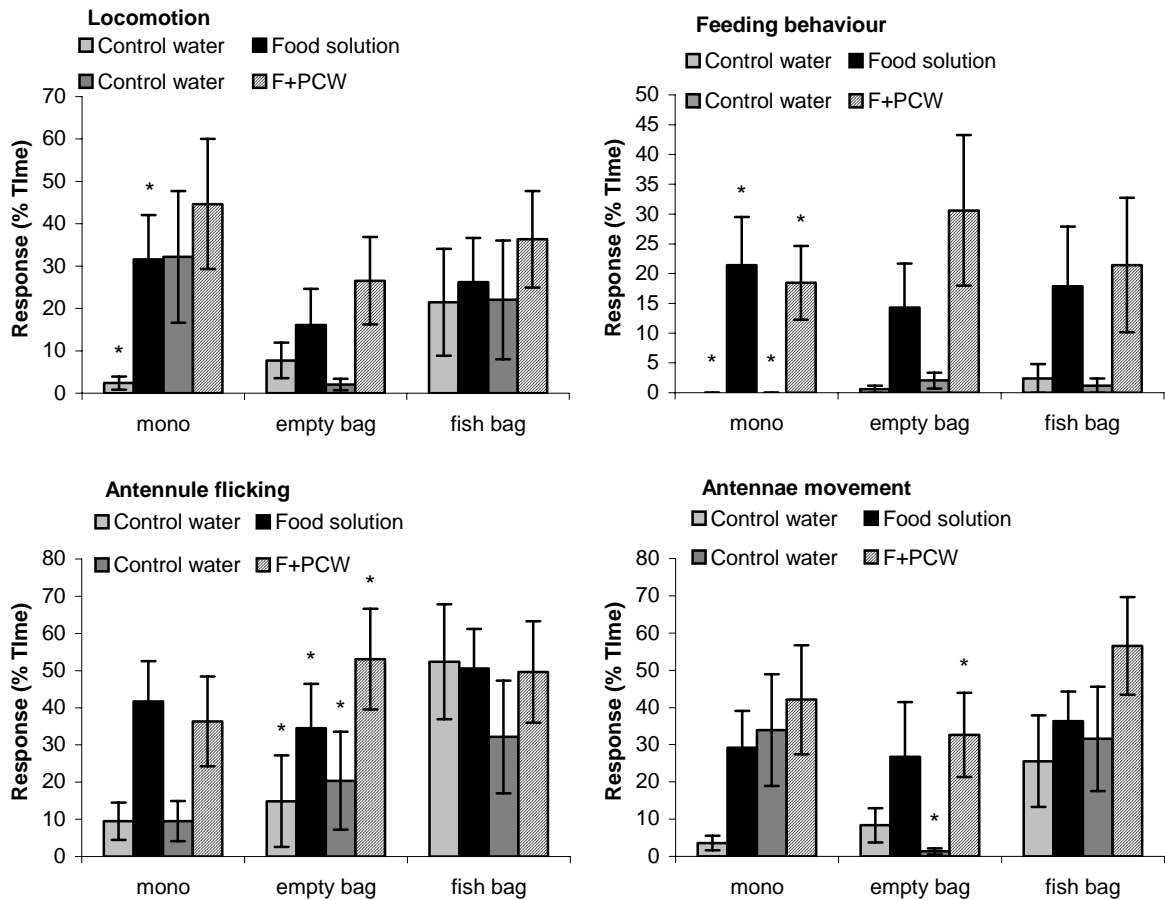
Reaction times were lower in all treatments for food and F+PCW solutions compared with control solution (Figure 5.2, Appendix B - Table III). The degree of change in reaction time between control and food solutions were  $138.75 \pm 47.33$  s ( $P=0.259$ ) for marron held in monoculture,  $159.38 \pm 43.63$  s ( $P=0.008$ ) where an empty bag was used, and  $187.5 \pm 28.21$  s ( $P<0.001$ ) where silver perch were held in bags. In response to the F+PCW solution, reaction times increased by  $196.88 \pm 41.41$  s ( $P=0.005$ ) in monoculture treatment aquaria,  $132.86 \pm 40.78$  s ( $P=0.051$ ) with empty bags in aquaria, and  $106.88 \pm 40.95$  s ( $P=0.056$ ) for marron held with bagged silver perch.



**Figure 5.2** Reaction times of marron held in 1. monoculture (mono), 2. with an empty bag, 3. with bagged fish, in response to control and test solutions (food, and F+PCW - food +perch culture water).

Data is the average response  $\pm$  SE, with significant variations compared between control water and test solution. Significant variations are identified by \*\* ( $P<0.01$ ) when differences existed between the control and test responses within each treatment.

Locomotion, feeding activity, antennule flicking and antennae movements of marron increased in response to both test solutions in all treatments when compared to control (Figure 5.3, Appendix B - Table III), with one exception - antennule flicking in the marron + bagged fish treatment responding to food. In this exception, antennule flicking was also high in response to control water.



**Figure 5.3** Behavioural responses of marron held in 1. monoculture (mono), 2. with an empty bag, 3. with bagged fish, in response to control and test solutions (food, and F+PCW) for locomotion, feeding behaviour, antennule flicking and antennae movements.

Data is the average response  $\pm$  SE, with significant variations compared between control water and test solution. Significant variations are identified by \* ( $P < 0.05$ ) when differences existed between the control and test responses within each treatment.

In monoculture, marron exposed to food alone displayed significant increases in locomotion ( $P=0.032$ ) and general feeding ( $P=0.032$ ), and marked increases in antennule flicking ( $P=0.054$ ) and antennae movements ( $P=0.051$ ). In response to conditioned water marron in monoculture increased feeding activity significantly ( $P=0.021$ ) and showed marked increases in antennule flicking ( $P=0.057$ ). In the marron + empty bag treatment, antennule flicking was significantly increased in response to both test solutions (Food  $P=0.019$ , F+PCW  $P=0.040$ ), compared with control. In response to the food and culture water solution, antennae movement was

significantly increased ( $P=0.037$ ), and higher results were seen in locomotion ( $P=0.053$ ) and general feeding movements ( $P=0.063$ ). When marron responses were examined in the presence of silver perch held in bags no statistically significant findings were apparent, however shelter, locomotion, feeding, antennule and antennae movements all increased in response to both test solutions, with the one exception previously stated. No significant changes in posture, cleaning or climbing were recorded in treatment groups (Appendix B - Table III).

#### 5.1.6.4 Comparison between test solutions and monoculture, empty bag and bagged fish treatments

No significant differences ( $P>0.05$ ) were found in behavioural responses of marron between test solutions (Table 5.1).

**Table 5.1** Magnitude of change between control water and test solutions in reaction time (s), behaviour and body posture (%).

	monoculture	marron + empty bag	Marron + fish
<b>Reaction Time</b>	0.9110	0.9830	2.2400
<b>In Shelter</b>	1.3420	Data sets identical	0.4470
<b>Locomotion</b>	1.1530	1.1530	0.8450
<b>General feeding movements</b>	0.5930	0.5080	0.4230
<b>Antennule flicking</b>	0.5600	0.5600	1.2600
<b>Antennae movement</b>	1.1830	0.1050	0.9800
<b>Lowered posture</b>	Data sets identical	1.0000	1.0000
<b>Intermediate posture</b>	0.9340	0.4050	1.2140
<b>Raised posture</b>	1.1530	0.1350	0.4050
<b>Cleaning</b>	0.5350	0.3780	0.1050
<b>Climbing</b>	0.9440	0.2720	0.4050

Comparisons among test odours (FOOD, F+PCW = food + silver perch culture water) within groups, used Kruskal-Wallis test.

No statistical differences were seen in responses of marron to either test solution ( $P>0.05$ ) between treatment groups (Table 5.2).

**Table 5.2** Magnitude of change between control water and test solutions in reaction time (s), behaviour and body posture (%)

	<b>FOOD</b>	<b>F + PCW</b>
<b>Reaction time</b>	1.4970	3.0040
<b>In shelter</b>	0.4480	2.5570
<b>Locomotion</b>	2.9100	0.5020
<b>General feeding movement</b>	0.9440	0.3990
<b>Antennule flicking</b>	4.4950	0.4380
<b>Antennae movement</b>	0.6670	0.9390
<b>Lowered posture</b>	Data sets identical	2.8750
<b>Intermediate posture</b>	0.2250	2.7820
<b>Raised posture</b>	0.2680	1.2760
<b>Cleaning</b>	2.8380	1.4650
<b>Climbing</b>	0.3210	0.3440

Comparisons between visual stimuli (MM = marron monoculture, MB = Marron and empty bag, MF = marron and fish in bag) for each test odour (FOOD, F+PCW = food + silver perch culture water), used Wilcoxon Signed Ranks Test (X2, df 2). \* P<0.05, \*\*P<0.01

A summary of results for this trial is provided in Appendix B, Table IV.

## 5.1.7 Discussion

### 5.1.7.1 Responses of marron to visual cues associated with silver perch held in bags

The behaviour of marron held in aquaria containing silver perch in bags (T2) showed a number of significant variations compared with marron in treatments without silver perch (T1 and T3). Marron displayed significant increases in antennule flicking and antennae movements, choice of low posture and increased climbing when exposed to cues associated with bagged silver perch, compared to marron in treatments without silver perch (T1 and T3). The behaviour of marron in T2 is consistent with anti-predator responses. Hazlett (1990) and Gherardi et al. (2002) showed that in freshwater crayfish, increased use of antennules is seen with detection of environmental signals pertaining to threat. Lowered posture has previously been correlated to responses to predatory cues in the crayfish *Orconectes virilis* (Hazlett and Schoolmaster 1998), and escape responses (Lawrence and Smith 1989, Mathias and Smith 1993b, Herbaholtz et al. 2004) or avoidance of high risk areas (Brown et al. 1995), such as climbing, is a documented predator avoidance strategy.

Visual detection of threat is commonly used in aquatic environments (Brown et al. 1997, Watson 1999), controlling a range of anti-predator behaviours in many species (Herrnkind 1968, 1972, 1983), including decapods (Bollens and Frost 1989, Diaz et al. 1999, Hazlett and McLay 1999, Woodley and Peterson 2003). Visual cues are often the primary source of information in environments where vision is high, such as in systems of low turbidity (Watson 1999) providing early accurate information (Culp et al. 1991, Brown and Godin 1999, Hazlett and McLay 2000, Bouwma and Hazlett 2001). The evolution of marron in clear-water rivers and streams in the south-west of Western Australia supports these findings, where visual location of potential threats may be the most effective early warning system. As predators of marron are limited (Morrissy 1997, FWA 1999, Allen et al 2002) and generally confined to terrestrial species (Rowland 1995b), such as birds and water rats, the use of chemical triggers is arguably much less important, and may explain the lack of avoidance responses in the previous chapter.

Although marron behaviour was altered when held with bagged silver perch, the responses to food solutions showed no variations with other treatments. As predator avoidance responses are often characterised by feeding inhibition (Rahel and Stein 1988, Brown et al. 1999, Bouwma and Hazlett 2001), this suggests that marron did not associate cues from fish in bags with high or immediate threat. Observed behavioural changes to visual cues may simply be related to curiosity. Another explanation is that responses of marron were not detected through analysis of behaviour. As in Chapter 4, crayfish may increase alertness, or readiness for flight or fight, which may not be detected as a significant change in observed behaviours (Hazlett 1994a, Listerman et al. 2000, Li et al. 2000). Crayfish have been shown to continue feeding behaviour following identification of risk (Hazlett 1999, 2000b), presumably relying on rapid avoidance responses, such as tail-flips, to escape attack.

#### **5.1.7.2 Chemosensory detection of food odour**

Chemical communication is a well-known and widespread ecological phenomenon mediating a variety of interactions between organisms and their environment (e.g. Maynard Smith 1993, Andrew and Savage 2000, Grasso and Basil 2002). Recognition of chemical cues associated with potential food sources has been demonstrated in many decapod species (Tierney and Atema 1988, Barnes 1997, Giri and Dunham 1999, Hazlett and McLay 2000, Moore and Grills 1999, Hazlett 2000a, Grasso and Basil 2002) and associated with typical behavioural changes including increased searching-locomotion (Tierney and Atema 1988, Giri and Dunham 1999, Hazlett and McLay 2000, Grasso and Basil 2002), feeding behaviour (Hazlett 1999, 2000b, Gherardi et al. 2002, Hazlett 1971) and use of chemosensory devices (Tierney and Atema 1988, Hazlett 1990, Grasso and Basil 2002). The ability of marron to detect and recognise cues relating to food was apparent in findings in this study, supporting observations made in Chapter 4. Marron in all treatment groups responded positively to cues in both test solutions examined, with significantly faster reaction times and significant increases in feeding activity, locomotion, antennule flicking and antennae movement, compared to control solutions. Antennules and Antennae are the primary device used by freshwater crayfish in detecting chemical cues (Hazlett 1971, Tierney and Atema 1988, Grasso and Basil 2002, Hazlett et al. 2002).

### 5.1.7.3 Chemosensory detection of fish odour

Chemical information pertaining to predation risk is commonly associated with anti-predator behaviour by the receiver (Kiesecker et al. 1996, Kats and Dill 1998, Wisenden and Millard 2001, Diaz et al. 2001, Head et al. 2002). Typically, behavioural responses to predatory odours include:

- inhibited food-related responses (Hazlett 1994a, Brown et al. 1999, Hazlett and McLay 2000, Bouwma and Hazlett 2001);
- reduced locomotion or other movements (Hazlett 1997, Persons et al. 2002, Hazlett 2000a, Mirza et al. 2001);
- avoidance of risk areas (Brown et al. 1995, Persons et al. 2002), such as tail-flipping (Bethe 1897, Huxley 1880, Wiersma 1961);
- increased shelter (Appelberg et al. 1993, Baker and Montgomery 2001).

For each of the typical kairomone-induced avoidance behaviours listed above, the opposite reaction was displayed by marron in this trial in response to the F+PCW test solution, and no significant variation in responses between solutions (Food and F+PCW) was found.

The lack of variation between the behaviour of marron responding to food solution and responses to F+PCW solution, suggests that marron do not detect fish cues in silver perch culture water. Another explanation is that marron detect chemical cues from silver perch, but do not associate them with potential risk, or that risk level was not high enough to warrant behavioural change. In many species, recognition of threat from novel predators requires association of predatory cues with known risk cues, such as alarm odours (Mathis et al. 1996), and in some cases avoidance behaviour is only triggered following physical interaction with a predator (Chivers and Smith 1995, Diaz et al. 2001).

### 5.1.7.4 Cumulative effects from the combination of visual and chemical cues

Although marron behaviour was altered by cues associated with silver perch in bags, the addition of chemical cues in perch culture water did not result in any cumulative effects. That is, marron exposed to both visual and chemical signals from silver perch showed no

variation in behaviour compared with treatments containing no silver perch. In fact, marron in all treatments, for both test solutions, increased feeding behaviour, locomotion, and use of sensory systems (antennules and antennae). These behaviours are indicative of food-related responses (Hazlett 1971, Tierney and Atema 1988, Hazlett 1990, Grasso and Basil 2002), not avoidance Brown et al. 1999, Hazlett 2000a, Hazlett and McLay 2000, Mirza et al. 2001). This demonstrates that foraging holds a higher hierarchical standing for marron than behavioural responses to both silver perch odour and visual cues from bagged silver perch.

### 5.1.8 Conclusions

Results from this study support findings in the previous chapter which demonstrate the ability of marron to detect and respond to cues in the test solutions provided, however as no significant differences were found between test solutions, it is still unknown whether detection of chemical cues from silver perch, found in their culture water is made. The questions remaining are whether marron detect allelochemicals from silver perch and do not associate the cues with risk (which if true may mean segregation is required, e.g. cage culture) - or do not interpret cues as a high enough risk to warrant a change in behaviour (which would further question what level of risk is required produce a reaction in marron and would avoidance strategies be effective). The most important finding of this trial was the apparent avoidance responses displayed by marron when exposed to visual cues from silver perch held in bags.

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**The null hypothesis  $H_0$  (5.1)** was accepted, as although marron detected visual cues from silver perch in bags, whether they could discern chemical cues associated with silver perch in the F+PCW solution was unclear

**The null hypothesis  $H_0$  (5.2)** was rejected as although marron did not demonstrate avoidance responses to chemical cues from silver perch (as stated by  $H_1$ ), responses were seen where visual cues were presented (not stated by  $H_1$ ).



### 5.1.9 Limitations and recommendations

Examinations of the complexity of interactions between marron and fish were extended in this study, through incorporation of visual cues associated with fish, alone and in combination with chemical cues. Future studies need to further extend investigations into the ecological basis of interaction, incorporating additional sources of information in an arena that includes competition and natural behaviours of fish. To do this a number of modifications to experimental design need to be examined, these include:

#### **Larger systems with less restriction of predator behaviour**

Predator behaviour has been shown to effect prey response (Dugatkin and Godin 1992, Murphy and Pitcher 1997, Brown et al. 2000). The trial reported in this chapter may have been limited by behaviour of bagged fish, in so far as silver perch may have been anxious due to their environment and not concerned with predation of marron. Recommendations would be to trial responses in larger systems, where fish could be held in separate compartments to crayfish, and therefore move more freely.

#### **Increasing need for crayfish to respond to potential threat**

As crayfish have at their disposal the ability to rapidly respond to predation through tail-flipping, there may have been reduced need to demonstrate avoidance responses, as close refuge was provided allowing escape in the face of imminent danger. A way to increase the need for early avoidance strategies could be the addition of competition, where detection of threat in limited refuge may result in early competition for refuge. Future recommendations include the use of multiple animals with limited shelter.

#### **Increased duration of risk to crayfish**

Lima and Bednekoff (1999), noted that many laboratory experiments stimulate a scenario with extended periods of low risk and only occasional pulses of danger. That is in most cases, investigators hold prey without predators and study how prey respond when predators are added, as was the case in this trial. This protocol, chosen for practical purposes and not for a fit to reality, might incorrectly estimate the effects of risk in marron-perch polysystems where marron should experience more sustained predatory pressure from silver perch. Observation of crayfish behaviour over extended periods of sustained risk should enable better prediction of production outcomes in polyculture systems with silver perch. As behaviour is controlled by both the endocrine system, and the nervous system (Hazlett 1995), it makes sense that responses should be examined both as an initial reaction, and changes over time.

## **5.2 The effect of visual and chemical cues from silver perch on marron behaviour under cohabitation with the yabby, a congeneric crayfish**

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Previous trials have shown a lack of avoidance by marron in response to chemical and visual cues from a potential predator, especially when faced with food-derived cues. One explanation for these results is that marron increase alert status in response to potential threat, maintaining feeding and responding only when attack is imminent. One factor that may trigger avoidance responses in marron is competition, in that individuals competing for resources such as shelter may force marron to respond to potential threat more immediately. Competitive interactions and habitat use in aquatic systems are largely a function of predation risk (Miner and Stein 1996). The addition of a sympatric crayfish that is known to respond to exteroceptive cues from potential predators, such as the yabby (Gherardi et al. 2002), may also produce alarm responses detected by marron. Alarm cues have been shown to produce responses in normally non-reactive animals (Gazdewich and Chivers 2002). In a previous study, comparing responses of marron and yabbies, it was shown that both species will react to odour from each other (Gherardi et al. 2002). This may be due to co-inhabiting systems for the past 70 years (Lawrence and Morrissy 2000), phylogenetic inertia (Hazlett 1990), or related to similar methods of chemical detection (Rittschof 1993, Hazlett 1994b).

In this trial (T5:2), one marron and one yabby were held together in a 250L aquarium, with silver perch held in the same system and separated by partitions allowing or preventing the transfer of visual and or chemical cues from fish. Large experimental systems were used in this trial, following suggestions that behaviour of fish and crayfish may have been limited by the size of aquaria used in previous studies. This trial aimed to determine if behavioural responses of marron to silver perch cues were influenced by competitive interaction, or alarm responses, of yabbies in response to cues from silver perch. Flow between compartments containing crayfish and those containing silver perch was constant, therefore any allelochemicals released by silver perch would be present for the duration of analysis, where as in previous trials solutions were introduced once at the beginning of each observation period. Chemical signals in aquatic environments have been shown to quickly decay (Lass 2001, Mesquita et al. 2003), which may have affected responses in previous trials.

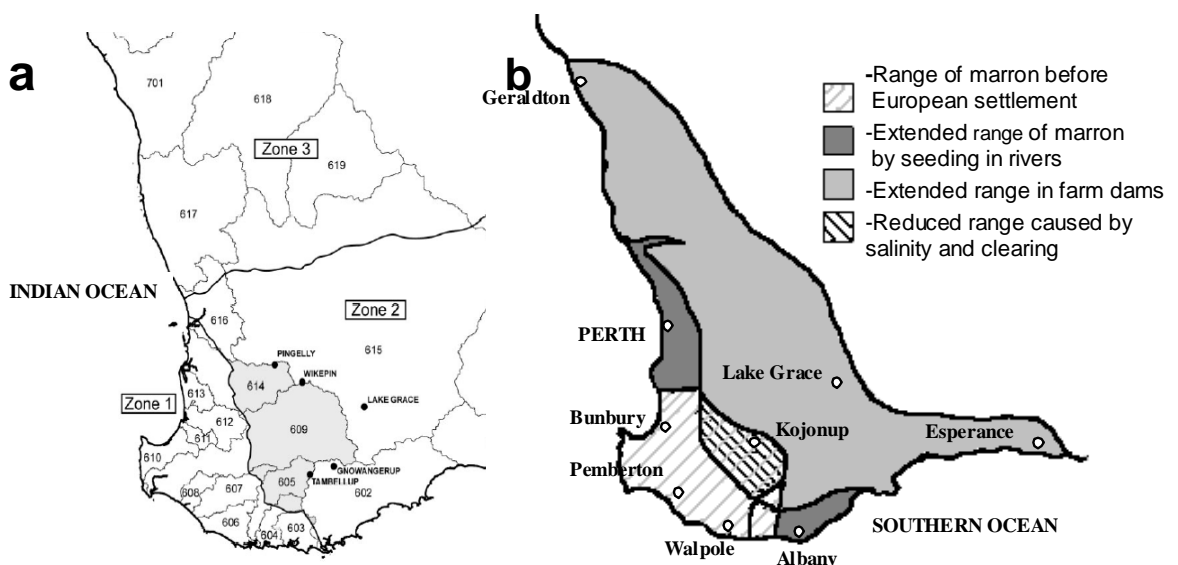
Behavioural observations were extended in this trial to view crayfish behaviour over longer periods than previous trials. This incorporated observation of night-time behaviour, which is of particular importance as marron are primarily nocturnal (Morrissy and Caputi 1981).

.The null hypothesis for T5:2 was:

$H_0$ : Marron will not display avoidance behaviour in response to cues presented from silver perch, regardless of cohabitation with yabbies. 5.3

### 5.2.1 Background

The invasive yabby (*Cherax albidus*) affects indigenous marron (*Cherax tenuimanus*) populations in Western Australia by its highly competitive behaviour (Gherardi et al. 2002, Lynas et al. 2004). While, past research has shown that cohabitation of these species usually results in displacement of marron (Height and Whisson 2004), a recent study of Lake Moyanup in Western Australia reported marron re-establishing itself alongside a resident yabby population (Whisson 2003). A contributing factor to this finding could be the presence of crayfish predators within the system, a factor described by Pöckl and Pekny (2002) as strongly influencing displacement of crayfish species. Stimuli from potential predators like non-native silver perch (*B. bidyanus*), invoke predator-avoidance responses increasing competition within and between prey species (Werner 1991, Kotler et al. 1994).



**Figure 5.4** Distribution of yabbies (a) and marron (b) in the south-west of Western Australia. (a) Zones 2/3 are permitted culture zones for yabbies (FWA 2002b). (b) Natural and extended habitat of marron (FWA 1999).

In aquatic environments, accurately assessing predation risk will ultimately determine the success of species like freshwater crayfish (Pfeiffer 1977, Brown and Godin 1999, Delgado et al. 2002). Understanding the nature of this recognition then becomes important in explaining the relative status of component species within multi-species systems. There are several sensory modalities utilised in recognising predators in aquatic environments, including visual cues (Brown et al. 1997, Hazlett and McLay 2000), tactile (Culp et al. 1991), aural (Rekwot et al. 2001, Vester et al. 2004), and chemical (Kiesecker et al. 1996, Brown and Godin 1999, Mirza et al. 2001). Chemical cues are particularly important to nocturnal species like freshwater crayfish, and include scents released by predators (Chivers et al. 1996b, Hazlett and Schoolmaster 1998, Kats and Dill 1998) and odours given off by prey damaged during predation (Howe and Scheikh 1975, Hazlett 1994a, Chivers and Smith 1998).

Recent studies on freshwater crayfish species residing in south-west Western Australia have focused on chemo-detection abilities and avoidance strategies in response to conspecific alarm odours and chemical cues released from potential predators (Gherardi et al. 2002, Height and Whisson 2004). Results indicate that individual yabbies display a high level of behavioural plasticity, while marron has demonstrated behavioural modifications to chemical cues in food odour (Gherardi et al. 2002, Height and Whisson 2004), indicating a potentially higher level of predation risk from non-indigenous species. The aim of T5:2 was to observe responses of marron and yabbies to multiple cues (visual and/or chemical) from non-indigenous silver perch - a potential predator of both crayfish species (Whisson 2000, Prokop 2002). The direct influence of these cues on intraspecific interactions and predator avoidance behaviour was examined under limited shelter conditions to promote competition.

## **5.2.2 Research design**

### **5.2.2.1 Experimental systems and stock**

Marron, *C. tenuimanus* (89.4±6.2g) and yabbies, *C. albidus* (63.9±6.2g) of comparable physical body and claw sizes were reared in monoculture ponds and transferred to holding tanks at the South-West Aquaculture and Environment Centre in Collie, Western Australia (33°S, 115°E). Marron were sourced from Pemberton (Forest Fresh

Marron Pty Ltd), and yabbies from Mulataga Aquaculture, Perth (Mulataga Pty Ltd). Glass observation tanks (250L, Plate 5.3) were partitioned and one compartment stocked with a single crayfish of each species (both sexes) and a single piece of shelter (PVC pipe - length 160 mm x diameter 75 mm). Partitions were either permeated or solid - to allow or prevent the exchange of chemical cues from a single silver perch (323.6±82.5g) placed in the adjacent compartment. Dye tests were carried out on all tanks to confirm water exchange was, or was not, occurring between compartments, as designed. Where exchange was permitted, complete mixing of water throughout the aquarium was observed in approximately 30 s (Dye test, Appendix E). Partitions were clear or darkened to manipulate visual signals from fish. Five treatments were tested (Table 5.3, Plate 5.3) and replicated in five homogeneous tanks. One male and one female crayfish were stocked in four of the five treatments, with the final treatment examining single sex interactions. In a replicate trial on the following day the sex of crayfish introduced to aquaria was reversed from day 1.

**Table 5.3** Experimental design showing treatment allocation of cues from silver perch

Treatment	Central Partition Design	Water Flow	Silver Perch	Stimuli Tested
1: Control	Plastic mesh (10 mm)	YES	NO	Crayfish only
2: Visual	Plastic mesh / Clear Glass	NO	YES	Visual cues
3: Chemical	Plastic mesh / Opaque Glass	YES	YES	Chemical cues
4: Vis/Chem	Plastic mesh	YES	YES	Visual/Chemical cues
5: Single Sex	Plastic mesh	YES	YES	Visual/Chemical single sex

T1 - Control (T2 = with fish)

T3 - Chemical cues

T4/T5 - Visual & Chemical cues



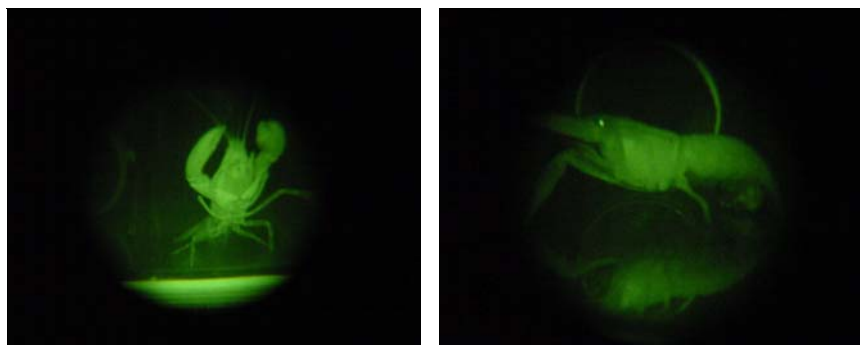
**Plate 5.3** Visual (left), chemical (centre) and visual-chemical (right) treatment systems

Aquaria were filled with 230L water at 20.1±0.08°C (Appendix A). Each aquarium was aerated using two Aquaclear 150 filter-pumps (without media), one in each

compartment. All aquaria were visually isolated to minimise disturbances to crayfish. Silver perch were not fed for three days prior to testing, and marron for 1 day prior, with both species not fed over the two-day trial period. As with all studies examining response to chemical cues, chlorinated water was cured for use in experimental systems to prevent introduction of external chemical information.

### 5.2.2.2 Experimental procedures

Behavioural observations were carried out in three time periods; 1. Following introduction of crayfish to aquaria, 2. Following introduction of silver perch to aquaria containing crayfish, and 3. Nocturnal behaviour of crayfish recorded after silver perch had been in systems for 4 h. Marron and yabbies were introduced simultaneously to fishless aquaria between 0900 and 1130 h, where behavioural observation were conducted immediately after the addition of marron and yabbies to each system. A settlement time of 4 h was provided to allow acclimatisation of crayfish to aquaria prior to the introduction of fish. Night time behaviour of crayfish was observed using night vision goggles (Plate 5.4), between 1900 and 2100 h.



**Plate 5.4** Top: night-vision goggles used in nocturnal observations. Bottom: yabby and marron observed through night goggles

Behavioural reactions to treatments were recorded using two separate observation protocols, a '5-minute test' and a '2 hour test'. These tests examined different aspects of crayfish behaviour prior to, and following, fish introduction.

### **5.2.2.3 5-minute test**

The 5-minute test involved recording crayfish behaviour every 15s over a 5 min. period, following protocols outlined in Section 4.1.5. The 5-minute test was carried out in time period 1, following simultaneous introduction of crayfish to aquaria, and in time period 2, following the introduction of silver perch to systems. The 5-minute test was not carried out in time period 3 as observation of minute details, such as antennule flicking, was difficult to accurately discern using night vision goggles.

In addition to the standard behaviour protocols described in Section 4.1.5, analysis was extended to incorporate interaction behaviour between the crayfish. The additional records were: number of approaches, whether interaction was aggressive or non-aggressive (NAI), and which species was the aggressor when conflicts were observed.

### **5.2.2.4 2-hour test**

The 2-hour test was a simplified behavioural analysis carried out on all systems for 30s every 15 min., over 2 h. The 2-hour test was conducted in each of the three time periods:

- 1) following introduction of crayfish,
- 2) following introduction of silver perch,
- 3) 4 h after introduction of silver perch - to observe nocturnal behaviour.

Observations made for each tank were; tank position of marron, yabby and silver perch (plotted on a plan-view of the aquarium to show relative position of each species); shelter use; number of conflicts (and dominant species); number of non-aggressive interactions (NAI); shelter evictions and climbing on tank divider (screen).

### 5.2.2.5 Water quality

Total ammonia (ppm), salinity (ppt), conductivity (mS), pH, nitrite (ppm), nitrate (ppm) and temperature (°C) were recorded daily. All levels remained within optimum ranges for test animals with no significant variation between experimental systems (Appendix A).

### 5.2.2.6 Statistical analysis

The percentage time spent in each behaviour over the 5-minute and 2-hour tests was calculated then arcsine transformed prior to analysis (Zar 1984). Analysis of variance (ANOVA) between treatment means for each behaviour, for both species, was conducted and *post hoc* significance ( $P < 0.05$ ) tested (Selvanathan et al. 2000). Where variances were equal significance was determined by Tukey's HSD (reported), Bonferroni and Scheffe's F-Test, where equality was not assumed Dunnett's T3 (reported) and Tamhane were examined (Selvanathan et al. 2000). In the first time period, prior to introduction of silver perch, the analysis described above was used to compare background differences between systems and blocks. Comparisons between species responses to treatments, and between sexes and days were made using independent t-tests (Selvanathan et al. 2000).

Comparisons were also made between crayfish behaviours recorded with the 5-minute test in the first time period and behaviours observed in the control treatment in the second time period. This was done using independent t-tests for each crayfish species to determine if general controlled behaviour was altered over time (Selvanathan et al. 2000).

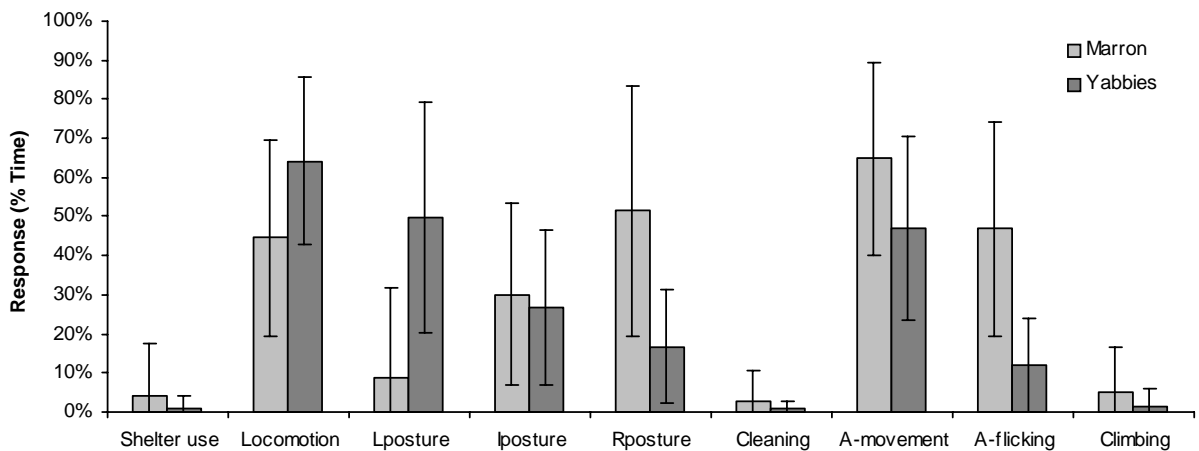
\* Behaviour of marron and yabbies following introduction to aquaria was compared between aquaria, with no significant variations found ( $P > 0.1$ ). This was done to ensure that variations in screen design between compartments had no influence on crayfish behaviour prior to introduction of silver perch in the second time period.



### 5.2.3 Results

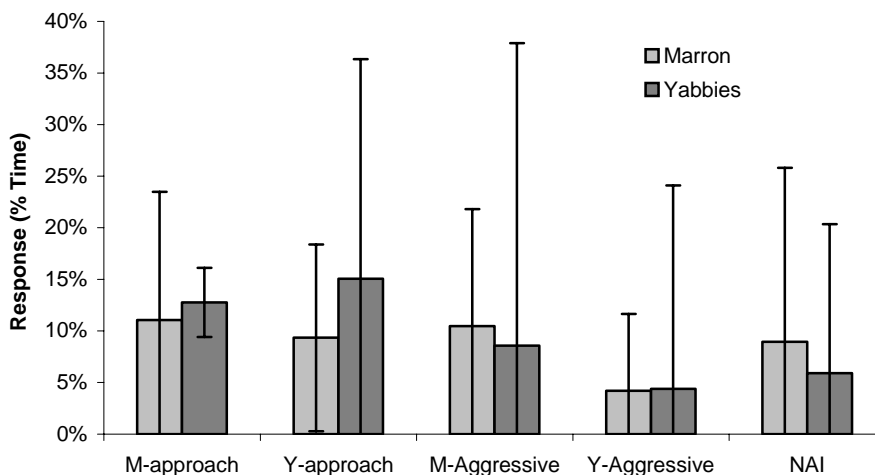
#### 5.2.3.1 5-minute test: crayfish behaviour following introduction to aquaria

The behaviours of marron and yabbies, recorded following introduction to experimental systems, showed no significant variations between species in both individual behaviour (Figure 5.5) or interaction behaviour (Figure 5.6).



**Figure 5.5** Behavioural responses of marron and yabbies following introduction to aquariums

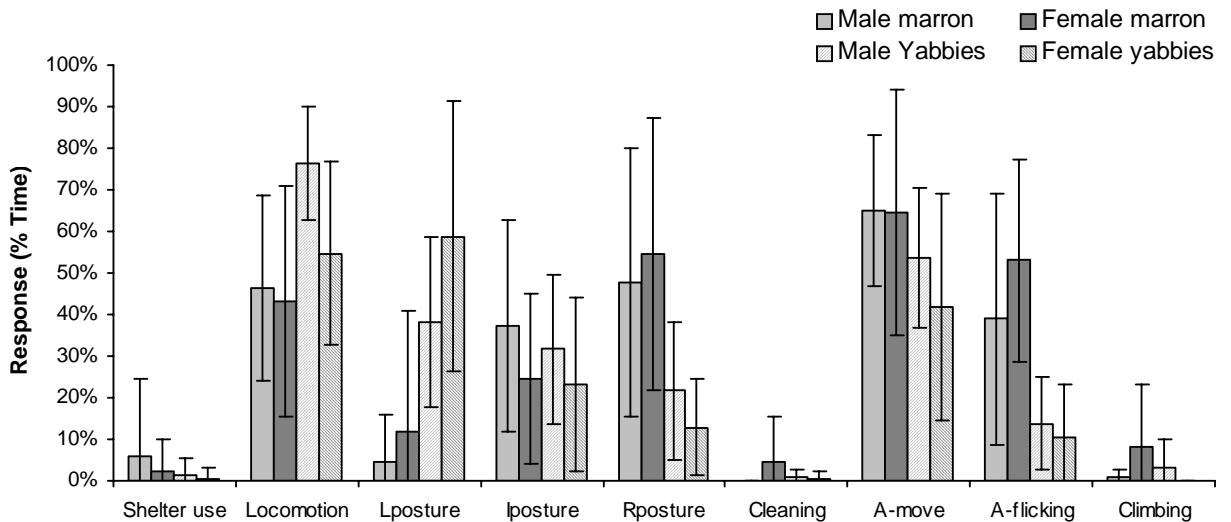
Data is time spent in each behaviour ( $\pm$  standard error). Lposture = low posture, Iposture = intermediate posture, Rposture = raised posture, A-movement = antennae, A-flicking = antennules.



**Figure 5.6** Interaction responses of marron and yabbies following introduction to aquariums

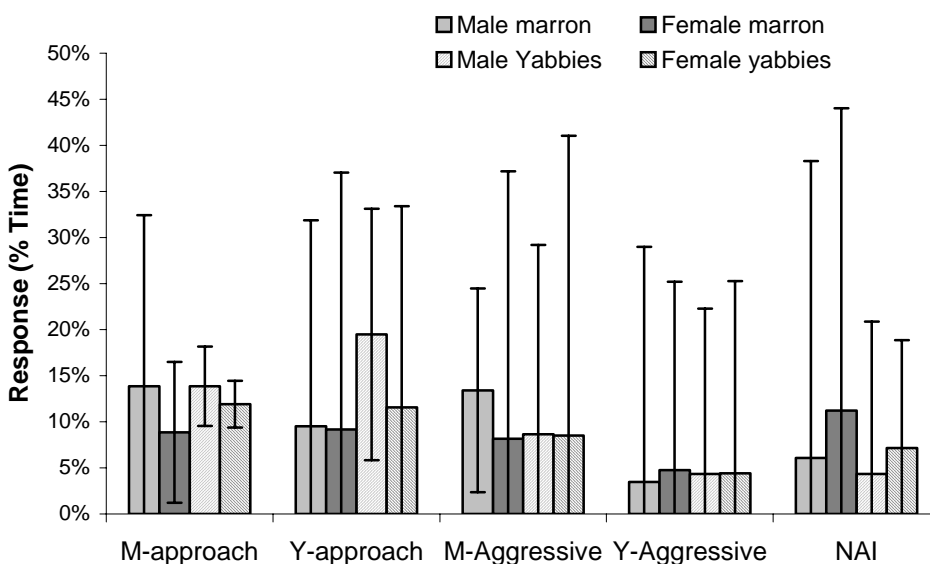
Data is time spent in each behaviour ( $\pm$  standard error). M = marron, Y = yabby, NAI = non-aggressive interactions

No significant variations between behaviour of males and females, for both species, were found following introduction to aquariums, in individual behaviour (Figure 5.7) or interaction behaviour (Figure 5.8).



**Figure 5.7** Behavioural responses of male and female marron and yabbies following introduction to aquariums

Data is time spent in each behaviour ( $\pm$  standard error). Lposture = low posture, lposture = intermediate posture, Rposture = raised posture, A-movement = antennae, A-flicking = antennules



**Figure 5.8** Interaction responses of male and female marron and yabbies following introduction to aquariums

Data is time spent in each behaviour ( $\pm$  standard error). M = marron, Y = yabby, NAI = non-aggressive interactions

High standard errors in all data (Figure 5.5-5.8) signify large variations in behaviour between individuals within each species, as was seen in T4:1 and T5:1.

### **5.2.3.2 5-minute test: comparing control responses of crayfish in time period 1 and 2**

Comparisons between control behaviours of marron and yabbies recorded immediately following introduction, compared with observations made within the control (no fish) treatment following introduction of silver perch revealed a number of significant changes. These changes indicate alterations in general and interaction behaviours after 4 h of cohabitation (being the time lapsed between time period 1 and time period 2). The behavioural differences between the two time periods were a significantly higher time spent in locomotion and increased use of antennae for both species ( $P < 0.001$ ) recorded following introduction of crayfish to fishless aquaria, than compared to 4 hours later. In addition, yabbies approached marron significantly more in the first time period ( $P < 0.01$ ), resulting in significantly higher non-aggressive interactions overall ( $P < 0.001$ ). Marron also chose raised posture more often in the first time period ( $P < 0.01$ ) and lowered posture in the second time period ( $P < 0.05$ ).

No differences between sex in either species occurred between the control behaviours recorded in either time period using the 5-minute test ( $P > 0.1$ ).

### **5.2.3.3 5-minute test: Response of crayfish to silver perch cues**

Both marron and yabbies displayed significantly faster reaction times when presented with visual, chemical and visual/chemical cues from silver perch ( $P < 0.05$ ), compared to control treatment responses (Figure 5.9, Appendix B Table Va/b).

#### **Marron responses to silver perch cues**

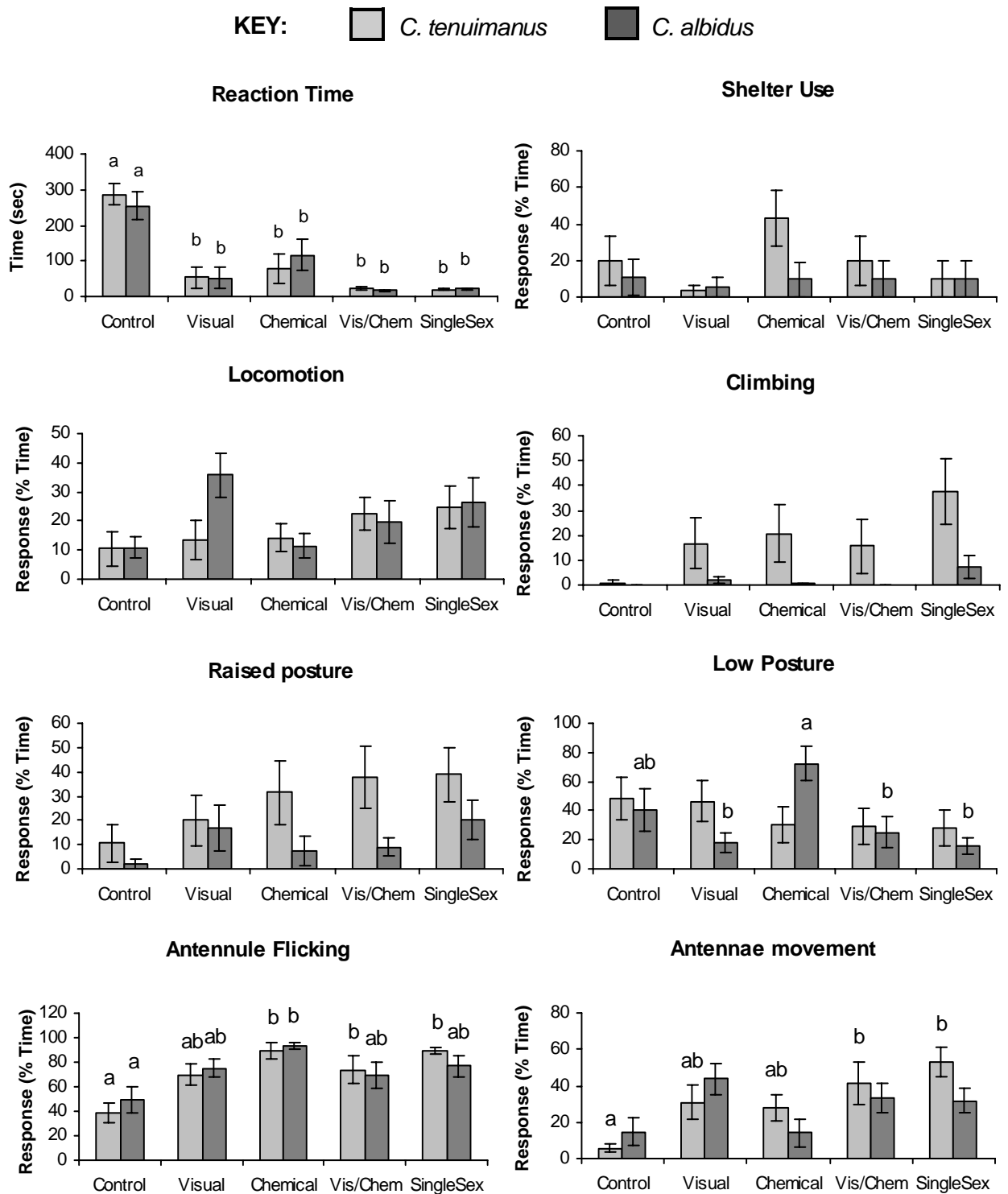
Use of antennae and antennules increased in response to all cues from silver perch tested, compared to control (Figure 5.9, Appendix B Table Va/b), with significant increases between control and visual + chemical treatments (T4 and T5) for both antennae and antennules, and also between control and chemical cues alone for antennule flicking ( $P < 0.05$ ).

### **Yabby responses to silver perch cues**

In responses to silver perch cues, yabbies demonstrated similar reactions as were seen in marron (Figure 5.9), with increased use of antennules in response to all treatments compared to control, however only significant ( $P < 0.05$ ) between control responses and reaction to chemical cues alone. Antennae movement in yabbies was also increased when responding to fish cues (Figure 5.9), however no significant differences were apparent ( $P > 0.05$ ), and little difference existed between response to control *versus* chemical cues alone. Yabbies chose low posture significantly more in response to chemical cues than compared to all other treatments ( $P < 0.05$ ) (Figure 5.9).

### **General responses to silver perch cues**

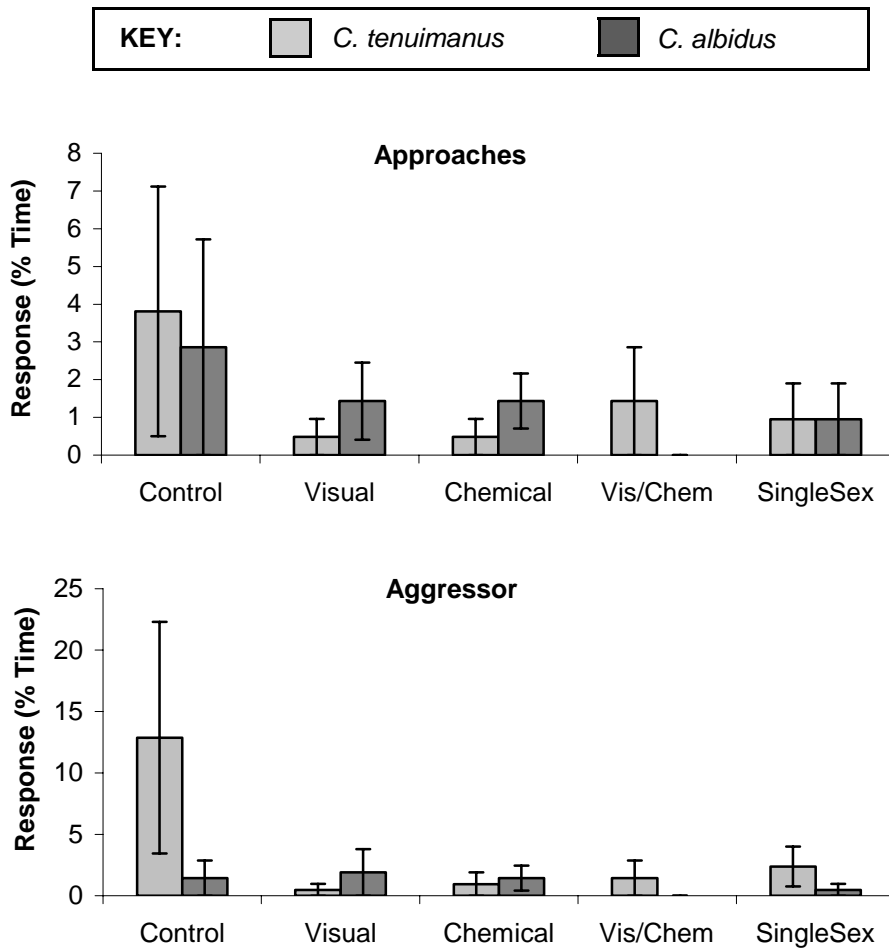
No significant differences were seen in response of either crayfish to treatments in shelter usage, locomotion, climbing, feeding, cleaning, raised or intermediate posture (Figure 5.9), however a number of general trends were apparent: Shelter was rarely occupied by yabbies across all systems, with similar results seen in marron. However, marron utilised sheltered more in the chemical treatment than other groups (Figure 5.9). The amount of locomotion recorded in both species generally increased where combined cues were tested (T4 and T5), although a marked increase was recorded in yabbies responding to visual cues alone. Climbing appeared to increase in marron in response to all fish cues tested, with little climbing observed in control (Figure 5.9). Yabbies were rarely observed climbing across all treatments. Finally, raised posture was most common in marron in the chemical, and chemical and visual treatments (T4 and T5) compared to response in control and visual treatment groups (Figure 5.9). Yabbies rarely chose raised posture, and showed little difference between groups (Figure 5.9). Cleaning and feeding behaviours were not included in Figure 5.9 as were rarely recorded and showed no significant differences between treatments ( $P > 0.1$ ).



**Figure 5.9** Behaviours of crayfish (marron and yabbies) in response to a range of exteroceptive cues from silver perch.

Data is mean time spent in each behaviour for crayfish within each treatment. Where letters are different across treatments for each species a significant difference was found.

In the interaction behaviours recorded for both species, no significant variations were seen across treatment groups for either species (Figure 5.10).



**Figure 5.10** Interaction responses displayed by marron and yabbies within each treatment. Data is the mean ( $\pm$  SE) recorded for all individuals of each species in each treatment over trial period.

#### 5.2.3.4 5-minute test (time period 2): comparison of responses to silver perch cues between species

The general behaviour and interaction responses displayed by crayfish in response to silver perch cues were characterised by increased locomotion ( $P < 0.05$ ) by yabbies, and increased use of intermediate posture by marron ( $P < 0.01$ ) when visual perch cues were presented, and by a lowered posture ( $P < 0.05$ ) in yabbies in response to chemical cues (Table 5.4).

**Table 5.4** Variation in response of marron and yabbies to cues from silver perch.

Behaviours	TREATMENTS									
	Control		Visual		Chemical		Vis/Chem		Single Sex V/C	
	p value		p value		p value		p value		p value	
Reaction to fish	0.529	M>Y	0.943	M>Y	0.533	Y>M	0.202	M>Y	0.714	Y>M
Shelter	0.581	M>Y	0.749	Y>M	0.086	M>Y	0.556	M>Y	1.000	M=Y
Locomotion	0.989	Y>M	<b>0.047</b>	<b>Y&gt;M</b>	0.654	M>Y	0.810	M>Y	0.885	Y>M
Low Posture	0.766	M>Y	0.071	M>Y	<b>0.045</b>	<b>Y&gt;M</b>	0.808	M>Y	0.281	M>Y
Intermediate posture	0.109	Y>M	<b>0.007</b>	<b>M&gt;Y</b>	0.401	Y>M	0.189	Y>M	0.142	Y>M
Raised Posture	0.281	M>Y	0.760	M>Y	0.123	M>Y	0.064	M>Y	0.180	M>Y
Cleaning	0.905	Y>M	0.855	M>Y	0.343	M>Y	0.129	M>Y	0.365	M>Y
Antennae Movement	0.280	Y>M	0.339	Y>M	0.278	M>Y	0.414	M>Y	0.056	M>Y
Antennule Flicking	0.495	Y>M	0.648	Y>M	0.591	Y>M	0.546	M>Y	0.362	M>Y
Climbing	0.343	M>Y	0.221	M>Y	0.144	M>Y	0.211	M>Y	0.061	M>Y
Approach	0.825	M>Y	0.407	Y>M	0.290	Y>M	0.343	M>Y	1.000	M=Y
Aggression	0.265	M>Y	0.485	Y>M	0.736	Y>M	0.343	M>Y	0.289	M>Y
NAI	1.000	M=Y	1.000	M=Y	0.320	Y>M	0.825	M>Y	0.207	M>Y

Subscript 'M' (marron) or 'Y' (yabby) denotes the dominant species.

Although not statistically significant ( $P>0.05$ ), marron utilised shelter more in response to chemical cues ( $P=0.06$ ); climbed more and used antennae more in the single sex treatment ( $P=0.061$ ,  $P=0.056$ , respectively); displayed raised posture more in response to visual + chemical cues (T4) ( $P=0.064$ ); and chose lower posture in response to visual cues ( $P=0.071$ ) than yabbies.

### 5.2.3.5 Comparisons between sexes and days

The responses of marron and yabbies recorded between the two trial days, between time periods, and within each treatment, showed no significant variation ( $P>0.1$ ). Comparison between males and females of both species for each treatment and time period also showed no significant variations ( $P>0.05$ ), with one exception, female marron showed increased locomotion ( $18.1 \pm 8.09\%$  of time) compared to males ( $3.81 \pm 1.7\%$  of time) in the control group in the second time period ( $P=0.036$ ). This difference did not appear to affect comparison between treatments or species.

### 5.2.3.6 2-hour test: behaviour of crayfish across all time periods

Analysis of interspecific aggression between both crayfish species (encounters and subsequent fights) showed a number of significant outcomes. Aggressive encounters were more frequent following introduction of crayfish to fishless systems compared to interactions following introduction of fish ( $P < 0.001$ ) and at night ( $P < 0.01$ ) (Table 5.5). Marron were the dominant species following aggressive encounters in all three time periods at  $P < 0.01$ ,  $P < 0.05$  and  $P < 0.001$ , respectively. In total, fifty-four fights were recorded in the 2h following crayfish introduction, 15 following addition of fish and 22 at night (Table 5.5). For these three tests, marron was the aggressor or dominant crayfish in 88%, 93% and 95% of conflicts, respectively. Non-aggressive interactions (NAI) (Table 5.5) were also highest in the period following introduction of crayfish (30 records), and rarely seen at night (4 records) Comparison of all interactions over the three time periods showed that 64.3% of encounters were aggressive when only crayfish were present, 48.4% following introduction of silver perch and almost 85% at night.

No significant differences were seen between interactions recorded between blocks or between treatments in each of the time periods. The only remarkable finding between treatments was seen following introduction of silver perch, where no encounters were recorded when crayfish were exposed to chemical cues alone.



**Table 5.5** Variation in individual and interaction responses of crayfish to exteroceptive cues from silver perch.

		Aggressive encounters			NAI	% time in shelter		Shelter eviction	Screen (M:Y)
		Dominant species		No.		M	Y		
		M	Y		M			Y	
<b>TEST PERIOD 1: Initial crayfish interaction</b>					<b>Recording time 0900-1130</b>				
Block	(1)	12	10	2	5	33.3	0	0	14:5
Block	(2)	12	10	2	5	0	0	0	17:7
Block	(3)	9	7	2	6	2.2	11.1	0	13:1
Block	(4)	11	8	3	8	11.1	4.4	0	12:1
Block	(5)	10	5	5	6	8.9	2.2	0	22:9
<b>TOTALS</b>		<b>54</b>	<b>40</b>	<b>14</b>	<b>30</b>	<b>25</b>	<b>8</b>	<b>0</b>	<b>78:23</b>
<b>TEST PERIOD 2: Following introduction of perch</b>					<b>Recording time 1400-1630</b>				
Control	(1)	7	7	0	1	44.4	37.8	0	17:0
Visual	(2)	4	3	1	5	22.2	17.8	0	19:0
Chemical	(3)	0	0	0	5	71.1	2.2	1	22:0
Vis/chem.	(4)	2	2	0	3	11.1	13.3	2	31:3
Single sex	(5)	2	2	0	2	33.3	13.3	1	18:10
<b>TOTALS</b>		<b>15</b>	<b>14</b>	<b>1</b>	<b>16</b>	<b>82</b>	<b>38</b>	<b>4</b>	<b>107:13</b>
<b>TEST PERIOD 1: Nocturnal activity in presence of perch</b>					<b>Recording time 1900-2100</b>				
Control	(1)	6	6	0	1	8.9	4.4	6	11:8
Visual	(2)	5	3	1	1	11.1	11.1	0	19:8
Chemical	(3)	4	4	0	0	4.4	2.2	3	11:7
Vis/chem.	(4)	2	2	0	2	4.4	11.1	4	26:11
Single sex	(5)	5	5	0	0	11.1	6.7	4	21:8
<b>TOTALS</b>		<b>22</b>	<b>20</b>	<b>1</b>	<b>4</b>	<b>18</b>	<b>16</b>	<b>17</b>	<b>88:42</b>

Cell data was pooled across 10 tanks in each treatment (over 2 days) and 9 data points per tank (45 possible records). Shelter data has been displayed as a percentage of time in shelter. Shelter evictions were all by marron, therefore no descriptors are included. Screen (M:Y) = number of marron on screen : number of yabbies on screen. M = marron, Y = yabby. NAI = no aggressive interactions.

Analysis of shelter acquisition, use, and evictions showed a significantly higher use of shelter by both species following introduction of silver perch cues, compared with the other time periods ( $P < 0.01$ ). The combined shelter usage (marron and yabbies) following addition of crayfish was 7.25% of time in the first 2 h - increasing to over 25% following introduction of fish - and dropping to 7.5% at night. Yabbies sheltered for 37.8% of time in the control treatment, reducing use of shelter to 17.8%, 13.3% and 13%

in the visual, visual and chemical and single sex treatments and almost never sheltering in the presence of chemical cues. Contrastingly, marron inhabited shelter in over 70% of records when only chemical cues were present. Marron also dominated shelter under single sex conditions (M-33%, Y-13.3%) although shelter usage between crayfish was approximately even in the control (M-44.4%, Y-37.8%), visual only (M-22.2%, Y-17.8%) and visual and chemical (M-11.1%, Y-13.3%) groups. General observation suggested marron were out-competing and evicting yabbies from shelter, especially when only chemical fish cues were present. This was supported by the observation of shelter evictions, which were only recorded in time periods 2 and 3, and only for marron removing yabbies. Marron displayed significantly more climbing on the screen between the crayfish and fish compartments than yabbies in all time periods ( $P < 0.05$ ), although direct observations suggested that this behaviour was associated with ordinary foraging.

A summary of results for T5:2 is provided in Appendix B, Table VI, VII.

## **5.2.4 Discussion**

Marron were the target species for polyculture research reported in this thesis and as such, much of the discussion for this trial centres on responses of marron to the various exteroceptive cues presented. The role of yabbies in this investigation was designed to examine how interaction and competition can affect marron behaviour. In saying this, attention to the behaviours exhibited in yabbies responding to the various cues from silver perch allows reference to the different evolutionary systems of marron and yabbies, and increases overall knowledge of freshwater crayfish perception and response.

### **5.2.4.1 Behaviour of interacting crayfish - when no fish cues were present**

Studies reported in this thesis, and also by Gherardi et al. (2002) and Height and Whisson (2004) have examined the baseline behaviour of both marron and yabbies when held alone in aquaria, each using the 5-minute test protocol (see Section 4.1.5). This was the first attempt to examine the effects of interspecific interaction on the baseline behaviours of both species. Comparison between results from these studies

with results from this trial shows that except for increased locomotion and antennae movements displayed by both species following introduction to aquaria (time period 1), individual behaviours of marron and yabbies (not including interaction parameters, i.e. approaches) were all within ranges previously described when held alone. It may be assumed that the increases in locomotion and antennae use seen in the first period were associated with exploration of new environment, and establishment of dominance between species.

When behaviours recorded using the 2-hour test protocol are examined a clear physical dominance displayed by marron is apparent, which was not obvious using the 5-minute analysis protocol. If it is assumed that the most accurate indication of dominance relationships between the two crayfish species would be seen in the second and third time periods, after species have established dominance hierarchies, results showed that marron were the victor in almost all aggressive encounters, monopolised shelter and screens, and shelter competitions always resulted in the exclusion of yabbies. Based on these results it could be concluded that cohabitation of the two species would result in marron out-competing yabbies. A number of studies have examined situations where yabbies have been introduced into systems containing marron (Morrissy and Cassells 1992, Pen and Potter 1992, Lynas et al. 2004). In these studies, introduction of the invasive yabbies usually resulted in displacement of marron (Height and Whisson 2004), where marron are adversely affected by the highly competitive (Morrissy 1983; Morrissy 1997, Lawrence et al. 2001, Lynas 2002, Lynas et al. 2004) and plastic behaviour of yabbies (Gherardi et al. 2002, Height and Whisson 2004). The observed physical dominance of marron over yabbies in T5:2 does not confuse previous findings, as it should be noted that direct interaction between competing crayfish species constitutes only part of the displacement scenario. For example, yabbies are favoured as an invader owing to a higher breeding frequency and burrowing capability (Lawrence and Jones 2002).

Behaviours of both crayfish species examined at night time showed no significant differences when compared with previous periods, however the number of aggressive conflicts increased and the use of shelter and climbing reduced. These observations are consistent with increased activity displayed by crayfish in this time period, being predominantly nocturnal or crepuscular (Morrissy and Caputi 1981, Molony and Bird 2002). As in the first period, increased activity would have directly increased the chance of encounter.

#### 5.2.4.2 Detection of fish cues

Both crayfish species were clearly able to detect cues presented from silver perch (visual, chemical, visual/chemical combination), with significant increases in reaction time, antennule flicking and antennule movement across all treatments compared with control.

#### 5.2.4.3 Responses to chemical cues from silver perch

As mentioned in the previous section, both crayfish species responded significantly to silver perch odours (Treatment 3), with faster reaction times and increased use of the primary olfactory device of freshwater crayfish - the antennules (Grasso and Basil 2002, Tierney and Atema 1988, Hazlett 1990). In addition, yabbies significantly increased use of a low posture in the chemical treatment compared with control systems. These observations support the chemo-detection ability of marron and yabbies suggested by Gherardi et al. (2002) and Height and Whisson (2004), and in T4:1 and T5:1.

Although eliciting significant behavioural responses in both species, chemical cues presented in this trial did not produce feeding activity in either species. In previous trials, where food and fish cue combinations were used (Gherardi et al. 2002, Height and Whisson 2004) feeding was significantly increased. Even if the dominance relationship between marron and yabbies prevented feeding in yabbies, it is still likely that foraging responses would be seen in marron if they perceived fish as food. Hazlett (1999, 2000b) reported that in other species of freshwater crayfish when faced with imminent predatory risk, behaviour is commonly inhibited, but rarely prevented. These findings provide evidence for the ability of marron, and yabbies, for chemo-differentiation of signals pertaining to food and those pertaining to silver perch. The ability of freshwater crayfish to detect odours associated with potential predatory species has been shown in many previous studies (Hazlett 1997, Hazlett and Schoolmaster 1998, Persons et al. 2002, Hazlett 2000a, Mirza et al. 2001).

Comparisons between marron and yabbies in response to chemical cues from silver perch showed that yabbies selected shelter significantly less than marron. Examination of shelter rates in the control tanks, suggest that this was due to

increased use by marron, rather than reduced use by yabbies, and that the different shelter rates were only apparent in the chemical treatment. The increased use of shelter is a common antipredator response displayed by many species (Kats and Dill 1998, Lima 1998, Woodley and Peterson 2003), including freshwater crayfish (Stein and Magnuson 1976, Appelberg and Odelstrom 1988, Blake and Hart 1993b), however, a behaviour not seen in previous trials involving marron (Gherardi et al. 2002, Height and Whisson 2004). Interestingly, previous trials have shown the reverse trend. Height and Whisson (2004) showed a significantly increased use of shelter by yabbies in response to chemical cues from freshwater cobbler and redfin perch, compared with marron. Although it is difficult to draw clear conclusions, it is plausible that marron were responding to an increased desire to shelter by yabbies, which may be evident in the first observations of shelter evictions in this period, which were only recorded in treatments containing chemical cues. Previous studies have reported that yabbies exhibits a higher degree of behavioural plasticity compared to marron when faced with chemical information (Gherardi et al. 2002 and Height and Whisson 2004), although there was limited evidence in this trial to support this.

#### **5.2.4.4 Responses to visual cues from silver perch**

Behavioural responses to visual cues (presented alone) were apparent in this investigation, with significantly increased reaction times in both species. Although no significant differences were seen in other behaviours, compared to control, antennule and antennae movement were increased for both species. This supports findings from T5:1, where significant increases in antennule flicking, low posture and climbing were also found in response to visual cues from silver perch (Section 5.1.7.1). The use of visual cues as the primary information source, especially in clear-water conditions indicative of the natural rivers systems in south-west Western Australia has previously been demonstrated (Culp et al. 1991, Brown et al. 1997, Brown and Godin 1999, Murray and Jenkins 1999, Hazlett and McLay 2000, Bouwma and Hazlett 2001). In addition, the use of visual information in threat detection is commonly reported in aquatic environments (Brown et al. 1997, Watson 1999).

Although detection of visual cues was apparent for both species, only marron showed significant responses, compared to yabbies or other treatments. Marron were shown

to move less and remain in an intermediate posture more than yabbies, and shelter use was markedly reduced when compared to control, chemical and chemical and visual cues treatments. This may be attributed to the distinct evolution of these species, with marron naturally occurring in clear-water systems, whereas yabbies are more often found in highly turbid environments (Johnson 1986) where visual information would be less essential.

#### **5.2.4.5 Responses to combined cues from silver perch**

As no significant differences existed between crayfish held where visual and chemical cues were presented together, these treatments will be discussed as one group.

Behavioural responses of marron and yabbies when exposed to multiple cues from silver perch supported the ability of both species to detect chemical and/or visual cues, with significant increases in reaction time for both. Comparison between species revealed no significant differences in responses, however, compared to control responses, yabbies exhibited a significantly reduced use of low posture in when cues were combined, and marron showed a significant increase in use of antennules and antennae. These differences compared with control may suggest differences in the weight given to the type and complexity of information by each species.

Although not significant, one important observation was that the speed of reaction in both species was faster when cues were combined, than compared with all other treatment groups, and had much lower standard errors - suggesting more uniform responses across the population. This would support other authors reporting that the use of multiple sources of information pertaining to one ecological event can produce a more confident response (Rowe 1999, Goncalves et al. 2002). This more definitive response when multiple cues were presented may suggest hierarchical learning depending on the nature of information received, similar to the hierarchy described by Nelson (1990).

#### **5.2.4.6 Differentiation of exteroceptive cues from silver perch by crayfish**

When the responses of crayfish to the various information cues presented in this trial were compared between treatments, to determine whether crayfish were capable of

differentiating cues, only one significant variation was found: increased use of low posture displayed by yabbies responding to chemical cues (Figure 5.9).

The response of yabbies to chemical cues, compared to responses in other treatments, may support differentiation between information media. In addition to significantly lower posture, yabbies utilised antennules more and reduced locomotion when only chemical cues were present, compared to other treatments (Figure 5.9). Both of these responses have previously been associated with detection of predatory odours (Grasso and Basil 2002, Hazlett et al. 2002). In addition, this was the only treatment where no aggressive interactions occurred (Table 5.5), suggesting that perhaps yabbies had reduced activity and were not encountering marron as often. However, yabbies showed no significant variations between responses when visual cues were presented alone, and when combined with chemical cues.

The responses of marron between treatment groups were less obvious, however a general trend of increased locomotion, antennae movements, raised posture and climbing was seen where multiple cues were present (T4 and T5), compared to all other groups. This results could suggest that marron were actively seeking, or avoiding, the source of the info-cues, and that confidence in responses was increased compared to where individual cues were presented alone. In some species often the first reaction is to take an aggressive or defensive stance (Field 1990, Hazlett and McLay 2000). An initial reaction of this kind may be indicative of species such as freshwater crayfish, possessing both an effective attack-defence system 'claws' and a rapid escape mechanism 'tail-flip'. When *H. rotundifrons* receives a strong tactile input from a predator, it displays alternative predator avoidance behaviour by spreading its chelipeds and stopping all movements (Field 1990, Hazlett and McLay 2000). The behaviours demonstrated by marron indicate a heightened level of aggression when silver perch cues were detected.

Both marron and yabbies displayed a more rapid reaction, with lower standard errors, when multiple cues were present. Multi-component signals have previously been associated with more definitive responses, as they afford the organisms more security through increased confidence in information (Rowe 1999, Goncalves et al. 2002).

#### **5.2.4.7 Comparing diurnal changes in behaviour**

The comparisons made between day and night-time behaviours of marron and yabbies are important as both species are predominantly nocturnal foragers (Morrissy and Caputi 1981, Molony and Bird 2002). An extensive literature search on laboratory behaviour trials involving freshwater crayfish failed to find evidence of nocturnal behaviour, which would present a general limitation in many studies.

In this study, nocturnal behaviour of crayfish resulted in reduced shelter use, reduced climbing, increased rates of eviction of yabbies, and increase in aggressive encounters. These results suggest that crayfish were more active at night, therefore not utilising shelter and resulting in more encounters. However, we must consider that the period used to compare night-time behaviour equates to 4 h after silver perch were introduced. Therefore, results could reflect acclimatisation of crayfish to the presence of silver perch. Also, natural nocturnal behaviours of crayfish could be affected by their introduction to systems only 8 h previously, therefore few conclusions can be made to natural behaviours in this period. However, based on results, further investigation of nocturnal behaviour is warranted.

#### **5.2.4.8 Effectiveness of avoidance responses produced by crayfish**

The effectiveness of avoidance responses displayed by crayfish in response to any of the cues presented is difficult to ascertain as threat is arguable. As with T4:1 and T5:1, crayfish have been shown to detect and potentially differentiate cues from silver perch however, no obvious avoidance behavioural was consistently found in either species. Common risk related responses include reduction in overall activity (Stein and Magnusson 1976, Kats and Dill 1998, Lima 1998, Hazlett 1999, Woodley and Peterson 2003), choice of the most complex shelter available (Stein and Magnusson 1976, Appelberg and Odelstrom 1988, Blake and Hart 1993b) and increasing competition (Werner 1991, and Kotler et al. 1994). In this trial, reduction in activity in the face of silver perch cues was not apparent, as locomotion increased from control in all treatments for each species. Use of shelter as an avoidance response was also not consistent with findings in this study, where no significant changes in shelter usage were found. Finally, the amount of interspecific competition decreased after



silver perch were added to experimental systems. This lack of obvious avoidance behaviours may signify limited avoidance strategies of the crayfish species examined, or as previously suggested, may be related to the suggestions by Hazlett (1999, 2000b) that some species only reduce normal behaviour in response to threat. In some cases, where no behavioural responses are recorded, there may still be physiological responses associated with heightened alertness or readiness for flight or fight (De Meester and Pijanowska 1996, Schapker et al. 2002). In contrast, the evolution of marron in predominantly predator-free environments (Morrissy 1997, FWA 1999, Allen et al 2002) may mean marron haven't been required to evolve predator avoidance tactics, thus leaving them vulnerable to predation in polyculture systems. Alternatively, marron may require detection of an alarm odour to elicit an avoidance response (Hazlett and Schoolmaster 1998), especially if cues are novel (Chivers et al. 1995, Chivers and Smith 1998). To confirm the existence of avoidance responses possessed by marron and yabbies and determine their effectiveness, studies involving direct physical interaction with predators are required, in both the laboratory and field.

### **5.2.5 General conclusions**

This trial confirmed the chemo- and photo-sensory ability of both crayfish species, and their capacity to differentiate and respond to environmental information based on the nature of stimulus (food versus fish cues). However, results showed an absence of significant avoidance behaviour in marron. These findings may be a function of the natural selection of marron species in fishless regions where it is the largest, dominant invertebrate; or they may reflect an alternate predator response mechanism such as tail-flipping, which would be consistent with increased alert status but lack of behavioural change to perceived threat. Outcomes from the 2-hour test support the need for more extensive behavioural analysis in future interaction trials, as dominance relationships appear to develop over time exceeding 5 min.

An understanding of the factors governing interactions between these congeneric crayfish species and identifying the triggers for predator avoidance in marron has obvious ecological ramifications for wild-stock conservation and in developing strategies for the uncontrolled release of non-endemic species into natural waterways.

An understanding of the ecological roles of aquatic species also has direct application in developing management tools that may be employed in marron polyculture systems to mediate negative interactions between cohabitants exhibiting overlapping feeding regimes. The most encouraging finding for polyculture of this species is that even though marron detect fish cues behavioural responses were not evident. Therefore, if cages were employed in polyculture with a predatory species, or system variables altered to reduce effectiveness of predatory strategies, marron would maintain growth as they would not be directing energy to avoidance.

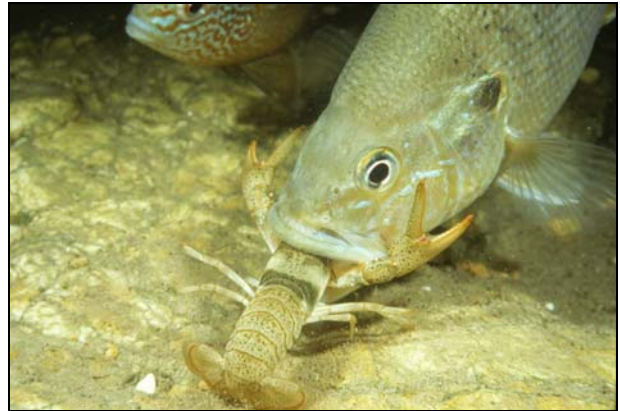
### 5.2.6 Recommendations

Results from T5:2 identify the need to examine marron behaviour under physical interaction with predators, to determine if marron display avoidance strategies, such as tail-flipping, and whether avoidance strategies are effective.

A second recommendation of this trial is to investigate genetic variability of crayfish to determine if certain individuals have more capacity for predator detection and avoidance, or related features. This suggestion comes from the high variation recorded in individual marron behaviour, represented by high standard errors, even under controlled conditions, in this and T4:1 and T5:1

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**The null hypothesis  $H_0$**  (5.3) was rejected. Marron detected both visual and chemical cues from silver perch, however avoidance behaviour in response to cues from silver perch was not supported.



### **Crayfish-fish interactions within a communal system**

*This chapter examines direct interspecific interaction between marron and two finfish (Murray cod and silver perch) under varied conditions of habitat complexity and light intensity in one laboratory (T6:1) and one field trial (T6:2).*

## **CHAPTER SIX**

### **Crayfish-finish interactions within a communal system**

Previous attempts at eliciting responses from marron exposed to chemical and visual cues from silver perch showed no discernable predator avoidance strategies. In order to determine whether this would equate to increased predation, marron were observed in communal systems with potential finfish predators.

This chapter incorporates two experiments. The first trial (T6:1) examined behavioural responses of marron to Murray cod, a known predator of crayfish (Allen et al. 2002). This trial was conducted in aquaria under varying conditions of shelter and light intensity. The second trial (T6:2) was conducted in earthen ponds, where marron and silver perch were held free-range under varied shelter regimes.

## 6.1 Predator-prey interactions between Murray cod and marron

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In this trial, Murray cod (*Maccullochella peelii peelii*) were chosen to examine the adequacy of predator responses used by marron (if any) as they are a strict carnivore and a renowned voracious crayfish predator (Allen et al. 2002). Due to this, It was hypothesized that the Murray cod would prey on marron more than the polytrophic silver perch. Murray cod were also chosen for this investigation as they are currently under review for translocation into and within Western Australia (FWA 2003b).

As foraging efficiency is a function of prey accessibility, vulnerability and abundance of alternative food sources (Mitchell and Hazlett 1996), shelter and light intensity were manipulated in this trial to examine their effects on predator-prey dynamics between marron and Murray cod. Turbidity, being negatively correlated with light intensity, has a profound influence on predator-prey interaction owing to its impact on reactive distances or maximum detection distance (Miner and Stein 1996). Similarly, shelter complexity affects capture and search time (Quammen 1984, Clarke et al. 2002, Gazdewich and Chivers 2002, Naranjo-Paramo et al. 2004), and therefore contributes energy cost to predators.

The null hypotheses for T6:1 were:

- |  |     |
|--|-----|
| <b><math>H_0</math>:</b> Marron survival is not influenced by the presence of Murray cod | 6.1 |
| <b><math>H_0</math>:</b> Shelter will have no effect of marron survival                  | 6.2 |
| <b><math>H_0</math>:</b> Light intensity will have no effect on marron survival          | 6.3 |

If survival of marron in the presence of Murray cod is shown to be influenced by factors including shelter and light intensity, this will demonstrate whether manipulation of system variables in ponds has the potential to increase polyculture production of marron in the presence of predatory finfish.

### **6.1.1 Aim**

This trial aimed to investigate the nature and intensity of interspecific interactions between marron and a crayfish predator, Murray cod.

### **6.1.2 Objectives**

1. To compare predation success of Murray cod on juvenile marron with or without shelter, and in low and natural light intensity.
2. To examine natural predator avoidance strategies displayed by marron in response to the novel finfish predator under varied shelter and light conditions.
3. To determine if marron are capable of learning avoidance responses to the threat from Murray cod.

### 6.1.3 Materials and methods

#### 6.1.3.1 Site and culture system

This experiment (T6:1) was conducted at the South-West Aquaculture and Environment Centre (SWAEC), located in Collie, Western Australia (see 3.1.1). Sixteen 250L glass aquaria (50 x 50 x 100 cm) were used for this experiment (Plate 6.1).

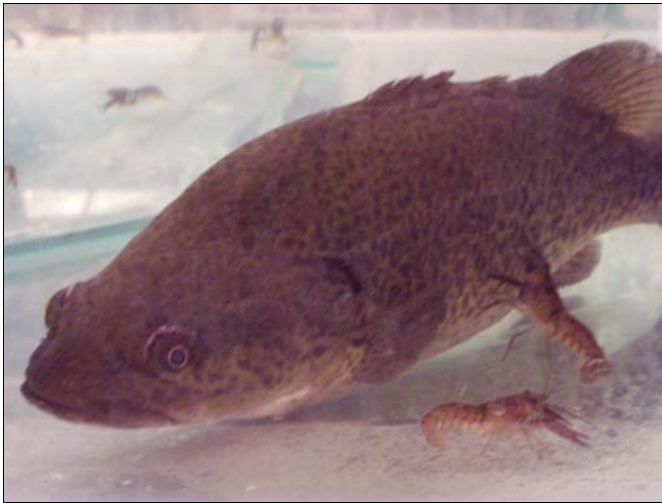


**Plate 6.1** 250L glass aquaria used in T6:1

#### 6.1.3.2 Experimental animals

Juvenile marron ( $4.24 \pm 0.7g$ ) were selected for this trial as this is the common stocking size in earthen ponds in the marron monoculture industry (Maguire 2004), and would be a life stage vulnerable to predation due to small size (relative to gape of Murray cod). Juvenile marron were removed from monoculture brood ponds in Pemberton ( $34^{\circ}S$ ,  $116^{\circ}E$ ) in April 2004 and transferred to holding tanks at SWAEC. Following a two-day acclimatisation in holding tanks marron were transferred to experimental systems. Twelve Murray cod ( $1090 \pm 182g$ ) (Plate 6.2) were sourced from a commercial grow-out facility at Ludlow(\*), Western Australia ( $33^{\circ}S$ ,  $116^{\circ}E$ ) and acclimatised in 5 tonne holding tanks at SWAEC for three weeks prior to commencement of the trial. Gapes of cod were  $>40$  mm (cv. girth of juvenile marron at maximum of 15 mm). Murray cod were introduced to systems 2 days after introduction of crayfish.

*\*Note: cod were raised in tanks on pelleted diets.*



**Plate 6.2** Murray cod (986g) next to marron (2.3g) in an experimental aquarium, showing size differential

### 6.1.3.3 Experimental design

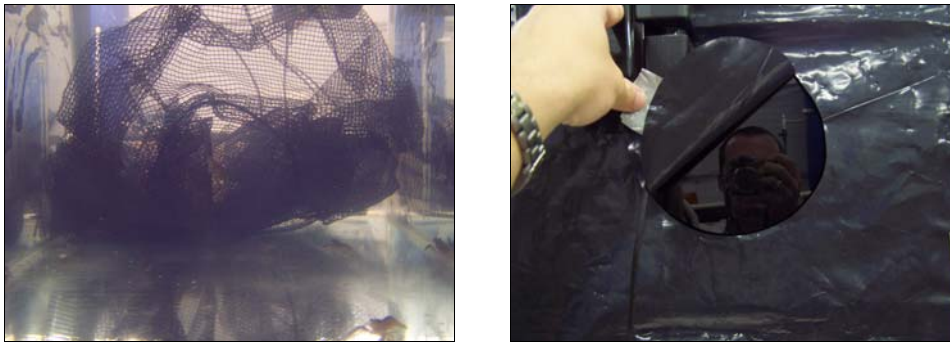
Twenty marron (1:1 sex ratio) and one Murray cod were placed into each of the sixteen experimental aquaria. A control (no fish) and three treatments were tested (Table 6.1):

**Table 6.1** Treatment groups used to compare marron-Murray cod interactions

	shelter	Light intensity	marron	Murray cod
Treatment 1	no	ambient	yes	yes
Treatment 2	yes	ambient	yes	yes
Treatment 3	yes	0%	yes	yes
Control	yes	ambient	yes	no

The control and treatments 1 and 2 were under ambient light conditions (12 hours daylight). Each group was represented in four replicate tanks (16 total). Synthetic loose-mesh marron hide material (Custom Networks Pty Ltd) was provided in treatments requiring shelter. Mesh hides offered increased complexity for juvenile marron compared with PVC pipe shelters. Shelter material covered approximately one quarter of each aquarium (Plate 6.3). In the 0% light intensity treatment all light was blocked using a heavy grade black plastic sheet. A plastic viewing window was made in one end, where night vision goggles (Night Optics D-2MV) were used to examine behaviour and survival (Plate 6.3).





**Plate 6.3** Left: loose meshing used as complex marron hide. Right: Viewing window in 0% light intensity treatment

Survival and shelter use were recorded twice daily (0900h and 1700h) for 14 days. Shelter use was recorded if marron were wholly within, or less than 50 mm from, shelter. Data were recorded for crayfish gender, which was determined by permanent silver marks placed on both sexes prior to commencement of trial (both sexes were marked to ensure no gender bias). Animals were not fed for three days prior to or during trial. Feed was not provided during trial in an effort to observe differences as state of hunger becomes more critical for both predator and prey.

#### 6.1.3.4 Statistical analysis

Survival between blocks was compared with one-way ANOVA, with *post hoc* testing consisting of Scheffe's F-test (reported), Bonferroni and Tukey. Survival was compared between treatment groups used ANOVA with Tamhane's T2 *post hoc* (Selvanathan et al. 2000). Shelter occupation between treatments and blocks was compared using univariate analysis under Scheffe, Bonferroni and Tukey (reported) *post hoc* tests (Selvanathan et al. 2000). Relationships between shelter and survival for treatments in each time period were assessed using one way ANOVA using Tamhane's T2 and Dunnette's T3 (reported). A two independent samples test with Mann Whitney U-Test was used to compare survival with time of day (mortality recorded at night and during day). All percentage data were subject to arcsine transformation prior to analysis (Zar 1984). Water quality was compared between ponds at each sample point (2 months) by one way ANOVA using Tamane's T2 (Selvanathan et al. 2000).

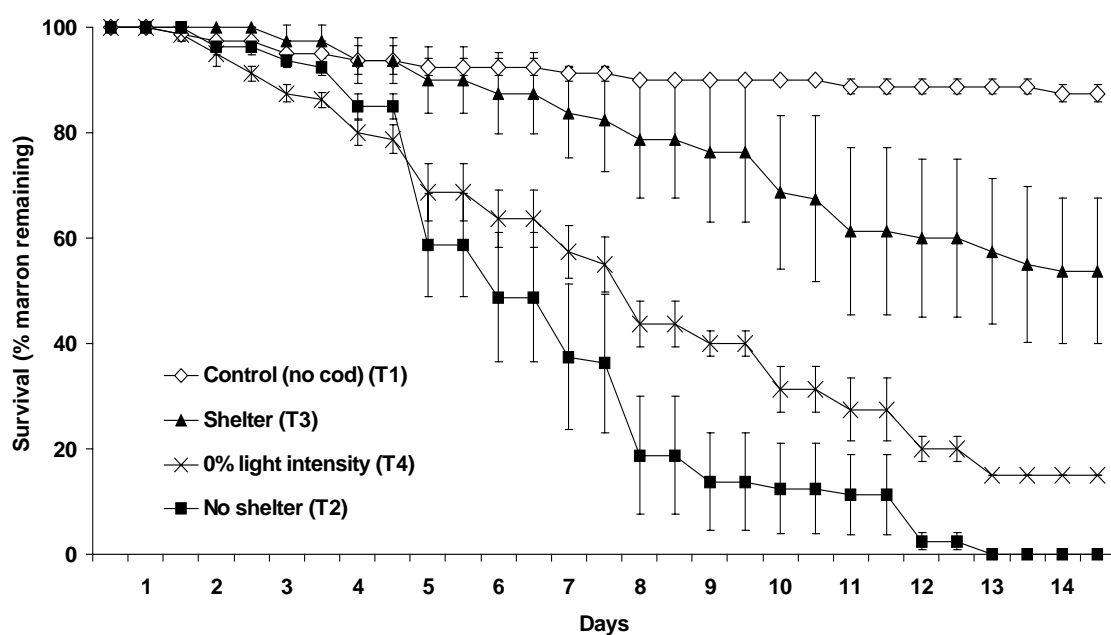
### 6.1.3.5 Water quality

All systems were maintained with two external biological-chemical filters and two air-stones for each aquarium. Water quality measurements - total ammonia (ppm), salinity (ppt), conductivity (mS), pH, nitrite (ppm), nitrate (ppm) and temperature (°C) were recorded daily. All levels remained within optimum ranges for Murray cod (NSW Fisheries 2005) and marron (FWA 1999) and no significant variation between systems, blocks or treatments was recorded (Appendix A). Water temperature across all systems was  $18.2 \pm 0.1^\circ\text{C}$ .

## 6.1.4 Results

### 6.1.4.1 Predation

Murray cod predated heavily on marron in all treatments (Figure 6.1). The highest mortality was observed when shelter was not provided, with no crayfish remaining after 12 days. Mortality when shelter was provided in 0% light intensity was also high, 85% after 12 days, followed by shelter (T3) which had 25-45% mortalities in three aquaria and 80% in one. Two or three mortalities were recorded in each of the four control aquariums, attributed to moulting and subsequent cannibalism.



**Figure 6.1** Survival of marron ( $\pm$  SE) over 14 days in all treatments.

Marron mortality was significantly higher during the night ( $P < 0.01$ ) in all treatments, with only 15 of the 195 total mortalities recorded observed during daylight hours. Of the 15 day-time mortalities, over half were recorded in the 0% light intensity group (Table 6.2). No gender bias occurred for crayfish mortalities ( $P > 0.1$ ).

**Table 6.2** Total marron mortalities recorded in each treatment during the day, and night

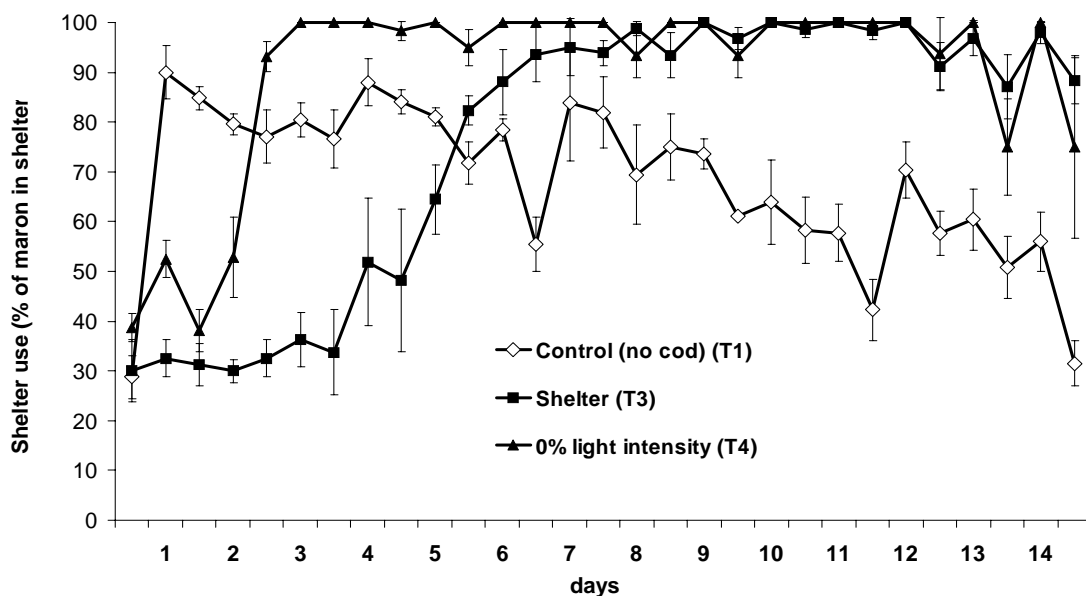
Treatment group	Marron mortalities during day	Marron mortalities during night
Control	1	8
Shelter	4	33
Shelter + 0% light intensity	8	60
No Shelter	2	78
<b>Total Mortalities</b>	<b>15</b>	<b>180</b>

Predation rates between treatments varied over time (Figure 6.1). Predation was strongest until day 4 in the 0% light intensity treatment, compared to control ( $P < 0.01$ ), no shelter ( $P = 0.014$ ) and shelter ( $P < 0.01$ ), respectively. However, overall mortality was greatest in T2, containing no shelter, being significantly different to the control and sheltered groups after day 5 ( $P < 0.01$ ) and compared to the 0% light treatment after day 9 ( $P < 0.05$ ). Predation levels in the sheltered treatment was significantly less than other treatments following day 5, and only greater than the control at day 14 and day 15 ( $P < 0.05$ ).

#### 6.1.4.2 Shelter occupation and behavioural observations

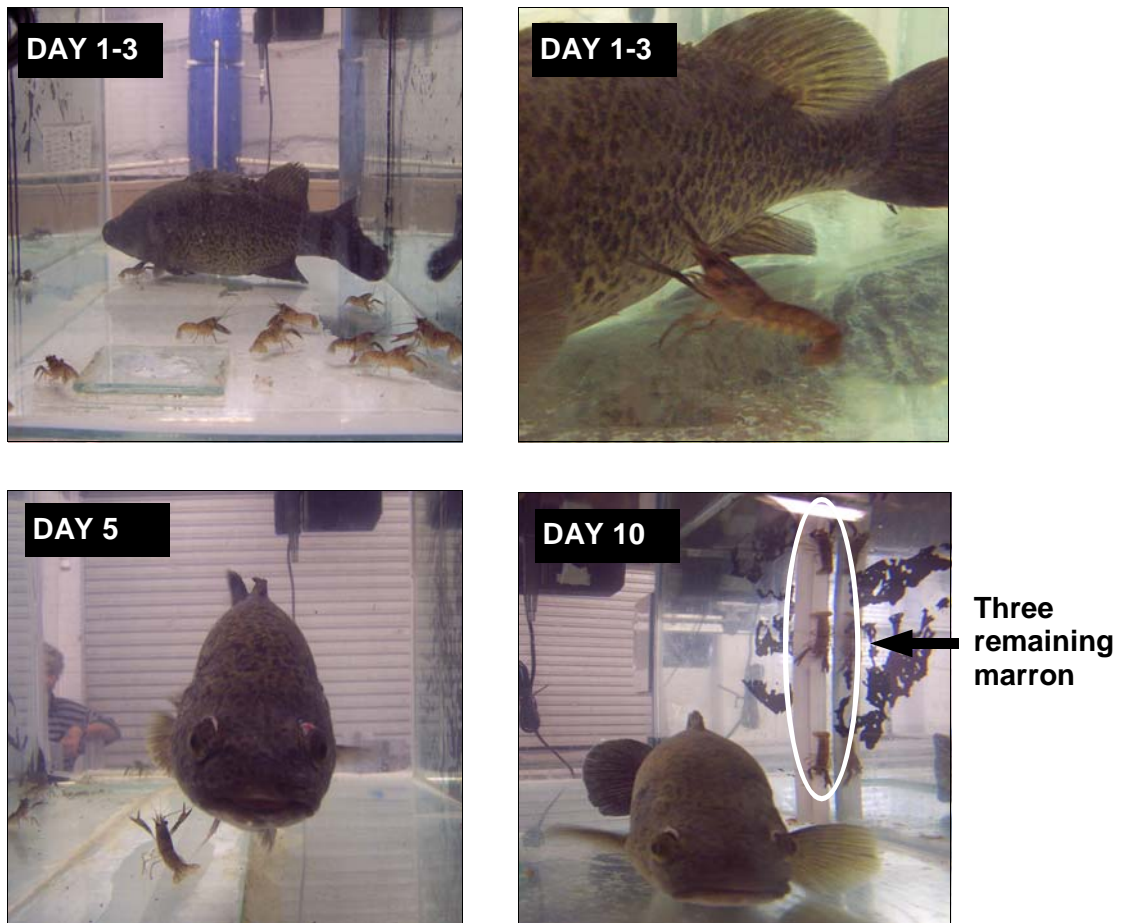
Shelter usage (Figure 6.2) in the four aquariums comprising the control group was approximately 80% over the first 8 days, and gradually declined thereafter (approximately 40% at day 14). Shelter use was relatively low in treatments containing fish until after the first predation events were recorded on day 4. On days 1 to 3 marron appeared unconcerned about the presence of the predator, with individuals

distributed evenly across the tank bottom (Plate 6.4). On occasions when cod approached marron (within 20 mm) the crayfish displayed strong defensive stances (Plate 6.4). There was almost 100% shelter use after 2-3 days in 0% light intensity (T3), and after 8 days in the shelter treatment (T2). Although no shelter was provided in T1, marron displayed avoidance behaviour after 4-5 days (Plate 6.4). In all treatments, shelter use decreased in the last 2-3 days of the trial. Note: data demonstrates an increased shelter usage, rather than increase percentage usage due to predation on individuals outside of shelter. In T4, the numbers of marron in shelter increased from  $7.5 \pm 0.7$  to  $17.5 \pm 0.3$  by day 3 (100% of remaining marron), and in T3, numbers of marron in shelter increased from  $6.0 \pm 1.2$  to  $16.25 \pm 1.2$  by day 6 (94% of remaining marron).



**Figure 6.2** Shelter occupation by marron in treatment groups. No shelter was provided in T2.

Shelter occupation was higher in the control group in the first two days compared to the 0% light intensity treatment ( $P < 0.01$ ), and for the first five days compared to marron in the sheltered treatments ( $P < 0.01$ ). Shelter use in the control was lower than other treatments following these periods ( $P < 0.05$ ). Comparison between treatments showed significantly more sheltering in the 0% light intensity group between day 2 and day 6 ( $P < 0.01$ ), although similar levels among all groups thereafter ( $P > 0.1$ ).



**Plate 6.4** Top: marron disregard presence of cod. Bottom left: defensive behaviour displayed by marron following approach by cod. Bottom Right: remaining individuals displaying avoidance, these were the final three individuals remaining in the tank.

### 6.1.5 Discussion

In previous chapters, marron have not displayed avoidance tactics however their ability to detect both visual and chemical cues pertaining to fish, was demonstrated.

#### 6.1.5.1 Predation

Although Murray cod were shown to successfully predate on marron in all treatments their effectiveness was reduced by both shelter and light. The role of shelter in reducing mortality is consistent with findings by Jones and Ruscoe (2000), where mortality rates of redclaw (*Cherax quadricarinatus*) were high when insufficient

amounts of shelter were provided in ponds containing silver perch. As 83% of marron were consumed in the 0% light intensity treatment, compared to natural light where over 50% of marron remained at the trial completion, there appears to be an advantage to the predator where visual detection is reduced. This is in contrast to the results from a number of studies, where prey have been shown to gain an ecological advantage at night as detection distances of predators are reduced (Vinyard and O'Brien, 1976, Confer et al. 1978, Gregory and Northcote 1993, Benfield and Minello 1996, Utne, 1997, Utne-Palm 2004). Closer examination of predation between the ambient and 0% light intensity treatments reveal that predation rates are relatively similar, although predation was more immediate following introduction of cod to the 0% light intensity systems. One argument for this result is that Murray cod are more stressed following introduction to full-light aquariums, and therefore less inclined to forage compared to Murray cod introduced to the darkened aquaria. With this said, significantly more marron were predated upon during the night in all treatments. As marron are generally more active at night, this may result in increased frequency of contact with the Murray cod. If the period of heightened nocturnal activity was prolonged by being held in 0% light intensity, this may explain greater mortality.

One factor that may have affected predation on marron was the use of pellet-reared Murray cod. It is unsure what effects Murray cod reared on crayfish as a primary food source would have on predation rates. However, in a pilot study carried out following this trial where twenty marron and twenty yabbies were introduced to a 250L aquarium containing one crayfish-reared cod the following observations were made over 4 h. Cod approached marron 51 times, resulting in 47 tail flicks and 3 mortalities. Yabbies were approached 22 times, resulting in only 2 tail flicks but 14 mortalities (Storer pers. obs.). Yabbies occupied shelter more than marron, which may explain reduced interaction with cod. Although this trial requires repeating in a more robust scientific manner, results do suggest potentially effective avoidance in marron, even compared to strategies employed by the invasive yabby - which evolved in the same river systems as cod.

#### **6.1.5.2 Avoidance strategies and learning**

The lack of sheltering by marron in the initial stages of this trial and increased shelter use of marron following predation of conspecifics by Murray cod demonstrates an initial

naivety by marron followed by rapid learning of avoidance. The avoidance strategies appeared relatively effective where refuge was adequate, with predation rates reducing markedly as trials progressed. As suggested in previous chapters, the lack of avoidance to potential risks by marron may be attributed to reliance of tail-flipping. The use of tail-flipping was not observed in this trial, although this is not unusual as predation events were rarely observed. The effectiveness of the tail-flip in the confined space of aquarium may be limited, as tail-flips are short bursts of speed generally used to rapidly leave danger areas. This may explain high mortalities of marron recorded where no shelter was provided, as tail-flips would be most effective if used to quickly retreat into close refuge.

#### **6.1.5.3 Effect of starvation**

One of the most common trade-offs animals experience is between foraging activities and the risk of predation (Werner and Anholt 1993, Skalski and Gilliam 2002). In most species, foraging activities increase the risk of predation (Wisenden et al. 1999), so choices regarding the levels of foraging activities must be made utilising cues about the risk of predation. One would predict greater risk taking as food motivation increases. Marron and Murray cod were not fed throughout trial duration, and all treatments showed reduced shelter use in the last few days of this trial. This may reflect increased foraging due to starvation. Shelter use by marron in control tanks was greatly reduced compared to treatment groups, dropping to less than 50% use after 14 days, compared to 80% in treatment tanks. The increased activity outside of refuge under controlled conditions may reflect active searching for food, which was inhibited by presence of Murray cod.

In contrast to these findings, Anholt et al. (2000) measured the activity levels of anuran tadpoles under combinations of levels of food availability and predation risk cues. They found the same relative magnitude of predation cue effects at all food levels, indicating no shifts in the nature of the interaction of the two inputs.

### 6.1.6 Concluding remarks

Although some marron remained after 14 days where shelter was provided, extrapolation of results (Figure 6.1) suggests that all marron would have eventually been consumed, especially as requirement to obtain food increased. In the context of field-based polyculture systems, the free-range cohabitation of Murray cod and marron appears impractical. Even if predation could be prevented under free-range conditions (e.g. cage culture techniques for Murray cod), the general stress and requirement of marron to shelter would greatly affect growth, survival and reproduction. One factor that may have influenced survival in this experiment was starvation. However, with naturally varying levels of starvation existing in most systems, and the need for marron to venture out of shelters to feed, this was not believed to be a major factor influencing extrapolation of results to polyculture.

Many aquatic animals have been translocated into Western Australia over the last century to improve recreational fishing (Allen 2002, FWA 2002b), control unwanted pests (Allen 2002), and develop aquaculture industries (FWA 1998, FWA 2002b). Adverse impacts of these translocations have included reduction in the abundance of some native species, threatened genetic integrity, and the introduction of pathogens (FWA 2003b). Murray cod, native to the Murray-Darling Basin (South East Australia), have already been approved for use in recirculating aquaculture systems in Western Australia (FWA 2003b). The potential for duoculture of Murray cod with the native marron is unknown, and the effects of accidental release of Murray Cod into local waterways unquantified. However, Murray cod are an aggressive ambush predator and are known to consume freshwater crayfish (Allen et al. 2002). In the event of accidental release of Murray cod, strong predation of marron is certain based on results in this trial. Further, stimuli from potential crayfish predators invoke predator-avoidance responses, potentially reducing foraging, increasing shelter competition and affecting other niche requirements, which has obvious ramification for polyculture production.

The most important finding to come from this investigation was the learning capabilities of marron, evident in sheltering behaviour, avoidance of high risk areas and reduce mortality in sheltered treatments. Although this may not produce benefits where marron and Murray cod are concerned, this may have important ramifications for the duoculture of marron and silver perch. For a polytrophic predator of crayfish, such as



silver perch, the tendency for them to quickly alter feed choice in conditions of increased cost of capturing prey is more plausible than for strictly carnivorous species (Sigler et al. 1984).

**The null hypothesis  $H_0$  (6.1)** was rejected. Murray cod predated strongly on marron in all treatments.

**The null hypothesis  $H_0$  (6.2)** was rejected as predation of marron by Murray cod was reduced where shelter was provided.

**The null hypothesis  $H_0$  (6.3)** was rejected, as higher mortality was recorded in the low light intensity treatments. This outcome was believed to be associated with the increased activity of marron at night, increasing encounter rate with Murray cod. As Murray cod are ambush predators they may rely less on visual cues.

### **6.1.7 Recommendations**

Further study into the duoculture of marron and Murray cod is warranted, focussing on the suitability of Murray cod to cage culture.

A strong recommendation of this trial is to examine interspecific interactions between marron and silver perch under varied shelter and light intensity conditions. Due to the influence of diurnal changes on species interaction dynamics and system conditions, it is recommended that these examinations be completed in the field.

## 6.2 Predator-prey interactions between silver perch and marron

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Although marron displayed a lack of obvious predator avoidance strategies when exposed to chemical and visual cues from silver perch in Chapters 4 and 5, the first trial in this chapter indicated possible learning under physical threat from Murray cod. Whether avoidance tactics evolved through interaction with Murray cod, or existing tactics were employed once marron associated Murray cod with predatory risk, is unknown. Marron survival in T6:1 demonstrated that the initial tactics employed by marron were not effective in preventing predation, and even following avoidance, predation events were still common. However, this result must be taken in context of environmental conditions. Marron were exposed to a large predator in a confined area and although use of habitat complexity significantly increased survival, starvation may have made remaining in shelter difficult.

To determine whether the avoidance tactics demonstrated by marron in response to a fish predator would equate to reduced predation in polyculture ponds, survival and growth of marron was observed in free-range pond systems with silver perch. Silver perch were chosen for this study, not only as the prime duoculture candidate with marron, but also as they are an omnivorous species (Grant 1987, Barlow et al. 1986, Whisson 1997) and therefore, more likely to alter preference for freshwater crayfish if costs associated with capture increase (Barlow et al. 1986). To examine this, crayfish habitat complexity was manipulated, under natural conditions of light and turbidity. Feed was supplied to satiation for both marron and silver perch, providing an alternate food source for silver perch and reducing time required by crayfish for locating feed.

In this trial (T6:2), berried marron (approx. 110 g) were introduced into ponds in November, where hatchling-juvenile marron would be released from tail shortly after. One female marron of this size is reported to release between 150 and 250 hatchlings (FWA 1999). Survival of marron between hatchling and juvenile stages in monoculture is highly variable (FWA 1999), although in optimal conditions Whisson (1997) reported 64 surviving juveniles per female.

### 6.2.1 Aim

The aim of this trial was to examine the effectiveness of avoidance tactics of marron to silver perch in earthen ponds under varying shelter conditions.

### 6.2.2 Objectives

1. To compare survival of 0+ marron and adult females in the presence of silver perch under no shelter and under high density shelter conditions
2. To examine growth rates of 0+ marron in the presence of silver perch under no shelter and under high density shelter conditions
3. To compare and contrast growth and survival of free-range silver perch between sheltered and un-sheltered ponds, and based on marron production.

The null hypotheses for T6:2 were:

**$H_0$** : Survival of both hatchling-juvenile marron and brood females will not be effected by silver perch 6.4

**$H_0$** : Shelter will not influence survival of marron in the presence of silver perch 6.5

**$H_0$** : Shelter will not effect growth rates of marron and silver perch 6.6

## **6.2.3 Materials and methods**

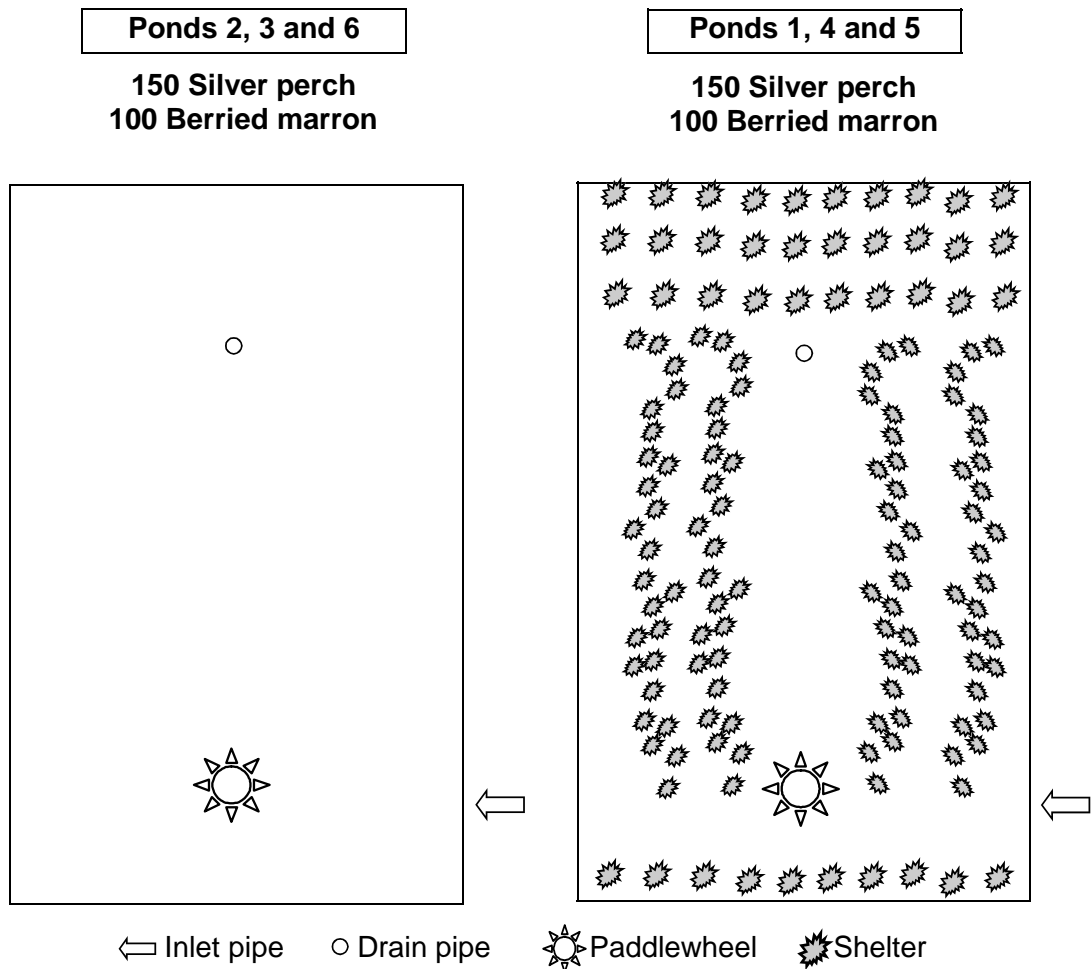
### **6.2.3.1 Culture system and site**

Trial T6:2 was conducted at the Collie Aquafarm field research site (Section 3.1.2.2). Ponds were emptied and left to dry for two weeks prior to the start of this trial, at which time 1 tonne of lime rock was added to each pond to increase alkalinity and calcium before being filled.

### **6.2.3.2 Experimental design**

One hundred berried marron (110g) and 150 silver perch ( $270.9 \pm 61.1$ g) were introduced to each of six experimental ponds (0.072 ha). As growth of berried marron was not a core objective of this study, initial weights were not recorded to reduce handling stress and time out of water for berried marron. To allow some degree of reference an average marron weight of 110g was assigned to each animal, based on results from sample population of 30 individuals not used in the study. Two treatments were examined in three replicate ponds; 1. 140 loose-mesh shelters (Section 3.1.2.2) per pond (approx. 1 per 5m<sup>2</sup>) and, 2. no shelter (Figure 6.3). Following detection of juveniles (length 20-30 mm) in shelters, ponds were drained and all stock collected, weighed and counted.

Treatments were randomly allocated in three replicated ponds.



**Figure 6.3** Design and allocation of sheltered and non-sheltered treatments ponds

### 6.2.3.3 Experimental animals

Marron and silver perch (Plate 6.5) used for this trial were raised in ponds at the Collie Aquafarm. Three weeks prior to the trial, all ponds were drained and stock collected and transferred to holding tanks at the South-West Aquaculture and Environment Centre (SWAEC) (Section 3.1.1). As female marron were newly berried they were transported to and from site in 600L fish transporters to protect eggs. Berried stock held at SWAEC were kept at low densities ( $1/m^2$ ) in 5 tonne flat-bottom fibreglass tanks. Water quality was kept within optimal ranges and holding systems were left in darkness.

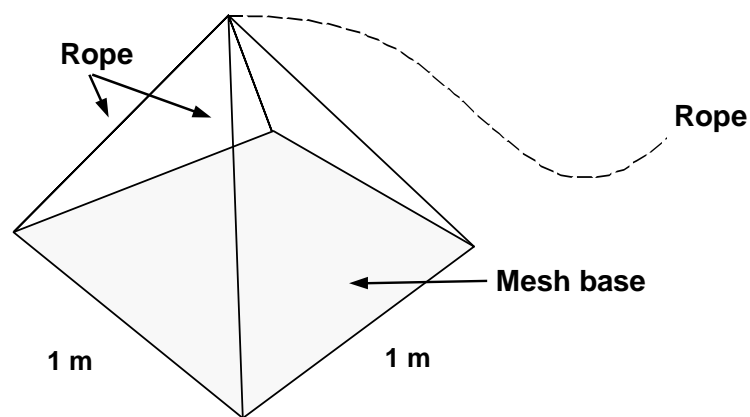


**Plate 6.5** Experimental animals. Left: berried marron (101g). Right: silver perch (364g)

The number of eggs/marron, estimated from a total count of eggs on 10 specimens to determine average fecundity, was  $119 \pm 13$ . The marron used in this trial were 2 yrs of age.

#### 6.2.3.4 Supplemental feed

Silver perch and marron were fed commercial preparations (Appendix C and D, respectively) three times per week, between 1600-1800 h. Marron and perch were fed at a rate determined by feeding animals in each replicate to satiation once per month (Table 6.3). Marron feed rates were determined using feeding trays located around each pond, which were 1m square mesh (300 um) feeding platforms (Figure 6.4). Platforms were monitored after 8 h and feed rates increased or decreased accordingly.



**Figure 6.4** Feeding platform used to determine feeding rate for marron in ponds.  
Clearance of feed placed on mesh base (shaded area) checked after 8 h.

Satiation levels for perch were initially determined 30 min. after feeding using feeding platforms installed in each cage (Section 3.1.2.2). However, as turbidity increased observation of general feeding behaviour, such as surfacing, was used to determine rate, as feeding platforms (0.75m under water surface) were no longer visible. Feeding was stopped 4 days prior to harvest to reduce gut contents.

**Table 6.3** Feeding rates for marron and silver perch

Month	Feed supplied (kg)						
	Marron	Silver perch					
	each pond	Pond 1	Pond 2	Pond 3	Pond 4	Pond 5	Pond 6
<b>December</b>	1.9	10.3	10.1	9.7	10.1	10.3	10.3
<b>January</b>	1.9	10.6	11.2	10.8	10.85	10.95	11.1
<b>February</b>	3.3	7.8	7.8	7.5	7.8	7.8	7.3
<b>March</b>	1.5	7.3	7.3	7.3	7.3	7.3	7.3
<b>Total</b>	<b>8.6</b>	<b>36</b>	<b>36.4</b>	<b>35.3</b>	<b>36.05</b>	<b>36.35</b>	<b>36</b>

December and March data was from 26 days and 22 days production, respectively.

### **6.2.3.5 Trial duration**

Marron were introduced on 29 November 2004 and harvested on 26 March 2005. Silver perch were introduced three days after marron to allow berried females to acclimatise to conditions and to locate and inhabit shelters where provided, giving a trial duration of 117 days.

### **6.2.3.6 Statistical analysis**

Silver perch and marron data were analysed for differences in weight and length using a one-factor ANOVA and Scheffe's F-test (reported), along with Bonferroni and Tukey, to rate significant difference between treatment means (Selvanathan et al. 2000). Comparison between treatments for marron and perch weight was compared using T-tests (Selvanathan et al. 2000). Independent samples t-tests were utilised in comparing length-weight ratios between treatments for both marron and silver perch, and Binomial Tests examined differences in survival of marron and perch, and number of juveniles, between treatments. Water quality treatment means were compared using a one-factor ANOVA and Scheffeis F-test (Selvanathan et al. 2000).

### **6.2.3.7 Water quality**

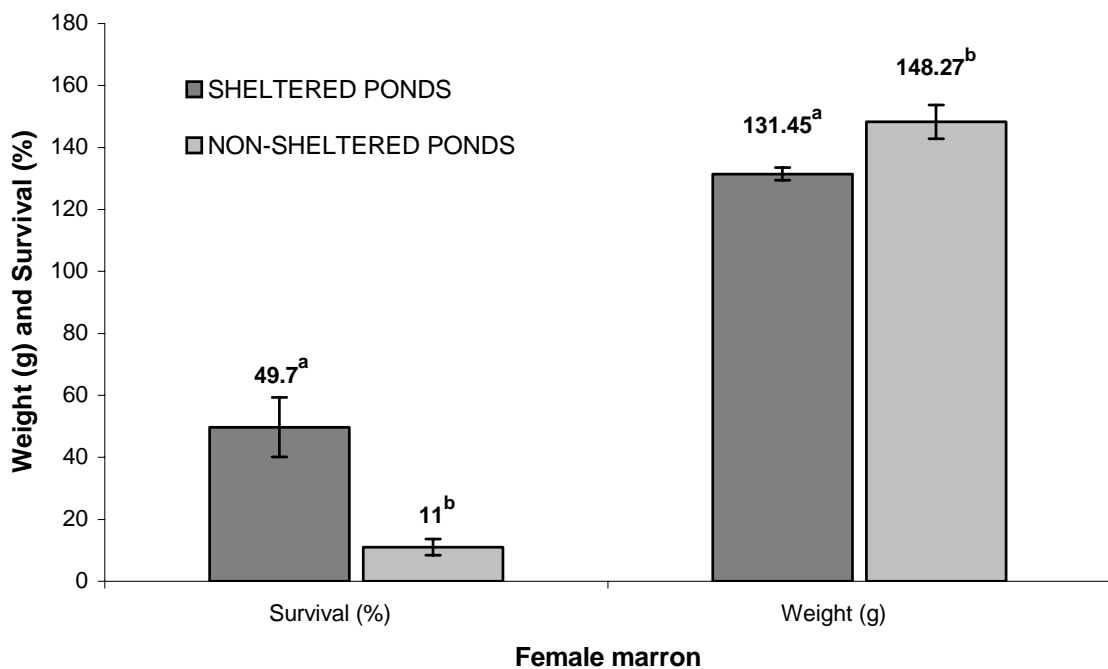
Water quality was monitored twice weekly, providing pH, dissolved oxygen, salinity, conductivity, and temperature data for each aquaculture pond (Appendix A). All parameters were within optimal ranges for both test species (Morrissy 1994, Rowland 1995).



## 6.2.4 Results

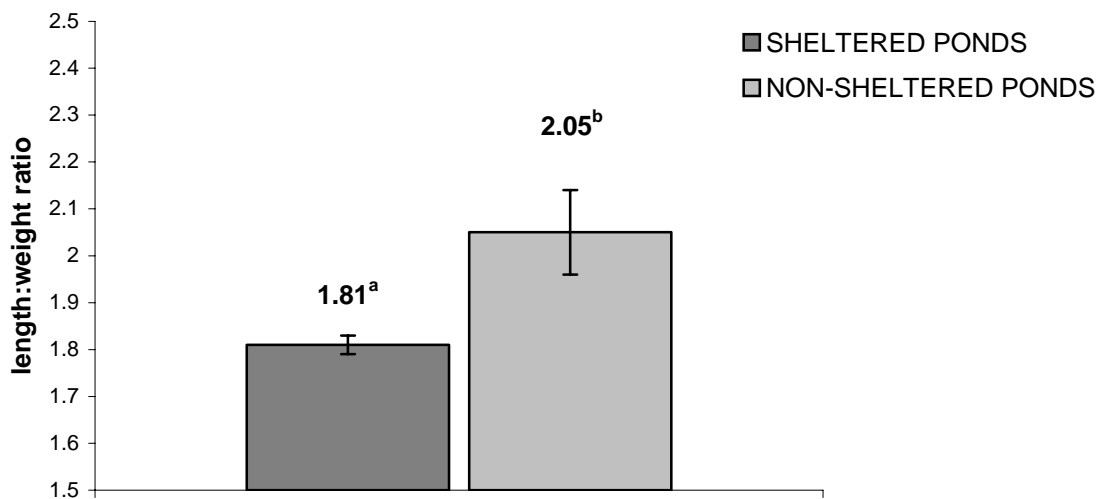
### 6.2.4.1 Female (adult) marron

Survival, average weight and growth over the 117 day trial period (Figure 6.5) showed a number of significant variations between treatments. Survival of adult female marron was low across all ponds, however significantly improved in the sheltered treatments, compared to non-sheltered ( $P < 0.01$ ) (Figure 6.5). Average weight was significantly greater in the non-sheltered treatment ponds ( $P < 0.01$ ) (Figure 6.5),



**Figure 6.5** Avg. survival (%) and weight (g) ( $\pm$ SE) of adult female marron over three replicate ponds in the sheltered and non-sheltered treatments, over 117 days. Significant differences were reported between treatments where different superscripts are provided.

The length-weight ratio of marron was significantly higher in animals harvested from non-sheltered ponds ( $P=0.013$ ) (Figure 6.6), which equates to marron in non-sheltered ponds being heavier than those in sheltered treatment ponds, at equal lengths.



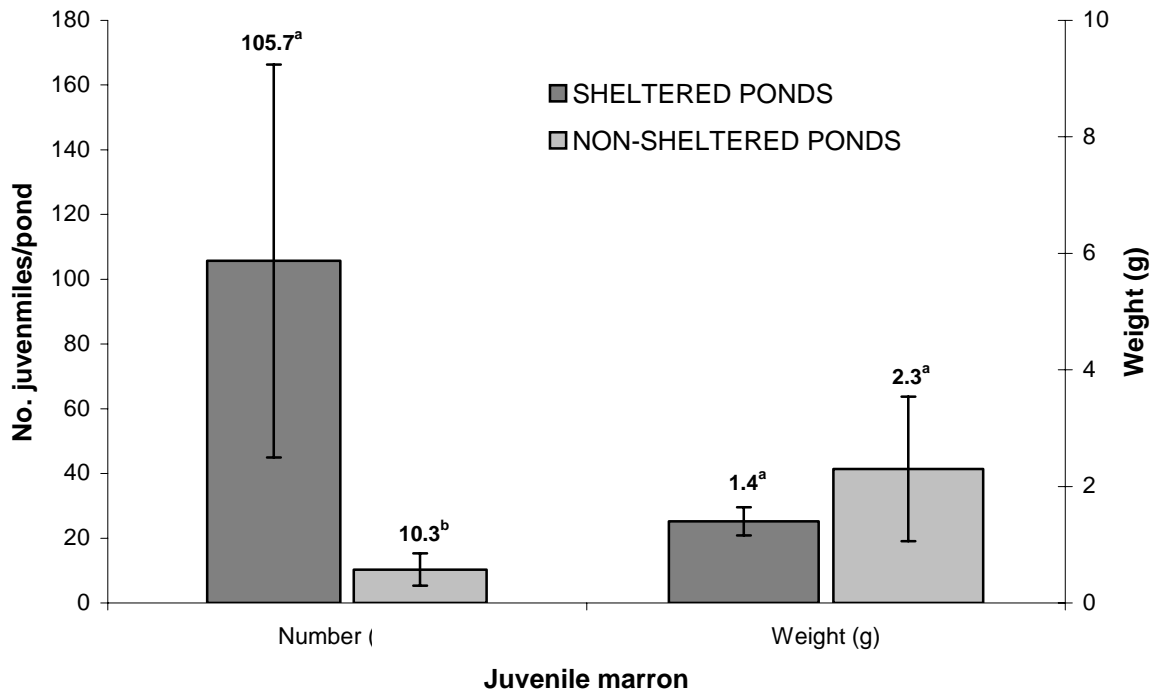
**Figure 6.6** length-weight ratios of marron in sheltered and non-sheltered treatments. Treatment means are significantly different ( $P<0.05$ ).

Marron harvested from the six ponds appeared to be in good condition, with <3% missing claws or legs, and all with high vigour (active, not sluggish). A large percentage of marron (>80%) were covered with algae (20% had moulted) .

#### 6.2.4.2 Juvenile marron

The numbers of juveniles collected in the three replicate ponds in each treatment were significantly greater in the sheltered systems ( $P<0.01$ ) (Figure 6.7), with 80, 175 and 80 marron collected in the three sheltered ponds, and 15, 5 and 11 in non-sheltered ponds. Based on mortality levels of brood females, this data equates to approximately 2.13 juveniles per surviving female in the sheltered treatment and 0.94 juveniles per surviving female in the non-sheltered treatment. Weight of juveniles was significantly higher in the non-sheltered systems at  $2.3\pm 1.24\text{g}$  ( $P<0.05$ ), compared with juveniles from sheltered ponds,  $1.4\pm 0.2\text{g}$  (Figure 6.7). The overall number of juveniles recovered from all ponds was greatly reduced from expected levels from monoculture operations

which, based on results from Whisson (1997), could have been in excess of 6400 individuals/pond, or accounting for survival of brood females; 3200 individuals/sheltered pond and 700/non-sheltered pond.

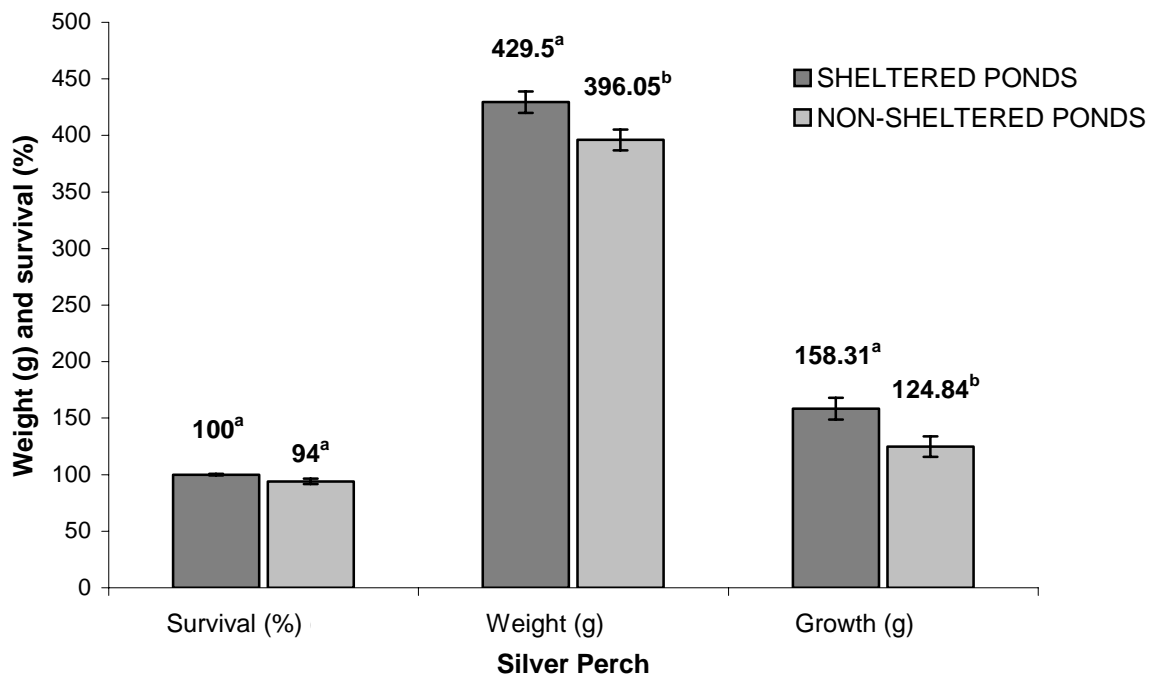


**Figure 6.7** Number and weight (g) of juveniles/pond in sheltered and non-sheltered ponds. Significant differences were reported between treatments where different superscripts are provided.

Juvenile marron were all harvested in good condition, as with adults, appendages were generally intact and vigour was high. No algal growth was apparent on juveniles.

### 6.2.4.3 Silver perch production

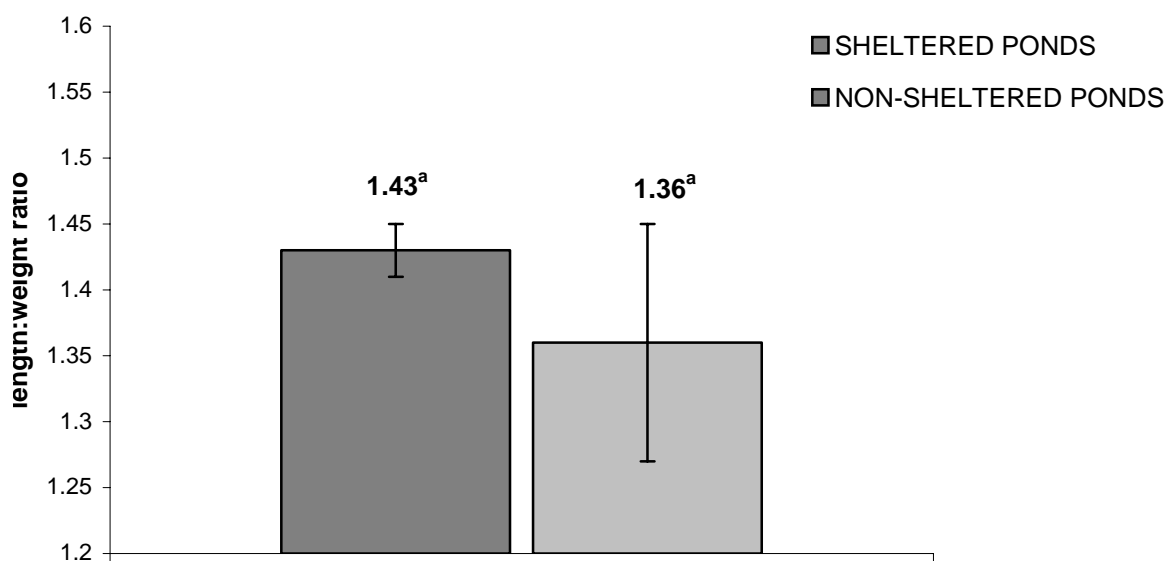
Production of silver perch in sheltered ponds was significantly greater in average weight (g) ( $P=0.013$ ) and growth (g) ( $P=0.012$ ), compared to non-sheltered ponds. Silver perch in sheltered ponds reached an average weight of  $429.5 \pm 9.58\text{g}$  compared to  $396.05 \pm 9.18\text{g}$  in non-sheltered systems (Figure 6.8). Survival of silver perch was high in all ponds,  $97 \pm 4\%$  (SD), with no significant variation between ponds or treatment groups ( $P > 0.1$ ).



**Figure 6.8** Survival (%), weight (g) and growth (g) of silver perch over three replicate ponds in the sheltered and non-sheltered treatments, over 117 days.

Significant differences were reported between treatments where different superscripts are provided.

The length-weight relationships between silver perch across treatment conditions showed no significant difference ( $P=0.147$ ) (Figure 6.9), however population variations (SE) were significantly increased in non-sheltered treatments ( $P<0.05$ ).



**Figure 6.9** Length-weight ratios of silver perch in each treatment group.

Significant differences were reported between treatments where different superscripts are provided.

#### 6.2.4.4 Additional observations

In previous trials conducted at the Collie Aquafarm, where marron were held in monoculture, a large number of dragonfly nymphs and tadpoles were evident during spring-summer. These species are commonly associated with negative effects on marron production, where tadpoles consume marron feed (Parker 1996), and perhaps target juvenile marron, and dragonfly nymphs are a confirmed predator of hatchling crayfish (Bird 1995, Jones 1995, Herbaholtz et al. 2004). In this trial, no observation of either species was made.

The presence of what appeared to be a single cormorant (*Phalacrocorax sp*) was noted intermittently throughout the trial duration. The cormorant was almost always observed on or around Ponds 3 and 6, both non-sheltered treatments. In order to determine an appropriate harvest time, a small number of pond shelters were checked weekly to observe numbers and sizes of marron. Almost no hatchlings and few juveniles were recorded in any of the checks made. Finally, filamentous green algae growth was apparent on shelters (Ponds 1, 4 and 5).

### 6.2.5 Discussion

#### 6.2.5.1 Silver perch production

Silver perch production (growth and survival) was similar to production data from previous trials based in earthen ponds. In this study silver perch, stocked at 2,083/ha in 0.072 ha ponds, gained on average between 125 and 158g (depending on treatment) over the 3-4 month trial period (Figure 6.8). In a study conducted by Rowland (1994), silver perch held in monoculture in 0.4 ha ponds (14,500/ha), increased 202g over a 7 month duration (September-March), grown from juveniles. Whisson (2001) reported average weight gains of 251g for silver perch cultured free-range in 0.1 ha marron ponds (1,800/ha), between November-July. Silver perch grown free-range with redclaw in 0.1 ha ponds between October and April displayed mean

weights of around 340g, being introduced at 18g (Jones and Ruscoe 1996), although survival was low (14.3%). Survival of silver perch was high in all ponds (94-100%), which is consistent with other studies where bird predation was not a major contributing factor (Rowland et al. 1994, Rowland 1995b, Jones and Ruscoe 1996). Whisson (1997) reported an average silver perch survival of 96% in tanks, and in separate study where perch were held free-range in three earthen ponds (0.1 ha) perch survival was  $92.4 \pm 3\%$  (Whisson 2000). The comparable growth and survival to silver perch monocultures (i.e. Jones and Ruscoe 1996) demonstrates that marron provide little to no negative effects from interaction. Similar results have been demonstrated with other species combination involving fish and crayfish. Red swamp crayfish (*Procambrus clarkii*) were not shown to influence survival of carp or tilapia fingerlings (Xinya 1995), and is consistent with previous studies examining interaction between marron and silver perch in tanks (Whisson 1997). In other situations, crayfish have had deleterious affects on cohabiting fish species, including spawning and feeding interference of tilapia by redclaw (*Cherax quadricarinatus*), and overall low production of fingerling catfish (*Ictalurus punctatus*) attributed to the presence of freshwater prawns (*Macrobrachium rosenbergii*) (Heinen et al. 1989).

Although survival of silver perch was high in all ponds, the single mortality recorded in the sheltered ponds compared to 27 perch unaccounted for in the non-sheltered ponds may be attributed to avian predation, as no carcasses were recovered.

As marron survival was reduced significantly in non-sheltered treatments compared to sheltered, it could be assumed that perch would display increased growth in these ponds. However, silver perch appeared to gain an advantage from culture in sheltered ponds, with average growth significantly reduced where no shelter was provided (Figure 6.8). The use of shelter within ponds may have contributed directly to the increased growth of perch in a number of ways. Silver perch being omnivorous may have gained increased feed and nutrition from algae observed growing on shelters. The shelter may have also reduced general stress levels, or stress associated with potential avian predation.

### 6.2.5.2 Marron production

A number of key differences were found in adult and juvenile marron production between the sheltered and non-sheltered treatment ponds. The most remarkable findings related to low overall survival of marron (adult and juvenile) compared to monoculture expectations, and increased mortality in ponds with no shelter.

The total number of juveniles recovered from all ponds were greatly reduced compared to monoculture broodstock-pond expectations. Female marron commonly produce between 150 and 250 prejuveniles (FWA 1999), with Whisson (1997) reporting survival rates of around 64 juveniles/surviving female. This data would equate to a potential 6400 juveniles in each experimental pond in this trial (based on 100 broodstock). An overriding factor was apparent, and several mechanisms may explain the low survival experienced in all ponds. These reasons include:

- Heavy silver perch predation on both juveniles and broodstock. Stein (1997) demonstrated that certain life-stages are more attractive than others to fish predators. With the loss of broodstock in all ponds, juveniles numbers could have been greatly influenced if predation occurred prior to release of juveniles (eggs-hatchlings), or similarly predation pressure on broodstock may have affected husbandry, i.e. reduced fanning or early release of eggs/pre-juveniles;
- Age of broodstock - broodstock in this trial were in their second year, with ideal brood-age around 3 yrs (FWA 1999);
- Handling of broodstock - the experiment required handling of fecund females. Handling stress can also lead to premature release of eggs and pre-juveniles from tail (Huner and Lindqvist 1991, Kuris 1991);
- High temperatures. Temperature may have been a contributing factor, as previously suggested by Whisson (2001). Marron are stressed over 24°C (Morrissy 1990) and in Queensland in the late 1990's environmental condition (particularly high temperatures) were attributed to collapse of the marron farming industry (Morrissy 1992a, Jones and Ruscoe 1996). In this trial, 42 days were recorded where temperatures exceeded 24°C, and three days over 26°C.

Low survival of juveniles has been reported in a number of freshwater crayfish species. Austin (1998) and Yeh and Rouse (1994) reported substantial losses in redclaw ponds,

up to 50%; Corey (1991) documented losses in the North American species *Orconectes propinquus*; and Morrissy (1970) stated high variability in the fecundity of marron. The factors affecting reproduction in decapods has been attributed to a number of factors, including physical dislodgement by abrasion, maternal activities and handling; infertility and interrupted development by genetic or environmental factors; and, infections, parasitism and predation (Huner and Lindqvist 1991, Kuris 1991).

It is difficult to draw conclusions from previous research into growth and survival of juvenile marron, in either polyculture or monoculture as most studies involved higher densities of marron stocked as juveniles. This appears to be the first study looking at juvenile production as a function of silver perch interaction in broodstock ponds. Whisson (1997) did report numbers and weight of juveniles retrieved from grow-out ponds, where 64 juveniles were recovered per surviving female, however number of berried females and fecundity could not be determined in this study. Studies examining survival of juvenile marron in monoculture operations have described a period of high mortality occurring in early grow-out of 0+ marron (Villarreal 1988, Bennison and Morrissy 1991, Morrissy et al. 1995a/b) and as marron mature, survival stabilises (Morrissy 1992b). This increased risk period for mortality of juvenile marron would have undoubtedly contributed to findings in this trial, compounded by polyculture interactions. Silver perch interaction has previously been attributed to reduced survival of 0+ marron (Whisson 1997). Therefore, if free range polyculture is carried out, the practice of stocking late 0+ marron should lead to higher overall survival.

Although the reasons for low survival of juvenile marron cannot be confirmed, observation of pond hides revealed few juveniles in the weeks and months preceding harvest. Due to this, it is assumed that marron were targeted at either broodstock or hatchlings stages, prior to development into juveniles. The ability of silver perch to predate on adult marron, which exceed gape size of the silver perch, has previously been demonstrated (Whisson 1997). In situations of low turbidity, silver perch have been shown to predate both on juvenile marron, and on larger marron - using their gregarious, schooling behaviour to attack large post moult individuals.

The survival of marron, both adult and juvenile, did show a significant improvement where shelter was provided (Figure 6.5 and 6.7). In sheltered ponds, survival of adult females averaged 49.7 individuals/pond and returned an average of 105.7 juveniles,



whereas ponds without shelter averaged only 11 adults and 10.3 juveniles/pond. In many studies, the addition of submerged refuge increased the opportunity for prey escape by restricting predator movements and obstructing sight (Gillinsky 1984, Diehl 1988), and in reducing crayfish activity and intraspecific interactions, lowering the risk of predator encounters (Westin and Gydemo 1988, Geddes et al. 1993).

These correlations between increased broodstock survival with juvenile survival suggest that the addition of shelter offered more protection of broodstock, which equated to increased number of juveniles. This supports the previous assumption that low overall survival was associated with predation of adult marron. In addition, as the number of juveniles per surviving adult was approximately 2.13 in sheltered ponds, compared to 0.94 in non-sheltered ponds, this also demonstrated that survivability of juveniles is increased once released from adult.

Although the addition of shelter resulted in increased survival of adult and juvenile marron in ponds, decreased average weight of marron was also recorded (Figure 6.5 and Figure 6.7), which was significant for adult females ( $P < 0.01$ ). The weight differences in marron grown with or without shelter may be due to a combination of a number of contributing factors. These include:

- Growth-density relationships: less competition in non-sheltered ponds where survival was reduced resulted in increased food availability, and reduced stress from less intraspecific competition. However, as feeding rates and shelter were relatively high for the final harvest numbers this is unlikely;
- Size selectivity of predators: silver perch may have targeted smaller individuals, and due to the increased mortality in non-sheltered ponds more smaller marron were removed - increasing average weight.
- Increased sheltering reduced foraging time. In T6:1, following identification of risk marron remained in shelter. In T6:2, this would equate to reduced foraging in ponds with shelter, however in the non-sheltered ponds marron may have foraged more resulting in increased growth, as sheltering was not an option.

The length to weight ratios of adult marron were significantly increased in non-sheltered ponds, which relates to increased weight per length over individuals in sheltered systems. One explanation may be reduced moulting in marron where shelter was not provided. During the inter-moult stage of freshwater crayfish, weight increases without

discernable change in length. Marron in the non-sheltered treatments may have resisted moulting to reduce vulnerability to predation. During moulting, and immediately following, marron are highly vulnerable to predators as their protective exoskeleton is soft, their chelae used in defence are soft, their activity is reduced, and the nutritional value to predator is said to increase markedly (Stein and Magnusson 1976, Dehli 1981, Blake and Hart 1993b). However, if marron were moulting more frequently in sheltered treatments, then overall weight of marron would be expected to be greater than in non-sheltered systems, which was not found.

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**The null hypothesis  $H_0$**  (6.4) was rejected. Mortality of both juvenile and brood marron was high in all treatments.

**The null hypothesis  $H_0$**  (6.5) was rejected as survival of brood and juvenile marron was increased where shelter was provided. Being omnivorous, it is assumed silver perch would be more inclined to choose alternate feed if marron demonstrated avoidance that would increase cost of capture to perch, in keeping with foraging theory.

**The null hypothesis  $H_0$**  (6.6) was rejected as growth of marron was not increased where shelter is provided. Whether this was due to reduced foraging as marron spent more time in shelter, or whether this was a function of prey size selectivity by silver perch, is uncertain. Silver perch displayed growth advantages when shelter was provided.

### **6.2.5.3 Additional remarks**

The presence of dragonfly nymphs and tadpoles were not observed in ponds in this trial, however in other monoculture investigations carried out in the same systems, large populations of both species were found (T7:1 and T7:2). These species have deleterious affects on marron production, due to predation on hatchlings-juvenile marron by dragonfly nymphs (Bird 1995, Herbaholtz et al. 2004), and competition for feed by tadpoles (Parker 1996). It is apparent from results in this trial, that although silver perch predate on marron, they also predate on the predators and competitors of marron. The introduction of a few silver perch in marron ponds, to target tadpoles and dragonfly nymphs, may prove advantageous when compared against some degree of predation on marron, especially in marron grow-out ponds - as larger marron would be at less risk from silver perch than juveniles. Likewise, if silver perch held in cages have similar effects on populations of tadpoles and dragonfly nymphs, this would prevent any impact to marron. Further investigation is required.



### **Marron-silver perch polyculture production in ponds**

*This chapter incorporates two field trials, a pilot study (T7:1) and a commercial grow-out trial (T7:2) used to gauge the impacts of a range of system variables on polyculture production of marron and caged silver perch*

## CHAPTER SEVEN

Results from laboratory studies in Chapters 4, 5 and 6 demonstrated a lack of effective avoidance strategies displayed by marron, and resulting high predation when held with predatory fish (Chapter 6). Following these results, field investigations described in this chapter focussed on the culture of caged silver perch in marron ponds. The use of cage culture was employed not only to protect marron from predation, but as marron do not appear to exhibit avoidance responses to exteroceptive cues from silver perch (Chapter 4 and 5), it was hypothesised that marron would not suffer from the physiological or behavioural stress that is often associated with perceived risk (Schreck et al. 1992, Schapker et al. 2002, Woodley and Peterson 2003).

The studies presented in this chapter explore recommendations from a previous study with marron and caged silver perch (Whisson 2000): expanding knowledge of growth-density relationships (stocking size and density of both marron and silver perch), and the effects of varied habitat complexity. Examination of cage culture conditions was also a key focus of trials in this chapter, following reports of reduced growth of silver perch when held in cages (Whisson 2000).

## 7.1 Effects of silver perch density in cages on polyculture production in ponds (pilot study)

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### 7.1.1 Introduction

Stocking silver perch in cages in marron ponds is an attractive option because interspecific interaction is avoided, bird predation is eliminated and management of stock is more effective than free range practices (Whisson 2000). However, in studies conducted to date, growth of silver perch is clearly reduced when held in cages (Rowland 1995c, Whisson 1999), with the growth-density relationship requiring further research due to its profound impact on system yields and profitability (Whisson 2000).

The first pond trial (T7:1) examined the polyculture of marron and caged silver perch in earthen ponds, where the impacts of silver perch density (100/cage and 200/cage) on production of marron and silver perch was tested. As previous data has indicated inhibited growth of silver perch in cages (Rowland 1995c, Whisson 1999), silver perch stocking size was increased from fingerlings (Whisson 2000) to advanced juveniles. This was done to determine whether this size of silver perch was amenable to cage culture - with the idea of stocking larger perch in an attempt to culture market sized fish in one season.

The null hypotheses for T7:1 were:

**$H_0$ :** Growth of marron under cohabitation with silver perch will show no variation compared to growth in monoculture 7.1

**$H_0$ :** No growth-density effects will be observed for either species, based on the densities examined 7.2

### 7.1.2 Aim

The aim of this preliminary pond trial was to evaluate growth, survival and polyculture production of marron (*Cherax tenuimanus*) and juvenile silver perch (*Bidyanus bidyanus*) in earthen ponds, with perch reared in floating cages.

### 7.1.3 Objectives

1. To assess marron growth and survival in an earthen polysystem containing caged silver perch.
2. To examine growth of advanced juvenile silver perch (~200g) at two densities (100 and 200) in floating grow-out cages within marron ponds.
3. To gather data regarding synergistic effects of caged silver perch on marron, and determine any correlation between marron growth rate and perch density.
4. To discuss results in light of communication factors documented in previous laboratory trials (T4:1, T5:1, T5:2, T6:1)

#### 7.1.4 Experimental design

Research was conducted in six experimental aquaculture ponds at the Collie Aquafarm (Section 3.1.2.2). All ponds were equipped with bottom drainage, paddlewheel aeration and mesh shelters for crayfish (50 shelters per pond). One floating fish cage (15m x 1.5m x 0.75m) (Section 3.1.2.2) was placed in the centre of each pond (Plate 7.1).



**Plate 7.1** Aquaculture research ponds with paddlewheel and fish cage.

Marron and silver perch were sourced from monoculture ponds in Pemberton (34°S, 116°E) and immediately introduced to ponds. Fifty marron ( $71.5 \pm 0.4\text{g}$ ) were stocked in each pond on 15 March 2002. Silver perch ( $199.4 \pm 0.6\text{g}$ ) had previously been introduced to cages on 28 December 2001, according to following treatments:

Treatment	Marron (number/pond)	Silver perch (number/cage)
1	50	0
2	50	100
3	50	200

Each treatment was replicated in two ponds, allocated using a random block design. Silver perch and marron were fed commercial preparations (Appendix C and D) three



times per week. Silver perch were fed at a rate determined by feeding each treatment to satiation once per month, while marron were fed the equivalent of 1.5 % of biomass per day in each pond. Thirty silver perch were randomly sampled from each cage bi-monthly and weighed individually. Marron were harvested on the 13-15 June 2002, and weighed individually, representing a grow-out period of 90 days. Silver perch were harvested and weighed on 16 July 2002 after 200 days.

Water quality was monitored twice weekly by recording pH, dissolved oxygen, salinity, conductivity, and temperature in each aquaculture pond. Treatment means were compared using a one-factor ANOVA (water quality data in Appendix A). Temperature averaged ( $\pm$ SE)  $21.9\pm 1.4^{\circ}\text{C}$  between December 2001 and April 2002, and  $14.8\pm 1.0^{\circ}\text{C}$  between May and July 2002.

### **7.1.5 Statistical analysis**

Silver perch and marron data were analysed for differences in survival, initial and final weight, increase in biomass, and combined pond yield using a one-factor ANOVA and Scheffe's F-test to rate significant differences between treatment means.

### 7.1.6 Results

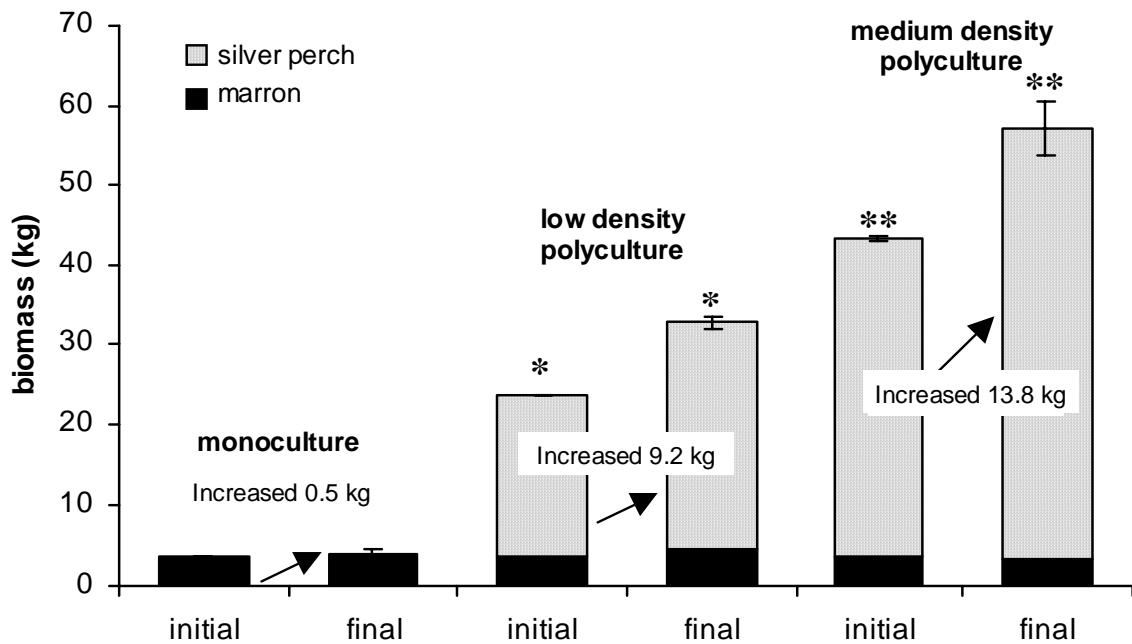
Marron reared in polyculture ponds with silver perch demonstrated a significant increase in final weight and SGR over the 90-day trial, compared to marron held in monoculture (Table 7.1). Marron survival averaged 75.7% in all ponds, with no significant differences between treatments ( $P>0.05$ ) (Table 7.1). Almost all marron mortalities were recovered from pond banks, above the water line, with injuries indicative of bird predation. No density effect was apparent for silver perch stocked in cages (Table 7.1), with a 41% average increase in biomass recorded over the duration of the trial, and no significant variations in survival or growth between treatments ( $P>0.1$ ). Silver perch survival was high in all ponds, averaging 97.4% (Table 7.1).

**Table 7.1** Growth and survival of marron and silver perch reared in polyculture ( $\pm$  SE)

	Marron, <i>C. tenuimanus</i>			Silver perch, <i>B. bidyanus</i>	
	0 fish/cage	100 fish/cage	200 fish/cage	100 fish/cage	200 fish/cage
<b>Initial weight (g)</b>	71.6 $\pm$ 0.5 <sup>a</sup>	71.2 $\pm$ 0.1 <sup>a</sup>	71.8 $\pm$ 0.3 <sup>a</sup>	200.1 $\pm$ 0.2 <sup>1</sup>	198.8 $\pm$ 0.6 <sup>1</sup>
<b>Final weight (g)</b>	100.5 $\pm$ 4.1 <sup>a</sup>	117.8 $\pm$ 1.6 <sup>b</sup>	107.2 $\pm$ 1.2 <sup>ab</sup>	286.2 $\pm$ 4.3 <sup>1</sup>	276.5 $\pm$ 24.9 <sup>1</sup>
<b>Survival (%)</b>	82 $\pm$ 11.3 <sup>a</sup>	80 $\pm$ 0.1 <sup>a</sup>	65 $\pm$ 24.1 <sup>a</sup>	98 $\pm$ 2.0 <sup>1</sup>	96.75 $\pm$ 1.8 <sup>1</sup>
<b>Pond biomass (kg/ha)</b>	4.1 $\pm$ 0.6 <sup>a</sup>	4.7 $\pm$ 0.1 <sup>a</sup>	3.5 $\pm$ 1.0 <sup>a</sup>	28.1 $\pm$ 0.1 <sup>1</sup>	53.6 $\pm$ 5.8 <sup>2</sup>
<b>SGR (%/day)</b>	0.39 $\pm$ 0.02 <sup>a</sup>	0.58 $\pm$ 0.01 <sup>c</sup>	0.46 $\pm$ 0.00 <sup>b</sup>	0.18 $\pm$ 0.02 <sup>1</sup>	0.16 $\pm$ 0.03 <sup>1</sup>

Values in the same row for same species followed by the same superscript are not significantly different ( $P<0.05$ ). Pond biomass for silver perch is identical to cage biomass

The marron - silver perch polyculture regime resulted in significantly higher pond yields over marron monoculture ponds ( $P<0.05$ ), with yields from medium density polyculture ponds increasing biomass by an average of 13.8 kg (Figure 7.1).



**Figure 7.1** Pond yields: marron monoculture *versus* marron-perch polyculture

\* $P < 0.05$ ; \*\* $P < 0.01$

No significant differences occurred between ponds for water quality ( $P < 0.05$ ) (Appendix A). Temperature during the culture period for silver perch averaged  $19.2 \pm 3.8^\circ\text{C}$ , with 108 days over  $20^\circ\text{C}$ . Temperature during the culture period for marron averaged  $18.0 \pm 3.2^\circ\text{C}$ , with 21 days over  $20^\circ\text{C}$ .

### 7.1.7 Discussion

Results from this trial were consistent with several other studies demonstrating significantly higher net yields from polyculture ponds compared to monoculture (Perry and Tarver 1987, Brummett and Alon 1994, Wahab et al. 1995, Jones and Ruscoe 1996). Further, evidence of synergism was seen with increased growth of marron when cultured in the same system with silver perch, compared to production in monoculture ponds (Table 7.1). While this result is only preliminary due to the low replication of treatments, it concurs with previous findings by Whisson (1998, 2000) and warrants further investigation at commercial densities.

Marron survival was affected by bird predation in some ponds, with evidence of eaten carcasses on pond banks, however levels in most ponds (~80%) compare favourably to

industry standards (Morrissy 1992b). Silver perch showed high survival in all ponds, equal or above documented levels (Rowland 1995b, Rowland et al 1984), and showed no sign of predation, almost certainly due to bird netting over the cages. However, the presence of avian predators on, or in the air above, cages may have increased stress to fish, warranting further investigation.

The use of floating cages in aquaculture ponds offers the farmer several benefits, including protection from bird predation, and management efficiencies in terms of feeding, grading, harvesting, and inspection (Karlsen 1993, Beveridge 1996, Whisson 2000). However, the negative effects of higher densities are compounded in cages (e.g. flyer/runt flattening of population distribution), with regular grading an important requirement of this type of culture (Beveridge 1996). Other studies have stocked relatively small silver perch (<20g) in cages, recording decreased growth at higher densities in all cases (Whisson 1998, 2000). In the present study, advanced juveniles (~200g) were stocked in cages to provide preliminary growth-density data for this size class. No density effect was apparent in terms of growth or survival when silver perch were stocked at 100 (1.36 kg/m<sup>3</sup>) or 200 (2.72 kg/m<sup>3</sup>) per cage, indicating that higher densities should be examined for this size class, with a view to single summer grow-out periods. However, growth of silver perch throughout all cages (0.16-0.18%/day) was lower than reported free-range growth data (1.20±0.02%/day, Whisson 2000), which is not unexpected as this trial was predominantly conducted under low water temperatures, towards the end of the growth season. Thus, given optimal conditions, increased growth may have resulted in density-effects.

### **7.1.8 Limitations and recommendations**

As this was a pilot study, stocking densities were kept low, and treatments were examined in only two replicate ponds. This was done to provide a research base for future work, without jeopardising large numbers of stock. Additional limitations exist as the facility used was in its first year of operation. In aquaculture involving benthic foragers such as marron, ponds may require a few years of operation before sufficient development of benthos is able to supplement the diet of crayfish (Morrissy et al. 1995b). Bird netting is recommended to reduce avian predation, however due to the expense of netting material, other options should be explored.

While the grow-out period for silver perch was 200 days, the timing of stocking and harvest only allowed a relatively short growing period, as silver perch require water temperatures above 25°C for optimum growth (Rowland 1994c). In this study, average pond temperature was 19.2±3.8°C, with only three months recording averages higher than 20°C. It is therefore recommended that further research be conducted over a complete growing season (October to April).

Improvement of cage conditions, incorporating stress alleviation and encouraging growth of natural feed, may increase growth of silver perch and should be examined further, and as no growth-density effects were found, increased densities should be examined.

#### 7.1.9 Concluding remarks

This trial was conducted using remediated water from an acid mine lake (Section 3.1.2.2). The trial reported here has, for the first time, demonstrated the potential for commercial aquaculture as a beneficial end use option for final mining lakes within the Collie Coal Basin. Water quality data indicated that remediation was successful, providing a 5 ML aquaculture farm with water that sustained aquatic life and facilitated fish and crayfish growth and survival over an extended period. Results from this initial pilot study has demonstrated the adequacy of the Collie mine lake water treatment system and Aquafarm ponds for use in subsequent investigations.

As no growth-density effects were apparent, further study should focus on increased density of both species. Continued examination of habitat complexity in respect to pond management and production potential is also supported, in particular a method of removing all shelters efficiently and quickly. Finally, the use of advanced sized silver perch to produce market sized stock demonstrated no negative affects on stock, further examination should be carried out over the full growth season (Oct-April) to determine whether market sized fish can be produced in one growth season.

**The null hypothesis  $H_0$  (7.1)** was rejected. Marron grown in duoculture with silver perch grew significantly more than monocultured marron.

**The null hypothesis  $H_0$  (7.2)** was accepted. No growth-density effects were observed for either species at the densities examined.

## **7.2 Effect of increased pond density and habitat complexity on polyculture production of marron and caged silver perch**

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Preliminary research conducted in the first trial of this chapter (T7:1) demonstrated successful polyculture of marron and silver perch in ameliorated mine lake water at relatively low densities. As no negative growth-density relationships were apparent, trial T7:2 examined increased densities of both marron and silver perch. Growth-density relationships for silver perch were examined through the use of two cages/pond (compare one cage/pond in T7:1). Multiple cages were examined to determine if production aspects were influenced more by relative density (in cages) or pond density, allowing comparison of results between treatments and within systems.

Habitat was included in silver perch cages for the first time, in an effort to improve cage conditions. The addition of habitat to cages was to reduce stress to silver perch from external disturbance, such as the presence of avian predators, and also to encourage growth of periphyton (assemblage of attached aquatic plant and animal organisms on submerged substrates), providing a supplemental feed for silver perch.

Growth inhibition of fish in cages has been attributed to reduced access to natural feed (Masser 1988), which could explain poor growth of caged silver perch reported in previous trials (Whisson 2000). Given the feeding biology of silver perch (Rowland and Kearney 1992, Lambert 1998), they would naturally target aquatic insects, detritus and crustaceans. The use of periphyton in aquaculture has previously been used with success, based on the finding that many herbivorous and omnivorous fish prefer feeding on benthic, epilithic or periphytic algae, rather than on small phytoplankton (Scott and Crossman 1973, Horn 1989, van Dam et al. 2002). Providing ponds with artificial substrates stimulates the growth of attached organisms that are more easily harvested by fish (Keshavanath et al. 2004) and several experiments in which artificial substrates were added have shown that periphyton can increase the production of fish compared to systems without substrates (Pardue 1973, Hem and Avit 1994, Wahab et al. 1999, Azim et al. 2001, Keshavanath and Wahab 2001, Keshavanath et al. 2001).

Note: In this trial, for the first time, commercial marron shelters were provided in attached lines. The use of single synthetic loose-mesh hides in marron ponds is a common practice, however hides must be removed prior to drain harvesting, as marron will often remain in hides on the banks, leaving them exposed to air and high

temperatures. If hides are left in ponds they can be annoying obstacles to the removal of marron. The addition of shelter lines assists in shelter removal prior to drain harvesting and are also an effective removal tool for sampling. Shelter harvests, prior to draining ponds, can reduce the number of marron forced into mud and sediment, which can have deleterious effects on the survival and condition of stock. *Vibrio* and *Aeromonas* bacteria multiply in gills due to trapped sediment (Morrissy 1995, FWA 1999, Lawrence and Morrissy 2000), often resulting in mortality or reduced marketability due to the increased onset of tail blisters (Storer 2002, Storer et al 2002b). Although this was not a research aim, results will be discussed in respect to management techniques for marron farming.

The null hypotheses for T7:2 were:

- $H_0$ :** Growth of marron under cohabitation with silver perch will show no variation compared to growth in monoculture **7.3**
- $H_0$ :** Habitat provided in floating cages will have no influence on growth of silver perch **7.4**
- $H_0$ :** No growth-density effects will be observed for either species, based on the densities examined **7.5**

### **7.2.1 Aim**

The aim of this experiment (T7:2) was to further investigate optimal stocking densities for polyculture of marron and silver perch in commercial-scale ponds, focussing on the effects from cage culture conditions and underlying factors previously described.

### **7.2.2 Objectives**

The specific objectives of T7:2 were to:

1. Compare growth, survival, condition, harvest sex ratio and population distribution of marron reared with caged silver perch at two densities.
2. Compare growth, survival and condition of silver perch reared in cages at 100 and 200 fish/cage, contrasting data with pond density.
3. Investigate the effect of cage shelters on the general behaviour, growth, survival and condition of silver perch.
4. Evaluate the influence of the fish cage itself on a polyculture system housing silver perch in cages.
5. Discuss implication for the production of market sized silver perch for a one-year grow-out cycle.



### 7.2.3 Materials and methods

Research was conducted in six experimental aquaculture ponds at the Collie Aquafarm (Section 3.1.2.2). All ponds were equipped with bottom drainage, paddlewheel aeration and mesh shelters for crayfish (70 shelters/pond, approx. 1/10m<sup>2</sup>). Silver perch were housed in two floating fish cages (15m x 1.5m x 0.75m) (Section 3.1.1) held in the centre of each pond (Figure 7.2). All ponds were dried and cleaned prior to the commencement of the experiment. One tonne of coarse lime rock was added to each pond prior to filling to maintain alkalinity and increase calcium throughout the trial period. Note: bird netting ponds is recommended, although not used in this trial as was outside budget.

#### 7.2.3.1 Experimental design

The experiment comprised three treatments, with two replicates allocated to ponds using a random block design. Treatments were:

1. 600 free-range marron and 0 silver perch
2. 600 free-range marron and 100 silver perch in two cages (i.e. 200/pond)
3. 600 free-range marron and 200 silver perch in two cages (i.e. 400/pond).

The densities chosen for this study were below commercial monoculture densities for both marron and silver perch, however the combined polyculture biomass was the highest tested to date with this combination of species.

Four shelter lines were introduced to each pond - two lines of 25 shelters and two lines of 10 shelters. Placement of the shelters was as per Figure 7.2, with shelters on each line approximately 1m apart. Shelter lines were initially placed 3-5m from the pond bank, at a depth of between 0.7m and 1.2m (Plate 7.2), however one shelter line was moved closer to the edge of each pond (<0.5m depth) after the first month (see 7.2.4.2). Thirty loose-mesh shelters were also provided in each fish cage (approx. 2/ m<sup>2</sup>) (Plate 7.3).

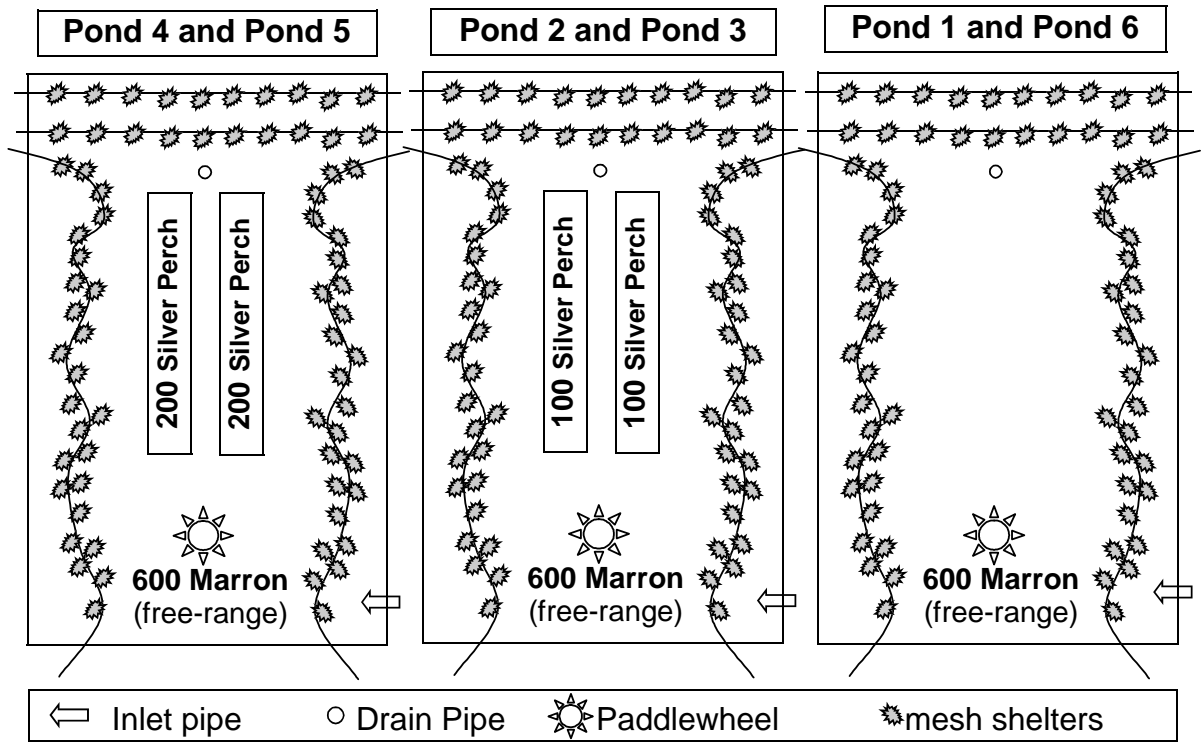


Figure 7.2 Treatment design and allocation to ponds



Plate 7.2 Aquaculture ponds at the Collie facility. Foreground: two floating fish cages. Background: monoculture pond. Shelter lines visible in both ponds



**Plate 7.3** Left: pond shelters arranged in lines, Right: shelter provided in fish cages

### 7.2.3.2 Duration

The experiment was conducted between March and November 2004. Silver perch were introduced to ponds between the 12 and 21 March, and marron one month later, between the 12 and 21 April. Final harvest was between the 10 and 19 November 2004. Total grow-out period was 243 days for silver perch and 213 days for marron.

### 7.2.3.3 Experimental animals

Marron and perch were sourced from monoculture ponds in Pemberton (34°S, 116°E). Marron (82.0±9.3g) were randomly distributed in all ponds at a stocking density of 0.83/m<sup>2</sup> (600/pond). Sex ratios of marron were exactly 2:3 (M:F) in each pond, based on availability of stock. Silver perch (184±35.6g) were weighed and distributed into floating cages. Population distributions of marron and silver perch at stocking showed no significant variation ( $P>0.05$ ).

### 7.2.3.4 Water quality measurements

Water quality was monitored twice weekly, providing pH, dissolved oxygen, salinity, conductivity, temperature and turbidity data (Appendix A) and treatment means were compared using a one-factor ANOVA.

### 7.2.3.5 Supplemental feeding

Silver perch and marron were fed commercial preparations (Appendix C and D, respectively) three times per week, between 1600-1800 h. Marron and perch were fed at a rate determined by feeding each treatment to satiation once per month (Table 7.2). Marron feed rate was determined using feeding trays located around each pond, which were 1m square mesh (500 um) feeding platforms (Figure 6.4). Clearance of feed placed on feeding platforms was monitored after 8 h and levels increased or decreased accordingly. Note: feeding rates were also subject to manipulation depending on phytoplankton densities, with reductions in feed made where secchi depth was recorded less than 300 mm.

Satiation levels for silver perch were initially determined 30 min. after feeding based on clearance of feeding platforms installed in each cage (Section 3.1.2.2). However, as turbidity increased, observation of general feeding behaviour was used to determine feed rate, as feeding platforms (0.75m under water surface) were no longer visible.

**Table 7.2** Marron and silver perch feeding schedule

Month	Feed supplied (kg)				
	Marron Each pond	Medium density perch Pond 2	High density perch Pond 3	Pond 4	Pond 5
<b>March</b>		4.3	4.3	8.7	8.7
<b>April</b>	2.2	15.2	15.2	30.4	30.4
<b>May</b>	6.0	7.0	6.4	16.2	15.2
<b>June</b>	2.2	4.7	-	6.1	9.4
<b>July</b>	4.4	2.6	-	4.7	3.9
<b>August</b>	4.1	2.8	-	5.5	6.6
<b>September</b>	3.2	6.2	-	9.6	12.4
<b>October</b>	5.3	4.1	-	9.1	9.6
<b>November</b>	2.2	2.2	-	4.9	5.7
<b>Total</b>	<b>29.503 kg</b>	<b>49.192 kg</b>	<b>25.928 kg</b>	<b>95.171 kg</b>	<b>101.77 kg</b>

Missing feed data for silver perch in Pond 3 was due to a fish-kill, explained in Section 7.2.3.8.

### 7.2.3.6 Sampling procedures and measurements

Weight, size (length and width) and survival of marron (*C. tenuimanus*) and silver perch (*B. bidyanus*) were recorded, with growth and biomass calculated. Length-weight and sex ratios of marron was also recorded at all sample points. Silver perch and marron were sample-harvested every two months, where 30% of silver perch per cage and 10% of marron per pond were examined. Marron sampling was done using shelter harvesting, where a two-hand net (1.5m x 0.75m and 5 mm x 5 mm mesh size) was placed under each loose mesh marron hide to capture marron as the hide was pulled above the pond surface. This sampling procedure was tested in ponds prior to this trial, with results showing that the sample population was significantly similar to pond population ( $P < 0.05$ ). Silver perch were sampled using a purpose built grader-net with slightly smaller dimensions than the internal dimensions of fish cages (1.45m x 0.7m) to prevent movement of fish past the grader (Plate 7.4). Silver perch were transferred to smaller cages adjacent to the pond edge to reduce time out of water during sampling. All stock was weighed using portable scales (0.01g), on moist soft mats, and returned immediately to ponds or cages. All stock was removed from water, weighed, length, sexed (in marron), checked for injuries, and returned to water within 10 s.



**Plate 7.4** Silver perch being harvested from fish cage using a purpose built grader-net

Final harvest was conducted between 17 and 26 November. All fish were removed from cages and basic morphometric measurements made on all individuals. As many marron as possible were removed from ponds using shelter harvest, the remainder were collected in drain harvesting, conducted between 0600 and 0900 h, when temperature and light intensity were low. Note: as many marron were berried in November collections, data were only collected from males and non-berried females. This was done so data were not biased by variations due to females carrying eggs.

### 7.2.3.7 Statistical analysis

Univariate one-way ANOVA using Tamhane's T2 method and Dunnett's T3 procedure (reported), was used to compare population distributions (initial and final) for both marron and silver perch between ponds and treatments, and also average growth (g) and length-weight ratios for both marron and silver perch between treatment groups (Selvanathan et al. 2000). Percentage survival between ponds was compared with Chi<sup>2</sup> (marron) and Binomial (silver perch) non-parametric tests (Selvanathan et al. 2000). Reproduction (percentage berried females) was compared with the Chi<sup>2</sup> test. Growth rates of marron and silver perch in each treatment between sample points were analysed with Independent samples t-test for each time period. Specific growth rates (SGR) of marron and perch were determined using the following formula:  $SGR = (\ln(W_f) - \ln(W_i)) * 100 / t$ , where  $W_f$  = final weight in g,  $W_i$  = initial weight in g, and  $t$  = growth period in days (Hopkins 1992). SGR is expressed as the percentage weight increase (g) per day. Feed conversions rates (FCR) were not determined for marron as survival could only be computed at final harvest. FCR for silver perch was determined as the amount of weight gained per kilogram of feed, where  $FCR = \text{pond biomass (kg)} / \text{feed (kg)}$ , over the same period. FCR's and SGR were compared with Independent samples t-tests.

### 7.2.3.8 Outlier analysis

On June 3 2004 (72 days after trial started), a malfunction was discovered in the water treatment system supplying water to Pond 3 (high density perch treatment), resulting in low pH in this pond. Following pond harvest, only 2% of the initial number of silver perch introduced to Pond 3 remained, compared to an average of  $92 \pm 7.5\%$  for all other ponds. Pond 3 silver perch data were subsequently removed from analysis. No impact from Pond 3 conditions was apparent in marron survival, therefore data is included in results for comparisons with production in other ponds, however data were not included in treatment comparisons, for obvious reasons.

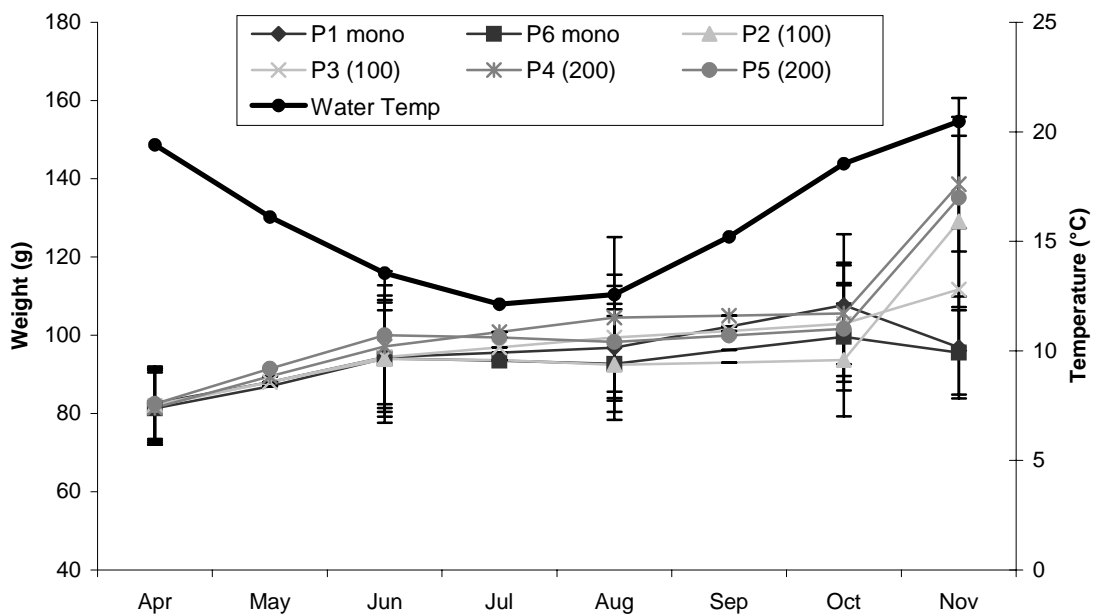
A discussion of factors contributing to the problems encountered in Pond 3 is provided in limitations (section 7.2.6).

## 7.2.4 Results

### 7.2.4.1 Marron growth

Growth of marron in all ponds was statistically similar ( $P>0.01$ ) during the first 6 months, however in the final sample point (October-November), where temperatures approached 20°C, marron reared in polyculture demonstrated significantly increased growth over monoculture ( $P<0.01$ ), and weight of marron in high density polyculture systems was significantly greater than in medium density ponds ( $P=0.024$ ) (Figure 7.3).

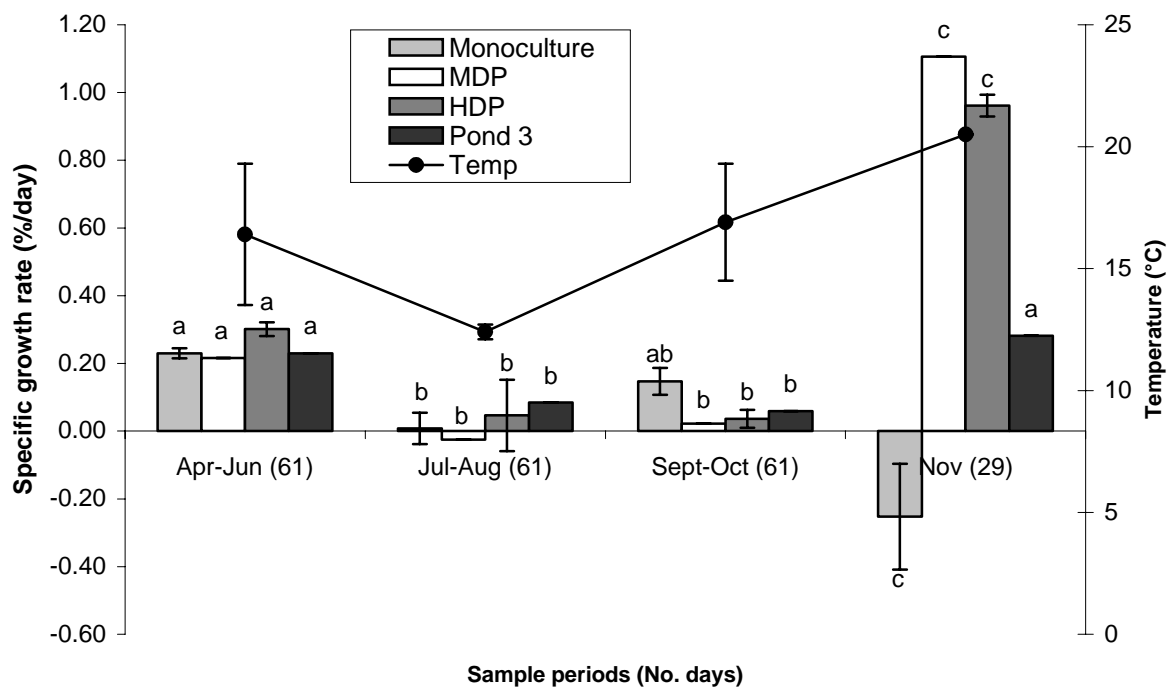
Marron growth was clearly influenced by water temperature. Comparisons of growth over time for each treatment showed significant increases between April and June ( $P<0.01$ ) and between October and November ( $P<0.05$ ), however no significant change between June and October ( $P>0.1$ ) (Figure 7.3). Marron in Ponds 2, 3, 5 and 6 showed negative growth between June and August, when temperatures were below 13°C, and marron from Ponds 1 (monoculture) and 4 (high density polyculture) showed only minimal increases.



**Figure 7.3** Average weight (g) ( $\pm$ SD) of marron grown in each treatment pond.

Comparison between marron growth in Pond 3 to all other ponds showed no significant variation with polyculture systems ( $P>0.1$ ), but significantly higher growth compared to monoculture ( $P<0.05$ ).

Specific growth rate (SGR) (see section 7.2.3.7 for formula) of marron in each sample period were compared between treatments (Figure 7.4). SGR was directly correlated with temperature (Figure 7.4), with significantly reduction between July and October ( $<15^{\circ}\text{C}$ ), compared to data in April-June and for November ( $P<0.05$ ), where temperatures were between  $15\text{-}20^{\circ}\text{C}$ . The most significant increases in growth rates were recorded in November ( $P<0.01$ ), where temperatures reached  $20^{\circ}\text{C}$ . In November, SGR of marron grown in polyculture were significantly higher than data recorded in previous sample periods ( $P<0.05$ ), and compared against data from monoculture ponds ( $P<0.01$ ).



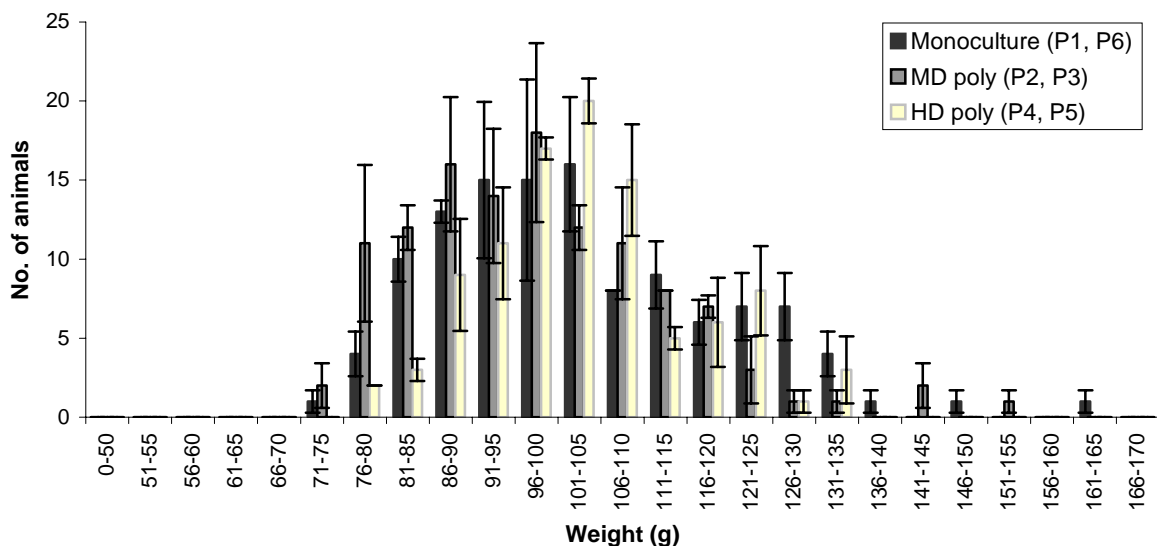
**Figure 7.4** Specific growth rates of marron in each treatment, and in Pond 3 (fish kill) for each sample period.

Data for marron in high density polyculture and monoculture ponds is the average of two replicate ponds, medium density polyculture only incorporates one pond, due to fish kill in replicate pond. Pond 3, where the fish kill occurred, is included for reference. Where different descriptors are present within each treatment a significant variation ( $P<0.05$ ) was found.



No significant differences in length-weight ratios of marron were apparent between ponds throughout the sample period ( $P>0.1$ ).

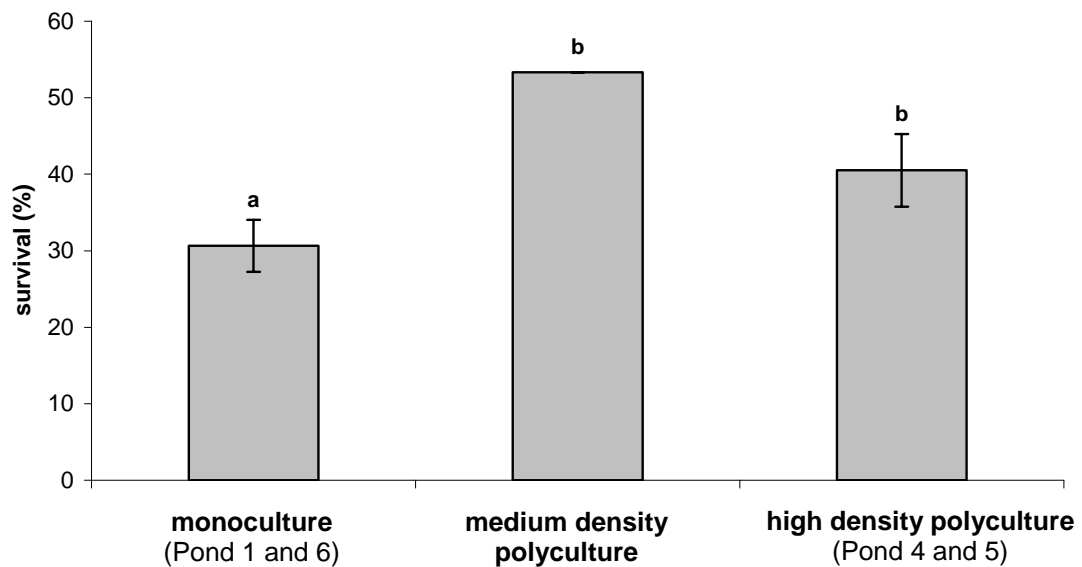
Population distributions were similar between all treatments ( $P>0.1$ ), except for a few fliers recorded in polyculture ponds (Figure 7.5). Data were only presented from October due to a large number of berried females in each pond in November, and weights from berried animals would have influenced weight distributions, which would not be indicative of optimal growth.



**Figure 7.5** Population distribution of marron in each treatment in October

#### 7.2.4.2 Marron survival

Marron survival was relatively low in all ponds, between 26.5-53.3% (Figure 7.6), although survival rates were higher in polyculture ponds ( $P<0.01$ ). Survival between medium and high density polyculture was statistically similar ( $P>0.1$ ).



**Figure 7.6** Survival of marron held in monoculture, and in medium and high density silver perch treatment ponds

Approximately 90% of marron mortalities observed in ponds were recorded in the first month, with numerous carcasses observed just above water level. Autopsy of mortalities revealed that 96% of individuals possessed either an endoskin or had recently moulted, being soft and possessing large gastroliths. The occurrence of dead moulting marron above the water level suggested avian predation (terrestrial predation was prevented by perimeter fence). This was consistent with damage to carcasses (Plate 7.5).

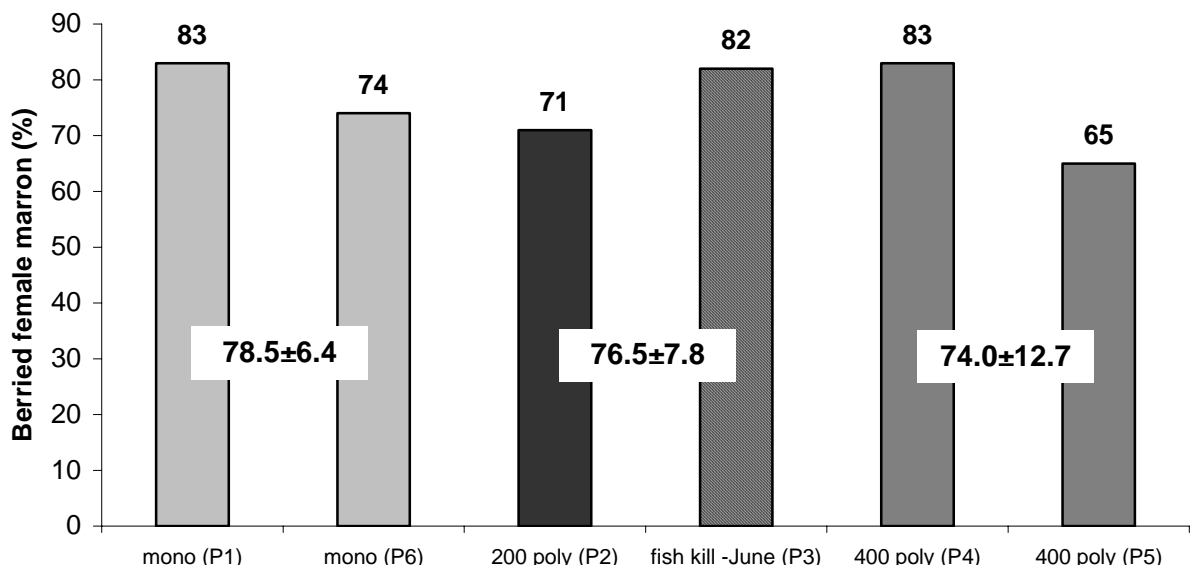


**Plate 7.5** Damage to the side of carapace, indicative of bird predation

Following these observations, one shelter line was placed along the bank of each pond (within 300 and 600 mm from waters edge) and no significant mortalities were recorded following its inclusion. In addition, regular checks of bank shelters revealed large numbers of moulting marron inhabiting the refuge.

#### 7.2.4.3 Marron reproduction

Marron reproduction was high in all ponds ( $76.3 \pm 7.5\%$  of all females) (Figure 7.7), with no significant variations reported between ponds or treatments ( $P > 0.1$ ). Fecundity was visually reduced in monoculture ponds, although as egg counts were not carried out this could not be quantified .

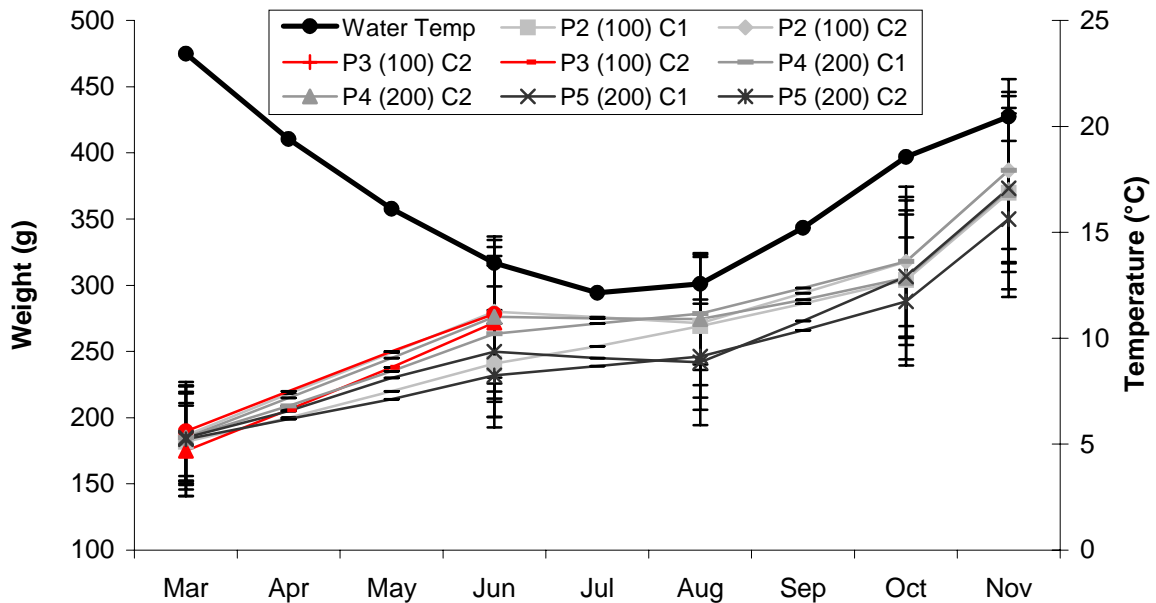


**Figure 7.7** Percentage of female marron berried in each pond

#### 7.2.4.4 Silver perch growth

Growth rate of silver perch showed no significant differences between ponds ( $P = 0.574$ ) (Figure 7.8), with average weight increasing from  $184.0 \pm 35.6\text{g}$  to  $373.1 \pm 62.5\text{g}$  across all ponds, over the 243 day trial period. Growth of silver perch in both treatments showed significant increases between March and June, and between August and November ( $P < 0.05$ ), however, no significant change was found between June and August. On average silver perch gained  $188.8 \pm 29.6\text{g}$  over the trial duration, with  $66.4 \pm 5.8\text{g}$  added

between October and November alone. No significant variations in growth or survival were apparent between cages in each pond ( $P>0.1$ ). Five silver perch were found free-range in Pond 2 in November, with counts showing that these fish escaped from cage 1.

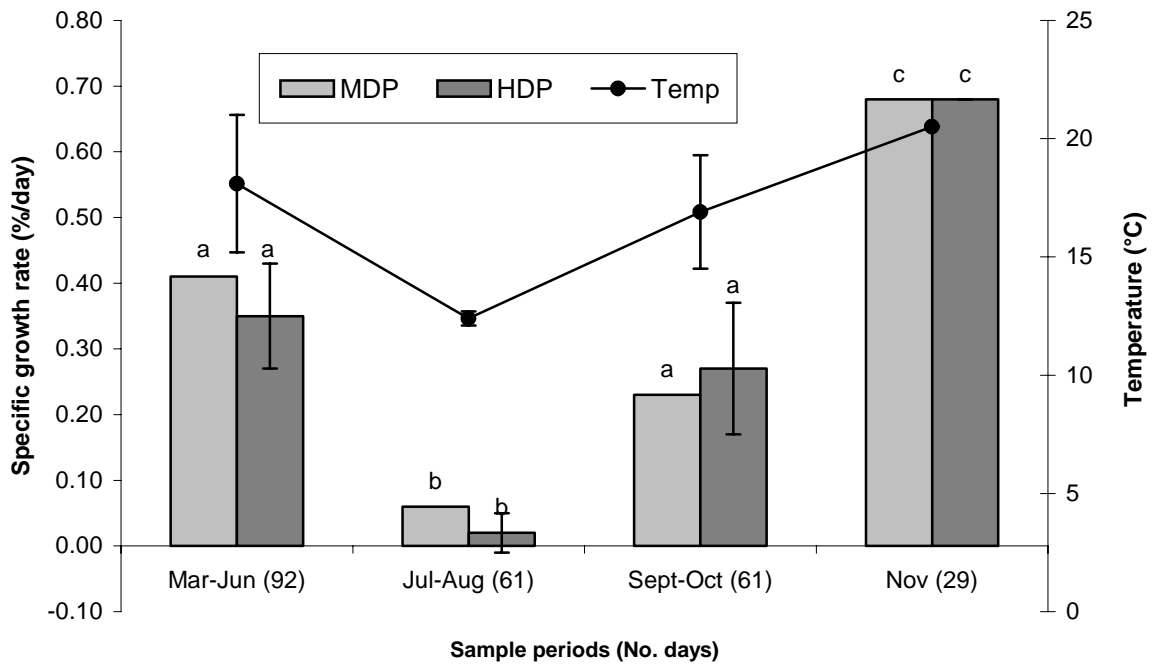


**Figure 7.8** Silver perch average growth ( $\pm$ SD) for each cage.

Key descriptors: i.e. P4 (200) C2 = Pond 4, 200 fish in cage 2.

Water temperature data demonstrated a direct correlation with growth of silver perch. Between June and August, when temperatures were below 15°C, silver perch showed negative growth in three ponds, and negligible growth in others. Highest growth was recorded where temperatures approached and exceeded 20°C (March-April and October-November).

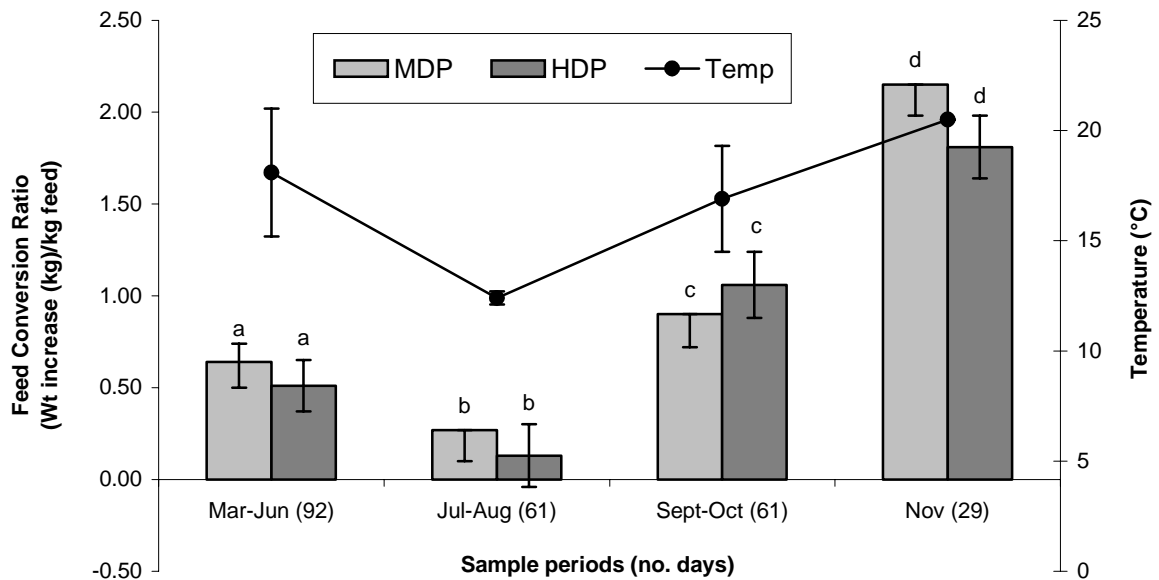
Specific growth rates (SGR) (see Section 7.2.3.7 for formula) demonstrated significant changes in growth rates between sample points (Figure 7.9), correlated with temperature. SGR was significantly reduced between July and August compared to all other periods ( $P<0.05$ ), and SGR significantly greater between October and November ( $P<0.05$ ) than all other periods. No significant differences ( $P>0.1$ ) were apparent between medium and high density cultures.



**Figure 7.9** SGR of silver perch in medium and high density ponds over each sample period along with average temperatures over the same sample periods

Data for high density polyculture is the average of two replicate ponds, medium density polyculture only incorporates Pond 2, due to fish kill. Where different descriptors are present within each treatment a significant variation ( $P < 0.05$ ) was found.

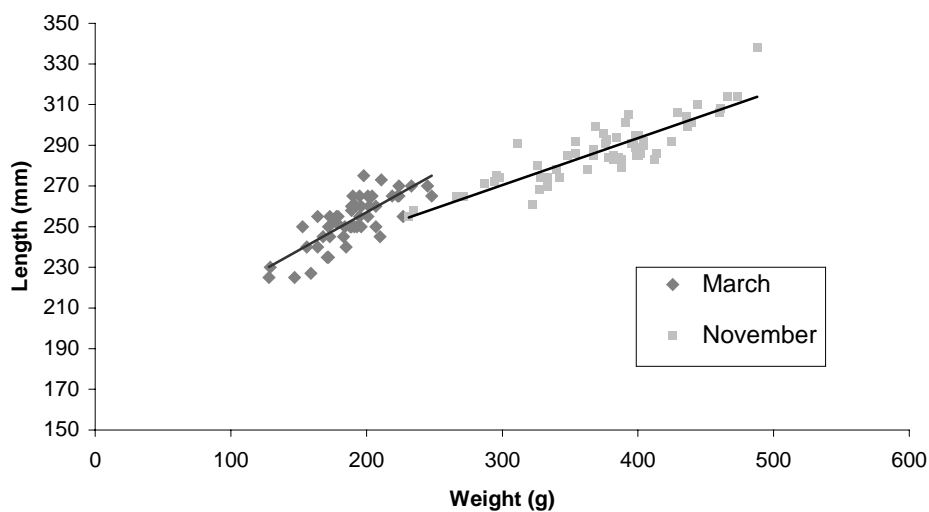
Feed conversion ratios (FCR) (see section 7.2.3.7 for formula) were calculated for silver perch in each sample period (Figure 7.10). FCR for silver perch showed no significant variations ( $P > 0.05$ ) between medium and high density treatments, however feed conversion was significantly reduced during July and August ( $P < 0.05$ ), and significantly improved in November ( $P < 0.01$ ), compared to other sample periods. FCR recorded through September-October were also higher ( $P < 0.05$ ) than all other periods, with the exception of November.



**Figure 7.10** Feed conversion ratios (Wt increase of fish per 1 Kg feed supplied) for silver perch in medium and high density cultures. Includes average water temperature data (°C) through each sample period.

Data for high density polyculture is the average of two replicate ponds, medium density polyculture incorporates Pond 2 data only, due to fish kill. Where different descriptors are present for each treatment a significant variation ( $P < 0.05$ ) was found.

Length-weight ratios for silver perch showed an increased spread in population distribution (Figure 7.11) compared to initial data, with weight of silver perch increasing at a greater rate than length.



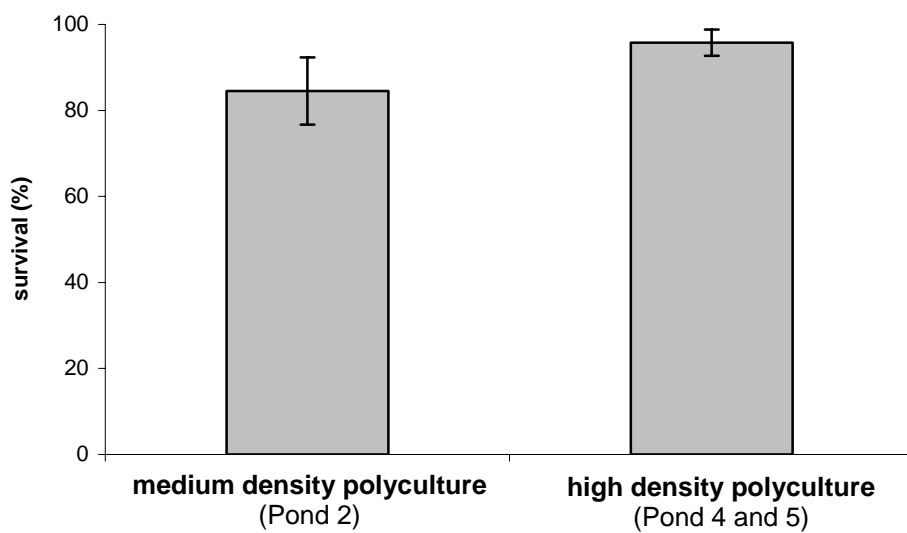
**Figure 7.11** Length-weight distribution of silver perch in March and November.

Data was taken from a sample population of 60 fish in each time period.

Population distribution showed no variation between silver perch grown in medium or high density polyculture ( $P>0.1$ ).

#### 7.2.4.5 Silver perch survival

With the exception of data from Pond 3, silver perch exhibited high survival in all ponds,  $92\pm 7.5\%$ , with no significant differences apparent between ponds or treatment groups ( $P>0.1$ , Figure 7.12).



**Figure 7.12** Survival of caged silver perch in medium and high density treatment ponds  
Values represent average of two cages in Pond 2, and four cages in Ponds 4 and 5.

#### 7.2.4.6 Additional observations

Tadpoles (*Litoria moorie*) and dragonfly nymphs (suborder Anisoptera) were observed in large numbers in the monoculture ponds (in excess of 1000 tadpoles and 1000 nymphs per pond), to a lesser extent in the high density polyculture treatments ponds (Ponds 4 and 5) (10-20 of both species), and neither species were collected in pond 2 (medium density treatment) (Plate 7.6). Both species were only recorded in the November drain harvest, and observed only a few weeks prior, which is consistent with breeding times.



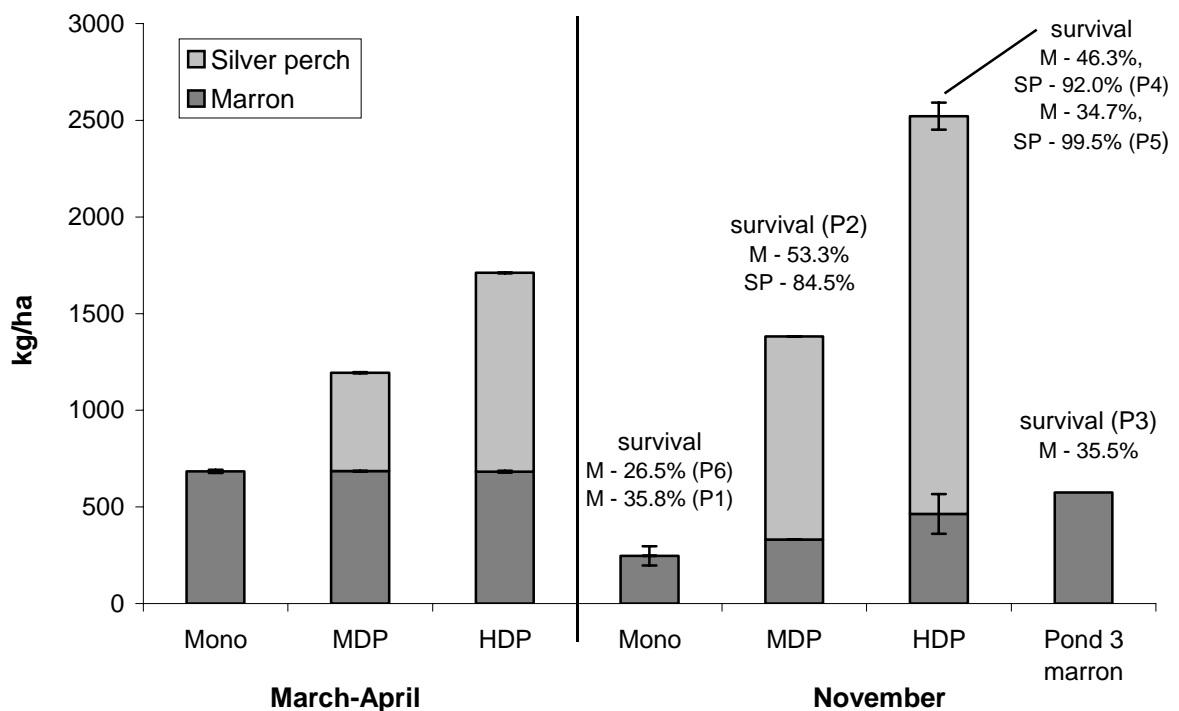
**Plate 7.6** Dragonfly nymphs and tadpoles collected in monoculture ponds



### 7.2.4.7 Polyculture production

Marron biomass and survival was significantly higher in polyculture ponds compared with monoculture ( $P < 0.05$ ) (Figure 7.13).

Silver perch displayed a significant increase in biomass over the trial duration ( $P < 0.01$ ), with high survival in all treatments (Figure 7.13). Silver perch increased in average biomass in the medium density ponds from  $509.4 \pm 2.95$  kg/ha to 1050.6 kg/ha (increase of 541.2 kg/ha) and from  $1027.2 \pm 1.97$  kg/ha to  $2057.9 \pm 69.5$  kg/ha (increase of 1030.7 kg/ha), in the high density ponds.



**Figure 7.13** The calculated biomass of marron and silver perch (kg/ha) for each treatment in March-April and November, including survival descriptors.

## **7.2.5 Discussion**

### **7.2.5.1 Silver perch survival**

Silver perch survival was high in all ponds ( $92.0 \pm 7.5\%$ ). These levels of survival were indicative of previous investigations where bird predation has not been a major factor (Rowland et al. 1994, Rowland 1995a, Whisson 1998, 2000, 2001). This was not unexpected, as climatic conditions through with the trial period (lower temperatures) are associated with lower disease (Anderson and Norton 1991, Soltani et al 1996) and better water quality, as wastes are reduced accordingly with lower feeding and digestion (Belkovskiy et al. 1991). The high survival and good condition of fish in both polyculture treatments supports the use of caged silver perch in marron ponds, where high predation in free range systems, seen in T6:2, is prevented. As survival of silver perch was highest in the high density polyculture, and no significant differences were seen in survival of silver perch between treatments, no density effect is apparent and continued investigations into increased densities is recommended.

### **7.2.5.2 Marron survival**

Marron survival in this trial (between 26.5-53.3%) was lower than results from higher density monoculture studies (Villarreal 1988, Bennison and Morrissy 1991, Whisson 1995a, Whisson 1999), where survival is commonly between 80-90%. The reduced overall survival of marron suggests an overriding factor affecting all ponds. A probable cause was bird predation, supported by high numbers of carcasses recorded on, or above, the water line in the first month of the trial (Section 7.2.4.2), and with injuries commonly associated with bird predators.

As marron mortalities were almost entirely made up of moulting or recently moulted individuals, this suggests that predators targeted marron at this stage in the growth cycle. During moulting, marron are often observed around edges of water bodies, due to avoidance of high cannibalism risk areas (Storer pers. obs.). However, this also leaves marron more exposed to terrestrial predators, as crayfish would be more visible in the shallower water. Moulting and soft post-moult marron have been shown to be exposed to greatly increased risk from predation due to these factors (Stein 1977, Dehli 1981,

Blake and Hart 1993b). In addition, the number of marron mortalities observed around pond banks was greatly reduced following the placement of one shelter line along the edge of each pond, and weekly observation of shelters showed large numbers of moulting marron inhabiting the shallow refuges. As a management tool, the use of bank shelters appears successful. However, it is suggested that bank shelters be used in conjunction with perimeter fencing to prevent access of terrestrial predators, i.e. wading birds or foxes, which may be able to remove marron from shelters placed in shallow water.

Barlow and Bock (1984) have shown that bird predation on outdoor aquaculture ponds will occur in 90% of farms by the third year of operation, even where farms are situated over 60 km from other permanent water bodies. As the Aquafarm site is nearing the end of the third year of operation, increased anti-bird predation measures for marron appear necessary if future trials are to be conducted without loss of experimental stock. In addition, bird predation is said to increase with increasing densities (Barlow and Bock 1984), as was the trend with successive Aquafarm trials.

The impact of polyculture on survival of marron does suggest some benefits from caged silver perch, as survival of marron was significantly higher in polyculture treatments compared to monoculture. It is unclear whether marron gain a competitive edge from interaction factors, for example increased nutrition due to nutrients in silver perch waste, or whether the presence of floating cages increases refuge complexity and so reduces the effectiveness of bird predation. If both factors increase marron survival, perhaps the latter plays a more influential role as survival of marron between polyculture densities showed no discernable difference.

The lack of significant variation in survival of marron and silver perch between medium and high density polyculture treatments shows no density effect, and suggests optimal stocking regimes for marron and/or silver perch exceeds those investigated.

### **7.2.5.3 Growth of marron and silver perch**

Specific growth rates of marron and silver perch between July and October (Winter) was low across all ponds (marron - Figure 7.4 and silver perch - 7.9), with net increases in average weight of  $1.7 \pm 3.9$ g for marron and  $5.6 \pm 4.9$ g silver perch over this period. A previous study conducted by Morrissey (1995) showed that growth of marron over these

months was marginal, if occurring at all (Table 7.3). *Note: Sept. was start of growth records in Table 7.3.* Morrissy (1995) reported optimal growing temperature for marron at around 24°C, whereas in this trial, only 29 days were recorded where temperatures were over 20°C, and only 3 days between 24 and 26°C. Similar results have been seen in silver perch (Whisson 2000), with winter conditions often resulting in reductions in weight, as fish utilise reserves to maintain survival. Weight reduction of silver perch was recorded in three of the six ponds studied between June and August (Figure 7.8).

Although growth rates were low, silver perch in all ponds displayed a significant increase in biomass over the trial duration ( $P < 0.05$ ), which is remarkable when considering that they experienced only 41 days over 20°C and 11 days above 24°C. Approximately 25°C is considered optimal for silver perch (Rowland 1994c). No density effects were apparent between the two treatment densities of silver perch ( $P > 0.1$ ).

**Table 7.3** The average weight and biomass increases of marron (0+,1+ and 2+) and feed delivery and conversion by month, with associated temperature (Morrissy 1995)

Age class		Month »								
		Apr	May	Jun	Jul	Aug	Sept	Oct	Nov	
	Temp °C »	16.8	13.4	10.8	11.8	12.2	15.9	19.2	19.2	
0+	Feed as %bw/day	1.3	0.7	0.5	0.4	0.4	1.9	2.3	3.6	
1+	Feed as g/m <sup>2</sup> /wk	20.1	12	9.4	8.2	8.1	4.2	6.7	14.7	
	Marron biomass(kg)	25.2	29.5	30.6	31.2	31.5	4.4	5.3	7.4	
	Marron mean weight (g)	52	58	64	68	71	7.2	10	13	
	Feed as %bw/day	1	0.6	0.5	0.5	0.5	0.4	0.7	1.5	
2+	Feed as g/m <sup>2</sup> /wk	31.2	20.3	17.8	16.5	16	8.5	4.6	29.7	
	Marron biomass (kg)	45.8	48	48	47.4	46.4	32.9	31.4	30.8	
	Marron mean weight (g)	156	169	173	174	175	85	91	95	

As was expected, specific growth rates of marron and silver perch in this trial were significantly higher between October and November, where temperatures exceeded 20°C, compared with growth in all other periods. In the final sample point, SGR of marron in polyculture ponds was  $1.04 \pm 0.1\%$ /day (Figure 7.4), which is equal or greater than growth rates recorded in previous monoculture trials with marron (Whisson 1995a, 1999). The high growth of marron and silver perch where temperatures were greater than 20°C is consistent with findings from Morrissy (1995) and Rowland (1994). The increased growth rates in October-November, and to a lesser extent in April-June,

is also consistent with significantly increased clearance and feed conversion rates recorded in these periods (Figure 7.10). Feed conversion rates (FCR) recorded for silver perch in September-October (around 1:1), and in November (approximately 2:1), were similar to previous studies with silver perch; where perch were stocked at either 7000 or 21000/ha in 0.1 ha ponds an average FCR of 1.6 to 2.0:1 was recorded (Rowland 1995b) and in 0.4 ha ponds at similar densities FCR was 0.7:1 (Rowland 1994a). The data recorded in November in this trial was comparable to that achieved by channel catfish cultures which are near 2.0:1 (Rowland 1994b).

The average weight of silver perch over the trial duration (approx. 8 months) increased by  $188.6 \pm 9.8$ g across all ponds, with no significant difference between treatments. This is similar to previous pond based monoculture studies where silver perch increased an average 202g in 6 months (Rowland 1994c) and 402g in 14 months (Rowland 1995a), despite growth in this trial predominantly recorded during winter, when growth is greatly depressed (Rowland 1994c).

The question of whether silver perch stocked at the size used in this trial could reach market size in one growth season is difficult to comment on as the trial was largely conducted outside of optimal conditions. However, inferences can be made based on growth data recorded for silver perch in November, where temperatures were close to optimum levels. Based on an average growth of silver perch between October and November (30 days) of +66.43g, and working on the assumption that growth would remain stable between September and April, silver perch would need to be stocked at around 100g. Using this stocking size, average size of silver perch should be 565g, which should allow for more than 80% of stock over 500g, based on population distribution assessments made in November.

#### **7.2.5.4 Marron reproduction**

As this trial was primarily conducted throughout Winter and into Spring, it allowed investigation of interaction effects on reproduction rates of marron. Percentages of females berried in all ponds were significantly similar, and equal to or exceeding levels expected in monoculture, with  $76.3 \pm 7.5\%$  of females berried (1.5 yr/old) across all ponds, compared to industry levels of 75% for 2.5 yr/old brood females (Morrissy

1992a). The high level of reproduction recorded was somewhat unexpected, as ponds were only in their second year of operation. Marron production in new ponds is reported as being sub-optimal in the first years of operation (Morrissy et al 1995b), due to insufficient benthos development - as marron are omnivorous and gain essential nutrition from detritus (Moloney 1996). In normal circumstances, benthic richness would develop in ponds as new water is supplied containing nutrients, organic matter and invertebrate species, and due to feeding and nutrients from stock (Morrissy 1992a).

#### **7.2.5.5 Impact of polyculture on marron production**

A definitive advantage to marron grown in cohabitation with caged silver perch was apparent in all ponds, with significantly higher survival, overall growth and specific growth rates of marron compared to their monoculture counterparts. Higher biomass from polyculture compared to combined monoculture, has been demonstrated in many studies (Guerrero and Guerrero 1977, Cohen et al. 1983, Scott et al. 1988, Brummett and Alon 1994, Wahab et al. 1995, Jones and Ruscoe 1996, Perry and Tarver 1997, Whisson 1999, 2001). Results in this trial, as supported by previous studies into marron and silver perch polycultures by Whisson (1998, 1999), indicate that the increase in overall biomass is predominantly due to increased marron production.

The superior growth displayed by crayfish in the presence of fish has been suggested as a function of increased nutrition from partially digested wastes products from fish (Yashouv 1971, Rouse et al. 1987), or from increased ecological stability due to more complex food webs (Cohen 1984, Rouse et al. 1987). In the latter, marron may have access to more diverse natural feeds as macro-invertebrate populations become more rich and diverse as a direct response to increased nutrients and associated phytoplankton. The synergistic advantages apparent in marron growth and survival were more remarkable when considering that significant growth was recorded in only one month of the trial. Note: Figure 7.5 showed flier animals in polyculture ponds, indicative of animals that have gone through an extra moult compared to the rest of the population (following step-wise growth patterns). Although all fliers detected were found in polyculture ponds, as this was represented by only a small percentage of the population, no definitive conclusions can be made. However, this does support improved success of marron in duoculture with silver perch.

The higher survival of marron in polyculture systems may be attributed to abiotic conditions, where marron gain a competitive edge over marron grown in monoculture due to cages, providing increased refuge from avian predators. Whether survival is increased by factors pertaining to ecological stability or directly from increased shelter is not a critical element of polyculture production management, however this may illustrate the need for greater habitat complexity in monoculture practices.

In addition to the apparent synergistic advantages to marron, the introduction of silver perch at medium and high densities showed no obvious density effects to either marron or silver perch. This was the highest silver perch number and biomass trialed in commercial sized marron ponds. However, when Whisson (2000) tested cage densities in excess of those examined in this trial, where silver perch were held at 180/cage and 380/cage, density effects were exhibited. It is difficult to draw direct comparisons between these trials, as Whisson (2000) introduced juveniles to cages, as opposed to advanced sized fingerlings in this trial. A number of factors may explain why density effects recorded by Whisson (2000) were not apparent in this study. One obvious explanation is that although pond densities of silver perch were increased, cage densities were less than trialed by Whisson (2000), as in this trial pond densities were divided between two cages. This may suggest that multiple lower density cages in marron ponds may be more profitable than single high density systems. Another possibility is that because trials in this thesis were conducted in the cooler off-season conditions, growth and activity of silver perch would have been reduced, which would influence density effects. In saying this, no effect was seen in the final data points where temperatures were adequate for good growth.

As survival, growth and condition of marron and silver perch showed no significant variations between treatments further investigations into increased densities of marron and/or silver perch is recommended. Future trials should compare growth of silver perch held in cages, where pond densities are fixed and cage densities altered through the use of multiple cages, as relative density, not pond density, may be the primary limiting factor in growth-density relationships. These comments must be taken in context with the timing of this trial, as optimal conditions would result in larger pond-cage biomass than tested in this trial and a density effect may become apparent.

When examining the results to determine if any density effects were apparent it is difficult to draw comparisons with the monoculture treatment as a negative specific growth was recorded in the final data point (Figure 7.4). This negative result was not expected as conditions, in respect to temperature and flow-on effects, were the most conducive to growth in this period. From this it is suggested that the significantly higher mortalities suffered in the monoculture ponds resulted in the skewed growth data, whereby the loss of a greater percentage of larger marron resulted in the illusion of decreased average weight.

A final impact of polyculture on marron production is also suggested, pertaining to populations of dragon fly nymphs and tadpoles. As previously mentioned, both these species have been reported for the varied adverse effects they can have on marron production. Specifically, tadpoles have been linked with competitive relationships with marron, both species targeting artificial pelleted feed (Parker 1996), and dragonfly nymphs are notorious predators of hatchling and juvenile crayfish (Bird 1995, Jones 1995) - obviously the latter is only problematic in brood ponds. The densities of each species were shown to be dramatically reduced in polyculture ponds, compared to monoculture. Although they still existed in polyculture systems, numbers were in the 10's-100's, as opposed to 1000's-10000's in monoculture systems. Silver perch have previously been shown to predate on both species when held in free-range (T7:1), and fish are generally considered an ideal natural bio-control for these species in marron ponds (Parker 1996). However this is the first report of clearance effects when silver perch are held in cages. One additional findings was in Pond 2, where five escapee silver perch were discovered at final harvest. In this pond, neither dragonfly nymphs or tadpoles were found. These findings suggest a secondary benefit from the culture of marron and silver perch not yet identified. This may have contributed to synergistic growth advantages of marron previous reported (Whisson 2000) due to a greater supply of feed available for marron (with loss of tadpoles) and higher survival of juveniles (through loss of dragonfly nymphs). Further investigation is recommended to determine if economical benefits exist (from increased FCR and survival of marron) from stocking a low number of free range silver perch (or other species), compared to any economic disadvantages from antagonistic interactions between silver perch and marron.



#### **7.2.5.6 The effect of habitat complexity on marron production**

A number of key observations were made throughout this investigation concerning the use of shelter lines. The lines were generally shown to be an effective tool for harvesting and sampling populations, and for easy removal of shelters prior to harvest. Removal of all 100 shelters from each pond took less than 10 min. for one person, where previous attempts at moving individual loose mesh shelters has taken between 20-30 min. (depending on levels of sediment, Storer pers. obs), and for removal of more traditional shelters, such as tiles and half tyres the job can take over an hour (Storer pers. obs). In the 30 pond samples of marron taken (6 ponds and 5 sample points), approximately 100-200 marron were removed from 1-2 shelters lines by carefully pulling lines close to one bank and dropping a 20m weighted net behind the shelter line. After shelter lines were gently shaken to dislodge marron and removed, the net was pulled to the bank. The entire process from dragging shelter lines in, to removal of the final marron from the net took between 7 and 11 min. This was shown to be an effective and efficient method for researchers needing to check sample populations of crayfish held in free range ponds, and could also be easily adapted for farmers partaking in either shelter harvest or assessing growth and stage of marron development. One effective management strategy was the use of shelters close to the bank to protect moulting marron from stress and direct predation. The reduction in observable mortalities was significant in this trial, and requires further investigation.

Finally, the presence of cages in ponds may have had a beneficial role in marron survival, where monoculture (without cages) suffered higher mortalities. The role of the cages as a refuge is further supported when compared with results in T7:1, where no variation in survival was recorded between monoculture and polyculture ponds, as in T7:1 empty cages were used in monoculture ponds. This finding requires further investigation as it could have ramifications for monoculture habitat management.

#### **7.2.5.7 The effect of cage shelters on silver perch production**

The addition of shelters to cages containing silver perch appeared to reduced feeding neophobia, with more rapid initiation of feeding responses, and increased duration of feeding compared to previous trials where cage shelters were not used (T7:1). Similarly, silver perch held with shelter did not demonstrate startle responses to

external disturbances, which are a common reaction when workers move around ponds. It is difficult to draw conclusions from these observations, as feeding and general behaviour of silver perch was not quantified. However, more conclusive evidence was apparent in feed conversion ratios (FCR) of silver perch. FCR of silver perch between October and November was between 1.81 and 2.15 (increase in weight of fish (kg) per kg of feed). These FCR data were higher than previously recorded for caged silver perch culture, where upper levels of between 1.24 and 1.48 have been reported (Rowland 1994b, Whisson 2000). The increased FCR of silver perch where cage shelters were provided may suggest increased amounts of supplemental feed. As high levels of filamentous algae were observed attached to cage shelters, along with associated invertebrates assemblages recorded within cages, both of which are natural feed for silver perch (Grant 1987, Barlow et al. 1986), this is supported. In addition, SGR of silver perch in T7:2 was approximately 0.7%/day (November data), where cage shelters were provided. This level was much higher than data in T7:1, with a maximum SGR of  $0.18 \pm 0.02\%$ /day, where no shelter was provided. This data based on fish of similar size, and temperature of both trials was approximately 20°C over period where FCR was calculated.

The use of shelter in production cages is rarely reported, but where used is has been reported to reduce effects from crowding (Deady et al. 1995, Flemming and Hone 1996). The role of shelter in negating stress from potential predation has also been shown (Appelberg et al. 1993, Baker and Montgomery 2001, Lass 2001), which may explain increased feeding responses of silver perch in T7:2. Continued investigation into cage shelters in silver perch culture is clearly required, however any studies must consider the potential adverse effects shelters may have on water circulation through cages, as water quality problems associated with poor circulation have previously been identified (Masser 1988).

### **7.2.6 Limitations**

Most of the trial period was outside of regular commercial grow-out season for marron and silver perch. This was due mainly to delays associated with malfunction (and subsequent replacement and installation) of the pump used to provide water to the Aquafarm. The mine lake utilised as a water source in trials in this chapter had been

filling naturally over the past two years, and recent increases in water level resulted in the pump moorings breaking. Once a new pump was sourced and a new mooring system designed the stock originally sourced for this trial had grown larger than required and population distributions varied too greatly for the study. Once new stock was located and transported to site the trial was initiated in March (optimal growing season between November and March). However, as little data exists on off-season production aspects for marron and silver perch, this trial offered valuable information otherwise difficult to collect on a commercial scale. In addition, the trial was extended into the first period of optimal growth conditions (October-November), where following a long period of acclimatisation and ecological stabilisation, optimal growth data for both species should be obtainable.

A further limitation of this trial was the loss of almost all silver perch from Pond 3 after only 72 days. The sudden mortality of fish was due to adverse water quality conditions, attributed to failure of the water treatment system which delivered water to Pond 3. All results and discussion pertaining to the fish kill in Pond 3 was presented in Storer et al. 2004b and documented by Ingram (2004). A more detailed description can be found in these publications.

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**The null hypothesis  $H_0$  (7.3)** was rejected. Marron grown in duoculture with silver perch grew significantly more over the trial period.

**The null hypothesis  $H_0$  (7.4)** was rejected. SGR and FCR of silver perch were and in excess of T7:1 where no shelter was provided, and similar to free-range data from literature (Whisson 2000).

**The null hypothesis  $H_0$  (7.5)** was accepted. No growth-density effects were observed for either species at the densities examined.

## ***Chapter eight***

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### ***Integrated analysis of behavioural observations***

## **CHAPTER 8**

### **Integrated analysis of behavioural observations**

While examining the nature of communication between marron and silver perch in Chapters 4, 5 and 6, several factors featured consistently in the behavioural responses of experimental subjects to the various exteroceptive cues tested. How these responses influence system dynamics (and production in culture systems) will be discussed in this chapter, which compares and contrasts all findings in light of previous research.

## 8.1 Resting behaviour of marron

Behaviour recorded in the control periods of each laboratory investigation in this thesis provided an opportunity to examine the resting behaviour of marron; that is, the behaviour of marron when not confronted by cues from food or potential predators. Resting behaviour of marron was examined between size classes and gender, when marron were held alone and under cohabitation with a congeneric crayfish. For discussion, marron behaviour recorded in T4:1, T5:1 and T5:2 was compared against behaviours recorded in two other trials involving marron - Gherardi et al (2002); and, Height and Whisson (2004). In these comparative studies crayfish behaviour was recorded using observation protocols outlined in Chapter 4 and 5, experimental set-up was replicated, and all studies were conducted in south-west Western Australia, allowing direct comparison based on experimental techniques and climate. The trial conducted by Gherardi et al. (2002) was located in Perth (32°S, 116°E), all other trials were carried out in Collie (33°S, 115°E). Temperature across all trials was 19.7°C-21°C.

### 8.1.1 Influence of size class on marron resting behaviour

Several consistencies were apparent in the resting behaviours exhibited by marron when held under controlled conditions in 25L glass aquaria in T4:1 and T5:1. Table 8.1 provides a summary of these results, with comparisons to the trials conducted by Gherardi et al. (2002) and Height and Whisson (2004).

Resting behaviour of marron was relatively similar between the trials conducted and the different marron sizes examined. Time spent in locomotion (range 11.2-25.2%, of time spent), antennae movement (range 6.9-18.8%), shelter ( $22.5 \pm 12.7\%$ ), climbing ( $14.6.0 \pm 8.9\%$ ) and cleaning (range 0-4.7%) was consistent across all trials. Feeding activity was also similar (range 0-6.1%) when results from Gherardi et al. (2002) were not included (Table 8.1). Increased feeding activity reported by Gherardi et al. (2002) ( $48.5 \pm 5.2\%$ ) may be attributed to a minor variation in the recording protocol used. As stated in Section 4.1.5, marron display a 'leg-sway' which may be interpreted as scraping (feeding behaviour), however this behaviour was not included in observations made in this thesis, or by Height and Whisson (2004). Gherardi et al. (2002) also demonstrated increased locomotion and reduced shelter usage by marron, compared

with other trials (Table 8.1). These variations in data may be due to human interpretation of recording protocols, or variations associated with location of trials (e.g. water source).

**Table 8.1** Behaviour of marron held under control conditions in 25L aquaria.

	<b>T4:1</b>	<b>T5:1</b>	<b>T4:1</b>	Height and Whisson 2004	Gherardi et al. 2002	<b>T4:1</b>
Marron size >>	<b>Small</b>	<b>Small</b>	<b>Medium</b>	<b>Medium</b>	<b>Medium</b>	<b>Large</b>
<b>BEHAVIOUR</b>	(mean ± SE)	(mean ± SE)	(mean ± SE)	(mean ± SE)	(mean ± SE)	(mean ± SE)
Shelter	35.7±16.1	12.5±8.5	36.9±16.3	12.4±5.4	4.2±4.2	15.0±13.4
Locomotion	11.2±6.9	17.3±8.5	19.4±7.8	11.8±2.2	25.2±6.6	18.7±10.3
Feeding	6.1±3.8	0.0±0.0	0.6±0.6	4.4±0.9	48.5±5.2	1.2±1.2
A-flicking	67.0±8.6	9.5±3.6	83.3±12.9	32.6±5.5	12.0±2.3	70.4±13.0
A-movement	8.2±6.4	18.8±8.3	6.9±9.7	17.5±1.2	<i>NR</i>	17.7±11.2
Low posture	25.5±15.7	0.0±0.0	12.5±8.2	31.3±5.6	15.1±16.8	41.7±18.6
Inter-posture	24.2±15.4	59.2±12.0	40.8±17.6	26.4±5.0	<i>NR</i>	33.7±16.5
Raised posture	50.3±18.8	40.8±12.0	46.7±17.6	16.5±1.5	39.6±8.5	24.6±14.4
Cleaning	1.7±1.1	0.0±0.0	1.5±1.2	5.3±2.9	<i>NR</i>	4.7±2.9
Climbing	1.0±0.7	15.5±8.5	16.7±12.6	25.8±0.0	<i>NR</i>	13.8±8.1

Sizes of marron are: small <8g; medium 30-90g; and large >200g. *NR* = not reported. Data are percentage of time spent in each behaviour. T4:1 = 1<sup>st</sup> trial in Chapter 4, T5:1 = 1<sup>st</sup> trial in Chapter 5

Antennule flicking showed the most variation between trials (45.8±31.9%). Closer examination of this data revealed that the large variation was due to differences between trials, as comparison of data between size classes within Chapter 4 showed relatively consistent results (73.6±8.6% of time spent). Antennules are reported to be the primary olfactory sensing devices in crayfish (Hazlett 1971, Tierney and Atema 1988, Grasso and Basil 2002); as such, variations in activity between trials may reflect differences in water chemistry. It is therefore recommended that a standard protocol for water quality be developed for future trials - an obvious method would be chlorination and subsequent de-chlorination of water to remove any biotic influences.

### 8.1.2 Resting behaviour displayed by male and female marron

Gender differences in the behaviours displayed by marron were compared in control periods in T4:1 and T5:1. In all trials, small and medium marron displayed no gender differences ( $P>0.05$ ) in behaviour or posture (Figure 4.2). Large marron showed only two significant gender differences, where large males preferred low posture ( $P<0.001$ ) and large females preferred intermediate posture ( $P<0.05$ ) (Figure 4.2).

As marron in T4:1 and T5:1 were held in solitude, the lack of differences were not unexpected, as gender variations are most commonly reported in response to intraspecific interactions, such as resource competition (Zayan 1974, Goncalves 1993, Halperin and Dunham 1994, Hazlett et al. 1996), reproductive behaviour (Francis 1983, Smith 1986) or dominance disputes (Peters et al. 1980, Beacham 1987, Page and Cooper 2004).

### 8.1.3 Marron behaviour under cohabitation with congeneric crayfish

An understanding of the way crayfish respond to interaction with other crayfish has ramifications for both commercial aquaculture and wild stock management. To address this, resting behaviour of marron, recorded in control groups in T4:1 and T5:1, was compared with data recorded in T5:2, where marron were held with yabbies (Table 8.2). The behaviour of yabbies, held alone, was incorporated into Table 8.2 from data obtained from Gherardi et al. (2002) and Height and Whisson (2004). Yabby resting behaviour was included to examine whether behavioural modifications are most common in marron or yabbies following cohabitation, and to gain insight into dominance hierarchies between the species. This relationship is particularly important in light of the invasion of yabbies into natural marron habitats in Western Australia (Campbell and Whisson 2002, Lynas et al. 2004).

Under cohabitation in aquaria, both marron and yabbies displayed altered resting behaviours in the period immediately following initial introduction, compared to behavioural data obtained in previous trials where crayfish were held alone (Table 8.2).



Table 8.2 Behaviour of marron held under control conditions in 25L aquaria with yabbies

	<u>NO</u> <u>INTERACTION</u>	<u>INTERSPECIFIC INTERACTION</u>				<u>NO INTERACTION</u>	
	<b>T4:1, T5:1</b> Average Data	<b>T5:2</b> (TP1)	<b>T5:2</b> (TP2)	<b>T5:2</b> (TP1)	<b>T5:2</b> (TP2)	Height & Whisson 2004	Gherardi et al. 2002
Crayfish size >>	<b>MM</b>	<b>MM</b>	<b>MM</b>	<b>MY</b>	<b>MY</b>	<b>MY</b>	<b>MY</b>
<b>BEHAVIOUR</b>	(mean ± SD)	(mean ± SE)	(mean ± SE)	(mean ± SE)	(mean ± SE)	(mean ± SE)	(mean ± SE)
Shelter	24.6 ± 17.4	4.00±13.4	20.0±13.3	1.0±3.4	11.0±9.9	75.0±7.3	8.9±1.0
Locomotion	15.6 ± 5.3	44.57±25.1	10.5±5.9	64.2±21.3	11.0±3.6	2.9±1.2	15.7±2.6
Feeding	2.50 ± 2.7	0.00±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.1±0.1	21.7±1.3
A-flicking	58.0 ± 35.9	46.86±27.5	38.1±8.0	12.0±11.8	49.1±10.9	58.5±5.5	16.3±3.5
A-movement	12.20 ± 7.5	64.76±24.8	5.7±2.1	47.1±23.5	14.7±7.8	2.9±1.2	NR
Low posture	21.9 ± 13.3	8.76±22.8	48.6±12.5	49.7±29.3	40.5±15.0	85.3±5.5	59.7±3.3
Inter - posture	33.6 ± 10.2	30.10±23.2	16.7±10.1	26.9±19.7	48.6±13.3	12.6±5.0	NR
Raised posture	31.6 ± 21.4	51.43±32.1	10.5±7.5	16.8±14.4	1.9±1.9	2.1±1.5	3.3±1.4
Cleaning	3.40 ± 2.7	2.67±8.1	4.3±2.9	0.8±1.8	4.8±5.1	6.9±2.9	NR
Climbing	21.3 ± 6.5	4.95±11.8	1.0±1.0	1.3±4.7	0.0±0.0	0.0±0.0	NR

Crayfish sizes are MM-medium marron, MY-medium yabby. TP1 = introduction, TP2 = 4 h after introduction. NR - not reported. Data are percentage of time spent in each behaviour. T4:1 = 1<sup>st</sup> trial in Chapter 4, T5:1 = 1<sup>st</sup> trial in Chapter 5, T5:2 = 2<sup>nd</sup> trial in Chapter 5..

The behaviour displayed by crayfish in the first time period (following introduction to aquariums) is indicative of generally heightened activity, with both species decreasing shelter use, selecting raised posture and increasing locomotion and antennae movement (Table 8.2). This behaviour has previously been associated with the development of dominance hierarchies between crayfish (Field 1990, Hazlett and McLay 2000), or simply a common period of searching the new environment (Tierney and Atema 1988, Hazlett 1990, Panksepp and Huber 2004). As the behaviour of crayfish in the 2<sup>nd</sup> time period had returned to levels indicative of resting behaviour (when held alone), no significant effects from cohabitation on the resting behaviour of crayfish, given a period of adjustment, were apparent. If nothing else, these results support allowances for 'settling time' when observing crayfish behaviour in communal systems. Whether interactions between marron and yabbies would influence responses to signals from factors such as food or potential predators is discussed in Section 8.3.

## 8.2 Perception of exteroceptive cues by marron

The roles of visual, chemical, tactile and other information media are varied and wide ranging, as reflected by the extensive reviews in Sections 2.4.1 to 2.4.4. Information cues can be produced and utilised by both predator (Liang et al. 1998, Brown et al. 2000, Powers and Kittinger 2002) and prey (Mathis and Smith 1993c, Brown et al. 1997, Wisenden 2000). They are affected by factors such as water quality (Atema 1995, Hay 1996, Mesquita et al. 2003) and flow dynamics (Atema 1995, Lass 2001, Powers and Kittinger 2002). Responses to cues vary depending on conspecific and heterospecific competition (Werner 1991, and Kotler et al. 1994), predator behaviour and status (Dugatkin and Godin 1992, Brown and Chivers 1996, Brown et al. 2000), sex of prey (Pocklington and Dill 1995), ontogenetic stage (Mirza and Chivers 2002), species involved (Halpin 1986, Mirza et al. 2001), previous interaction (Zayan 1974, Goncalves 1993), and by system variables, including shelter (Rittschof 1993, Welch et al. 1997, Baumgartner et al. 2003) and turbidity (Confer et al. 1978, Guthrie 1986, Utne-Palm 2004). The investigations carried out in this thesis were designed to encompass a range of individual and combined cues, under varying conditions.

When investigating the factors governing communication and interaction responses between species for the first time, a broad range of questions exist:

- What environmental triggers are involved in communication?
- Do combined cues elicit more confident and accurate responses?
- How do responses influence production?
- What role do system variables play in influencing interaction responses?

In previous studies examining communication in decapods, many information sources have been highlighted, each with different roles and carrying varying amounts of weight in the decision processes of different species. The primary information sources used by species in aquatic environments are reported to be; chemical (Dicke and Sabelis 1992, Hazlett 1994a, Burks and Lodge 2002, Gherardi et al. 2002), visual (Culp et al. 1991, Rosenthal and Ryan 2000, Mirza et al. 2001) and tactile (Hoffmeister and Roitberg 1997, Bouwma and Hazlett 2001, Persons et al. 2001). Authors have examined other information cues, including electrical and audio, however as the

investigations carried out in this thesis are the preliminary examinations involving marron, only the most common sources were examined, laying a foundation for future work.

### **8.2.1 Chemosensory perception in marron**

Chemical signals are one of the most studied information media in aquatic environments - providing strong, reliable information (Sorenson and Caprio 1998, Vet 1999, Wisdenson 2000), especially where vision is limited (Stoddart 1980, Chivers et al. 1996b). Chemicals carry information between species (allelochemicals) (Dicke and Sabelis 1988) and between conspecifics (pheromones) (Dicke and Sabelis 1988), and provide information pertaining to food (Tierney and Atema 1988, Hazlett 2003), shelter (Grasso and Basil 2002), potential threats (De Meester and Cousyn 1997, Wisenden 2000, Tomba et al. 2001) and reproductive partners (Yen and Strickler 1996, Vickers 2000, Diaz and Thiel 2004). As the use of cage culture of silver perch is a potentially viable management option for polyculture in marron ponds (Whisson 2000), chemical cues from silver perch may offer the most significant challenge to control if found to produce stress responses in marron. Problems associated with tactile cues can be alleviated by cages, and visual cues can be reduced with increased turbidity, however chemical cues are much more pervasive within an aquatic system. The most relevant questions regarding chemical communication of marron in polyculture centre on the ability of marron to detect and adequately modulate responses to novel cues associated with potential fish predators, primarily silver perch. In addition, the way marron respond to cues from food, with and without cues relating to potential risk, is particularly important as this relates to the effect of fish on marron production. The studies employed in this thesis aimed at determining the ability of marron to detect and respond to food-derived chemical cues, and the subsequent inhibition (if any) of feeding in response to potential kairomones.

#### **8.2.1.1 Detection and response to food odour**

Response of marron to food odours alone were examined in T4:1 and T5:1, and included comparisons between size classes. Table 8.3 details results from these trials and incorporates data from Gherardi et al. (2002). Preparation of food solutions was

standardised across all trials, following procedures outlined in Gherardi et al. (2002), allowing a valid comparison. Data from Height and Whisson (2004) was not included in Table 8.3, as behavioural response to food solutions were not published.

**Table 8.3** Magnitude of change between responses to control water and food solution in reaction time (s), behaviour and posture (%).

	T4:1	T5:1	T4:1	Gherardi et al. 2002	T4:1
Marron size >>	Small	Small	Medium	Medium	Large
BEHAVIOUR	(mean ± SE)	(mean ± SE)	(mean ± SE)	(mean ± SE)	(mean ± SE)
Reaction time	-152.1±50.4 *	-138.8±47.3	-144.4±53.2 *	-32.5±11.1	-148.1±41.0 **
Shelter	0.0±0.0	+4.8±4.8	+19.1±13.0	0.0±0.0	0.0±0.0
Locomotion	+36.1±11.5 *	+29.2±10.9 *	+17.3±8.2 ^	+15.8±3.3	+23.2±9.1 *
Feeding	+17.7±10.9	+21.4±8.1 *	+16.1±6.4 *	+18.5±4.2	+17.9±8.3 ^
A-flicking	+11.6±5.6	+38.1±11.6 ^	-12.5±5.7	+14.2±3.0 **	-22.0±8.6
A-movement	+26.5±11.2 ^	+26.8±10.5 ^	+17.3±7.6 ^	NR	+11.9±5.8
Low posture	-11.6±7.8	0.0±0.0	0.0±0.0	-19.0±6.5 *	-1.8±1.8
Inter-posture	+17.0±8.2	-30.9±13.3	+14.9±10.6	NR	+3.6±2.3
Raised posture	+21.8±13.7	+31.0±13.3	-14.9±10.6	-14.4±4.1	-1.8±1.8
Cleaning	+6.1±2.1	+3.0±2.0	0.6±0.6	NR	-0.6±0.6
Climbing	+5.4±3.1	+6.6±5.3	-15.5±11.0	NR	-1.8±1.3

T-tests compared differences between solutions in all trials. ^P<0.1, \* P<0.05, \*\*P<0.01. T4:1 = 1<sup>st</sup> trial in Chapter 4, T5:1 = 1<sup>st</sup> trial in Chapter 5. NR = no result published. Sizes of marron are: small <8g; medium 30-90g; and large >200g.

Results show that marron responded consistently to food-derived chemical cues in all trials. Behaviours recorded were typical of responses indicating increased searching (increased locomotion, antennae movement and feeding behaviour) associated with foraging (Sih 1987, Lima and Dill 1990, Kats and Dill 1998, Lima 1998, Woodley and Peterson 2003). This indicates that crayfish were readily detecting the presence of chemical stimuli, as has been documented for *O. propinquus*, *O. rusticus* and *O. virilis* exposed to food (Hazlett 1994a; 2000). Results concur with Height and Whisson (2004) where significant increases in marron feeding behaviour were recorded when food cues were added.

Comparisons between marron of different size classes showed similar responses to food cues, although smaller marron generally sustained responses longer (locomotion, antennule flicking and antennae movement) (Table 8.3). One likely explanation is the increased energy requirements and higher replenishment frequency in younger crayfish (Svensson 1993), foraging longer in search of food. In contrast, the reduced relative energy requirement, increased storage capability and increased experience of older individuals (Stein 1977, Dutoit et al. 1991, Greenberg 1992) may result in them giving up searching earlier, if unsuccessful in locating the food source quickly .

As both farm-reared (Table 8.3) and wild-stock (Height and Whisson 2004) marron responded to food solution, it is assumed that marron instinctively associate certain cues, at least in commercial pellets, with food. However, it is unknown whether marron have the ability to differentiate cues. For instance, as marron have few natural predators and are the dominant invertebrate in freshwater systems in south-west Western Australia (Morrissy 1997, FWA 1999, Allen et al 2002), they may associate cues from novel predators with food. The responses of marron to food, when presented with cues from potential predators is, discussed below.

#### **8.2.1.2 Detection and responses to food combined with fish kairomones**

The ability of marron to detect chemical signatures from silver perch, found in their culture water, was examined in T4:1 and T5:1. These trials were primarily targeted at expounding the role of fish kairomones on feeding responses displayed by marron, and as such fish cues were combined with food odours. Any inhibition of behaviour, especially feeding, in response to fish odour would have deleterious results for marron production in polyculture, even with caged fish. The responses of marron to silver perch kairomones combined with food is displayed in Table 8.4, representing changes in behaviour compared with control responses.

**Table 8.4** Magnitude of change between responses to control water and food solution with fish culture water combined with reaction time (s), behaviour and posture (%).

	<b>T4:1</b>	<b>T5:1</b>	<b>T4:1</b>	<b>T4:1</b>
Marron size >>	Small	Small	Medium	Large
<b>BEHAVIOUR</b>	(mean ± SE)	(mean ± SE)	(mean ± SE)	(mean ± SE)
Reaction time	-189±37.5 **	-197±41.4 **	-146.3±40.7	-248±19.7 **
Shelter	-15.0±11.9	-12.5±12.5	+13.1±7.0	-0.8±0.7
Locomotion	+34.7±11.9	+12.5±8.1	-29.8±11.1	+12.7±5.2
Feeding	+24.5±11.3 ^	+18.5±6.2 *	+15.5±7.6 ^	+0.8±0.7
A-flicking	+1.4±1.3	+26.8±11.8 ^	-13.1±12.4	+4.8±2.6
A-movement	+32.0±10.6	+9.7±5.9	-16.1±13.4	+11.1±4.4
Low posture	-20.4±13.6	0.0±0.0	+1.2±1.2	+3.2±2.8
Inter-posture	-35.4±13.0	+20.2±12.4	+26.8±9.0	-31.0±15.7
Raised posture	+31.3±14.1 ^	-20.2±12.4	-25.6±8.5	+31.0±15.7
Cleaning	+2.7±1.3	+4.2±3.5	+5.4±3.5	-7.9±4.6
Climbing	+20.4±13.6	-14.3±7.0	-9.5±6.5	+9.5±4.4

T-tests compared differences between solutions in all trials. ^P<0.1, \* P<0.05, \*\*P<0.01. T4:1 = 1<sup>st</sup> trial in Chapter 4, T5:1 = 1<sup>st</sup> trial in Chapter 5. Sizes of marron are: small <8g; medium 30-90g; and large >200g.

The ability of marron to detect cues found in the food + silver perch conditioned water solution (F+PCW) was confirmed, with significantly faster reaction times at P<0.01 in three of the four silver perch treatments (Table 8.4). These results supported Height and Whisson (2004), where significantly faster reaction times (P<0.05) to both redfin perch (*Perca fluviatilis*) and freshwater cobbler (*Tandanus bostocki*) solutions were reported. Redfin perch and cobbler are known predators on marron (Allen et al. 2002), with freshwater cobbler being the only large naturally occurring finfish in rivers and streams in the south-west of Western Australia (Allen et al. 2002), and redfin perch introduced to South-West waters over 100 years ago (Arthington and McKenzie 1997). Data from Gherardi et al. (2002) were not included as responses to kairomones were not tested.

The responses of marron to F+PCW showed similar trends as in reactions to food alone, however the behavioural changes to F+PCW were less pronounced. For example; in response to food - locomotion, feeding and antennae movement of marron showed increases in all studies reported (Table 8.3); however in response to F+PCW - only feeding behaviour showed consistent increases between the trials examined, and

only marginally in large marron (Table 8.4). Although feeding responses appeared unaffected by fish odours, the lack of other behavioural changes in marron responding to F+PCW, compared to responses to food, may suggest some degree of inhibition. Reduced feeding, but not cessation, has been shown in other crayfish in response to risk cues (Hazlett 1999, 2000b). One explanation is that crayfish may increase alert status - defined as the capability to escape the attack of a predator through an increased sensitivity to mechanical and light disturbance (De Meester and Pijanowska 1996). By utilising powerful tail-flips to rapidly escape imminent danger (Hazlett 1999, Herbaholtz et al. 2004), crayfish could be given an ecological advantage over other species, where they can maintain normal behaviour until avoidance is absolutely necessary.

In T4:1, direct comparative analysis of behavioural responses between F+PCW and food alone, detected two significant differences (Table 4.1). These were reduced locomotion in medium marron, and a faster reaction time exhibited by larger marron in response to F+PCW. Large marron also displayed a general reduction in feeding, locomotion and antennule flicking in response to F+PCW, compared to food alone (Figure 4.5). These results suggest that larger marron may reduce overall activity when exposed to fish cues, which is a typical response to potential threat (Ivlev 1961, Momot 1967, Hazlett and Schoolmaster 1998, Hazlett 1999, Schapker et al. 2002). These findings support other studies where larger, more mature, individuals display greater avoidance due to experience (Pfeiffer 1977, Brown and Godin 1999, Hazlett 1971). In T5:1, no discernable differences were found between responses to food and F+PCW, however, only small marron were utilised, displaying similar results to the same size class in Chapter 4.

In summary, results in T4:1 and T5:1 did not confirm any inhibitive effects from fish odours on behaviour of marron. In particular, small marron demonstrated no significant alteration in behaviour between food and food combined with fish cues, and although it was suggested that some behavioural modulation was made in larger marron, this was only backed up statistically by increased reaction time. As marron have evolved in systems devoid of natural predators (Morrissy 1997, FWA 1999, Allen et al 2002), they may not recognise silver perch odour, as chemical risk cues may be entirely novel. Regardless of whether marron are detecting danger or not, the lack of feeding inhibition is encouraging for polyculture using caged fish, as marron should not suffer unnecessary stress responses or be affected through behaviour alterations commonly associated with avoidance strategies.

### 8.2.1.3 Detection and responses to fish kairomones

In T5:2, marron were exposed to silver perch culture water, without food cues, to determine whether marron could detect signals pertaining to potential threat. Although chemical cues from silver perch elicited significant behavioural responses in marron (faster reaction time and increased antennule flicking) (Figure 5.9), they did not stimulate feeding activity. In previous trials, where food and fish cue combinations were used, feeding was significantly increased (Gherardi et al. 2002, Height and Whisson 2004). Hazlett (1999) reported that behaviour of *Orconectes virilis* is commonly inhibited when faced with imminent predatory risk, however does not completely shut-down. These findings provide evidence of the ability of marron to chemo-differentiate between signals pertaining to food and those pertaining to silver perch. The ability of freshwater crayfish to detect odours associated with potential predatory species has been shown in many previous studies (Hazlett 1997, Hazlett and Schoolmaster 1998, Persons et al. 2002, Hazlett 2000a, Mirza et al. 2001).

Although results indicate that marron can differentiate between chemical cues in silver perch culture water and chemical cues from food, as marron did not display significant avoidance responses upon detection of fish cues (Figure 5.9), the ability of marron to associate cues with potential threat was not supported.

### 8.2.2 Photo-sensory perception in marron

If marron do not interpret chemical signals from silver perch as potential risk, do they respond to other exteroceptive signals from potential predators? The use of visual cues by marron for detecting fish was examined in T5:1. This investigation compared the ability of marron to identify visual signals from silver perch, and examined whether responses could be associated with apparent risk status.

When exposed to cues from bagged silver perch, marron increased antennule flicking, antennae movements, and chose low posture more frequently, compared with marron in fishless treatments (Figure 5.1). These differences support detection of visual cues associated with fish in bags, with both the antennules (Tierney and Atema 1988, Hazlett 1990, Grasso and Basil 2002) and antennae (Panksepp and Huber 2004) shown to be the primary devices used to detect environmental signals. That is, once marron visually



detect fish they activate other sensory devices. However, behavioural studies have shown that freshwater crayfish use antennae for investigating 'novel system structures' (Panksepp and Huber 2004), which may mean that the increased activity of antennae may be a response to the bag, not the silver perch within. To address the finding of Panksepp and Huber (2004), direct comparisons were made between the 'fish in bag' treatment and the treatment containing 'bag only'. Results showed clear differences, with marron assuming lower posture and using antennae significantly more when fish were present in bags. Lowered posture has previously been recorded in responses to predatory cues in the crayfish *Orconectes virilis* (Hazlett and Schoolmaster 1998), with defensive stances in crayfish characterised by low posture, often with tail curled under body (Hazlett 1994a), as was seen in this trial. This suggests that marron were not only detecting visual cues from silver perch, but also responding to a potential threat.

The use of visual cues in threat detection is common in aquatic animals (Brown et al. 1997, Watson 1999), controlling a range of anti-predator behaviours in many species (Herrnkind 1968, 1972, 1983), including decapods (Bollens et al. 1994, Murray and Jenkins 1999, Diaz et al. 2001, Woodley and Peterson 2003). Visual cues are often the primary source of information in environments where vision is high, such as in systems of low turbidity (Watson 1999) providing early accurate information (Culp et al. 1991, Brown et al. 1997, Murray and Jenkins 1999, Bouwma and Hazlett 2001). The evolution of marron in clear-water rivers and streams in the south-west of Western Australia (Allen et al 2002) may support these findings, where visual identification of potential threats may be the most effective early warning system. As natural predators of marron are limited (Morrissy 1997, Allen et al 2002) and generally confined to terrestrial species, such as birds and water rats, the use of chemical triggers is arguably much less important, and understandable within an evolutionary context.

Whether the behavioural modifications displayed by marron in response to visual cues from bagged silver perch would equate to noticeable impacts on aquaculture production requires an examination of responses to the presence of food cues, to determine whether foraging is affected. Further, as behavioural responses of marron to visual cues from silver perch were detected in T5:1, an examination of combined cues (visual and chemical) is warranted. Although silver perch odour did not produce crayfish avoidance responses in T4:1, the combination of cues has been shown to elicit stronger, more confident responses in the receiver. Anti-predator behaviour displayed by *H. rotundifrons* (branchyuran crab) in response to tactile input is prolonged by the addition of chemical or

visual cues, however if visual and chemical cues are detected alone no reaction is evident (Field 1990, Hazlett and McLay 2000). This suggests, that although insufficient to elicit a response alone, some stimuli can increase the potency of other information media.

### **8.2.3 Combined exteroceptive signals**

Almost all researchers agree that behaviour is hierarchical, in that some elements have asymmetrical influence over the other elements (Dawkins 1976, Nelson 1990, Houston et al. 1993, Werner and Anholt 1993, Ydenberg 1998). It is predicted that animals assessing multiple sources of information concerning one ecological category (i.e. predation risk) will exhibit more contingencies (switches in asymmetry rules) (Hazlett 1996, Hazlett and McLay 2000). In previous sections the ability of marron to detect visual cues from bagged fish, and chemical cues from food has been demonstrated, however whether or not marron can differentiate chemical cues pertaining to potential threat (silver perch) was inconclusive.

In T5:1, behavioural responses of marron to multiple cues (visual and chemical) revealed no differences in response to F+PCW between crayfish held with or without bagged silver perch. In addition, marron exposed to the F+PCW, increased feeding behaviour, locomotion, and use of sensory devices (antennules and antennae), which are behaviours indicative of food-related responses (Tierney and Atema 1988, Hazlett 1990, Grasso and Basil 2002). These results suggest that visual cues are insufficient in inhibiting feeding, when presented alone, or in combination with chemical cues from silver perch.

In T5:2, a further comparison of the responses of marron to visual and chemical cues from silver perch was examined. In this trial, silver perch and marron were housed in larger compartments to increase freedom of movement (Plate 5.3). However, no significant differences were seen when comparing the responses of marron to cues presented alone, with the responses of marron to combined cues (visual and chemical). An incidental observation was that reaction times were faster and standard errors lower in marron responding to combined cues, compared to all other treatments. This may indicate an increased level of confidence in responses, as marron reacted more immediately and consistently. An increased confidence with combined cues has previously been described by Goncalves et al. (2002). Although not significant, a behavioural trends was apparent

when data was examined more holistically, where marron responded to combined cues with increased locomotion and climbing, choice of raised posture and increased use of antennae compared to cues separately (Figure 5.9). High variation in responses precluded low significance values. Large differences within populations were experienced in all laboratory studies in this thesis, and in trials conducted by Gherardi et al. (2002), and Height and Whisson (2004). Replication in each of these studies was based on eight animals per treatment, however evidence suggests that for this type of research, minimum replication number needs to be increased.

### **8.3 Effects of competition on responses**

T5:2 compared the responses of marron to visual and/or chemical cues from silver perch, under free-range conditions with yabbies. This trial was designed to determine if competition would force marron to respond more decisively to cues. One hypothesis stemming from results in T4:1 and T5:1, was that marron would not display clear avoidance responses to cues from silver perch as they rely on their ability to quickly tail-flip away from danger (i.e. towards shelter). In this trial, shelter was limited so that on detection of cues marron may be more inclined to claim shelter prematurely, as waiting for more imminent signs of threat may result in exclusion from refuge by resident (yabbies). Similarly, previous studies into yabby behaviour (Gherardi et al. 2002) have referred to a high behavioural plasticity exhibited by yabbies, and increased avoidance responses over marron when faced with alarm cues from crushed conspecifics (Gherardi et al. 2002). Earlier detection of potential threats by yabbies should result in a heightened response in marron, reacting to yabby behaviour.

In all comparisons between responses to the varying exteroceptive cues presented, no discernable differences were seen when comparing marron behaviour when held with or without yabbies. An examination of the interaction responses between marron and yabbies recorded using the 2-hour protocol in T5:2 (Table 5.5). Results demonstrated an overwhelming dominance of marron due to greater occupation of shelter, exclusively evicting yabbies from shelter, and being the victor in 34 out of 36 aggressive encounters following the introduction of silver perch to systems (Table 5.5). These results, taken together, suggest that marron behaviour is not inhibited by competition with yabbies.

#### 8.4 Effectiveness of marron interaction responses under predation pressure

Investigations in Chapter 4 and 5 demonstrated that marron can detect and differentiate both visual and chemical cues pertaining to silver perch, although displaying a distinct lack of avoidance responses upon detection of food-derived chemicals. These observations indicate that marron either do not interpret cues from silver perch as risk related, or that foraging holds hierarchical dominance over avoidance of potential threat. It can now be hypothesised that marron held with silver perch would be heavily predated on, unless avoidance responses of marron (if any) are triggered upon a more imminent predation threat.

To address this hypothesis, the effectiveness of potential avoidance strategies employed by marron were examined in two free-range trials with known crayfish predators - Murray cod (Allen et al. 2002) and silver perch (Jones and Ruscoe 1996, Whisson 2000, Allen et al. 2002). Previous research has highlighted the role of light intensity and shelter complexity in influencing interactions between predator and prey (Guthrie 1986, Rittschof 1993, Baumgartner et al. 2003, Utne-Palm 2004). As such, both factors were manipulated to gauge effects on marron avoidance strategies - given earlier findings of the complex nature of multiple exteroceptive cues (i.e. visual and chemical) and the importance of shelter.

Low survival of marron was observed in T6:1 and T6:2, which was not unexpected based on results from the previous laboratory investigations. In T6:1, marron mortalities reached 100% in 13 days, where no shelter was provided, and were greater than 80%, where shelter and 0% light intensity was trialed (Figure 6.1). In T6:2, free-range culture of marron and silver perch resulted in survival levels of between 11% and 49.7% of large marron across all ponds, along with low survival of juveniles (Figure 6.5) compared with industry averages (Whisson 1997, FWA 1999). In both field and laboratory trials, shelter afforded a distinct advantage to marron (Figure 5.1 and 5.6). However, predation was still significant at >40% and >50% mortality in shelter treatments for T6:1 and T6:2, respectively. Predation rates are likely to be understated within an industry context, as both laboratory and field trials were carried out over relatively short periods compared to aquaculture production cycles. Finally, where shelter was provided in 0% light intensity conditions, predation was greater than in ambient light (>80% mortality *versus* <50%). This suggests that marron survival is not advantaged by low light - a somewhat perplexing assertion (discussed in Section 8.5).

Although shelter showed the greatest benefits to marron, appearing to negate to some degree, the predation pressure by both Murray cod and silver perch, the high predation recorded would still suggest that free-range culture of marron in ponds with predatory fish (including omnivorous species such as silver perch) is impractical. Poor suitability of a number of crustacean species to polyculture with finfish has previously been described (Karplus et al. 1995, Kotha and Rouse 1997, Rouse and Kahn 1998), such as with many species of Penaeid prawns where polyculture has resulted in half the gross revenue of monoculture (Shang 1983). In these cases improved management practices can sometimes aid in negating negative interactions (Huner et al. 1983b, Whisson 2000). It is clear that successful polyculture of marron and silver perch relies on the development of management practices surrounding cage culture. The success of marron within this type of culture system is supported by laboratory results in Chapters 4, 5 and 6, as marron should show no negative impacts linked to avoidance behaviour from this type of culture system.

#### **8.4.1 Adaptability of marron to novel predators**

An interesting finding from behavioural observations in T6: 1, was the indication that marron could be 'learning' in response to threat from Murray cod. Following predation of conspecifics, marron were shown to occupy shelter, and where no shelter was provided marron remained in corners or along edges of aquaria (Plate 6.4). Previous studies in this thesis have shown a general disregard displayed by marron in the face of novel predator cues (Chapter 4 and 5), however these observations may suggest that marron require experience in order to associate novel cues with threat. The requirement of experience in order to formulate effective response has been seen in many other species (Mathis and Smith 1993b, Chivers and Smith 1998, Dicke and Grostal 2001, Hazlett 1971). In some cases, prey individuals must experience a predator cue (such as predator odour) and an danger cue (such as alarm odour or prey breakdown products) simultaneously before the predator cue is treated as a danger signal (Chivers et al. 1996b, Hazlett and Schoolmaster 1998, Grostal and Dicke 1999, Wisenden and Millard 2001).

Following development of avoidance responses seen in T6:1, marron survival was still significantly reduced, supporting the conclusion that free-range polycultures would not

result in high survival, of even 'experienced' marron. These observations warrant further investigation into the ability of experienced individuals to recognise threat cues following initial periods of interaction. Future studies could incorporate comparison between farm marron (used in trials) and wild stock marron, examining avoidance to natural predators, such as freshwater cobbler or redfin perch (introduced species in Western Australian waters). Perhaps genetic improvement programs targeting polyculture attributes in marron, such as avoidance responses, could provide a realistic opportunity to create an economic free-range polysystem.

### **8.5 Diurnal changes in behaviour**

Nocturnal behaviours of marron were recorded in T5:2, and indirectly in T6:1. Results highlighted variations in individual and interaction behaviour between day and night time observations which, if nothing else, demonstrate a potential flaw in many behavioural studies involving nocturnal species carried out only during daylight hours (e.g. Gherardi et al 2002, Hazlett et al 2002, Height and Whisson 2004).

Results showed that during nocturnal periods, the frequency of interactions between marron and yabbies was increased (T5:2) (Table 5.5), and predation of marron by Murray cod grew 12-fold (T6:1) (Table 6.2). The increased activity displayed by marron at night, being primarily nocturnal foragers (Morrissy and Caputi 1981, Molony and Bird 2002), would no doubt have contributed to the higher mortalities in this period when held with Murray cod, where frequency of interaction would have been increased. This may explain previous suggestions (Section 8.4) that marron are disadvantaged by low-light conditions.

## ***Chapter nine***

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### ***General discussion***

## **CHAPTER 9**

### **General discussion**

The research in this thesis was undertaken to assist Western Australian marron growers, and other rural industries, attempting to diversify their income base whilst optimising pond yields through a combination of marron and silver perch within a single system. An understanding of the ecological, biological and chemical processors contributing to production within these systems is crucial to successful planning and management of this diversified strategy.

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Although multi-species systems offer a range of business advantages, management is often undermined through increased complexity of culture. The trials carried out in this thesis were aimed at building an understanding of the communication between component species and relating the resulting interaction responses to production changes. A more thorough understanding of the way cultured species 'act' and 'react' will provide farmers with a greater ability to predict outcomes from manipulation of system variables, thereby reducing the time required to develop appropriate management strategies for optimising production.

This final chapter discusses the implications of results in this thesis for polyculture system management and more specifically, integration of silver perch into marron ponds in south-west Western Australia.



## 9.1 Implications for polyculture system management

One of the underlying reasons for investigating the interaction ecology of marron and silver perch in this thesis was to determine whether free-range polyculture conditions could be manipulated in a way that would reduce niche conflicts, whilst enabling optimal production of both species - given that silver perch displayed inhibited growth in cages (Whisson 2000, Storer and Whisson 2003). The results of laboratory and field trials (Chapter 4,5 and 6) strongly suggest that free-range polyculture is unlikely to be economical using current practices, as marron display poor avoidance strategies and suffer high predation, even where complex shelter and low light conditions were provided (Chapter 6).

Examining the ability of marron to detect visual and chemical cues from silver perch was also done to provide insight into whether marron would be negatively affected by stress responses from caged silver perch. However, the behaviour of marron in response to predatory cues supports the use of cage culture of silver perch, where lack of avoidance or obvious modification in behaviour of marron to both chemical and visual cues (Chapter 4,5) suggests that caged fish would have little to no negative effect on marron, and therefore marron production should not be negatively affected.

In light of these findings, two field trials were conducted within this thesis to investigate key variables in the production of marron and caged silver perch in polyculture (Chapter 7). Given that one of the main problems with holding fish in cages is inhibition of growth, this was also accommodated in research designs by examining a range of densities and stocking sizes, and through the addition of cage shelters. A core focus of field research was investigating growth-density relationships for both marron and silver perch, to determine maximum holding capacity for both species, under varying system conditions.

A review of the literature identified several key factors believed to be associated with depressed growth of fish in cages, these include: poor water quality (Huguenin 1997, Masser 1997), overcrowding (Huguenin 1997, Masser 1988, Whisson 2000), increased stress due to visual exposure to predators (Masser 1988), and limited access to natural feeds, especially for omnivorous species (Masser 1988). Assuming adequate water quality is maintained in ponds containing cages, poor water quality within cages is likely to be associated with insufficient water exchange between cages and ponds, which may

result in low levels of oxygen and high nitrogenous waste, localised within the cage (Masser 1988). Water movement through cages is affected by factors such as pond circulation levels, mesh size, algal fouling and stocking densities. In trials conducted in this thesis, problems associated with cage water quality were addressed: mesh size of cages was standardised, where the largest mesh size preventing escape of fish was used to maximise flow through cages, cages were aligned with paddlewheel aerators to maximise water throughput (Plate 7.2), and in T7:2, two cages were employed to reduce cage stocking densities while maintaining pond densities, thus reducing impedance of water flow by fish.

In the two field trials reported in Chapter 7 (T7:1 and T7:2), the other factors influencing production of fish in cages (overcrowding, stress due to high visibility to predators and access to natural feed) were examined. This was done through manipulation of stocking regime (i.e. stocking size, cage densities and pond density) and habitat complexity within cages. Cage shelters were tested for the first time in silver perch culture to investigate their effect on stress, and in an attempt to encourage epiphytic growth, which could be accessed as feed by silver perch. Cage shelters were monitored for any affects on water quality due to resistance of flow through cages. Total pond yields were examined under various density regimes, and the role of shelter (amount and placement) was investigated. Ultimately, marron were the primary species in all research, with the underlying aim of commercialising polyculture through maximising yields in existing marron farming operations. As such, discussion primarily examines research outcomes related to marron production.

### **9.1.1 Density interrelationships associated with marron production**

The potential for density effects on marron production under polyculture regimes was examined in field trials in Chapter 7. Results from these trials were compared to data from the only other reported trial using commercial-sized floating fish cages to culture silver perch in marron ponds, conducted by Whisson (2000). Unlike trials in this thesis, Whisson (2000) examined production over the optimal growth season, and introduced juvenile marron and silver perch to systems (as opposed to advanced fingerlings used in this thesis).

A clear advantage to marron grown in polyculture was apparent in all trials conducted. Marron production showed significant increases in growth rate (T7:1 and T7:2), pond yield (T7:2, Whisson 2000) and survival (T7:2, Whisson 2000), when silver perch were present in the system (Table 9.1). Comparison between densities of silver perch showed no negative effects on marron production (final weight, survival, yield) across all trials (Table 9.1). Further, results showed positive density relationships in marron production, where a significant increase in weight and pond yield was recorded for marron grown in the highest perch density (0.56/m<sup>2</sup>), compared with 0.28/m<sup>2</sup> (T7:2). This result is supported by Yashouv (1971), who documented increased growth of benthic species in the presence of silver carp (*Hypophthalmichthys molitrix*), attributing higher growth to nutritional faecal deposition from carp - resulting in higher polyculture yields.

**Table 9.1** Marron production from polyculture with different densities of silver perch

Whisson (2000)		Chapter 8		November-July					
marron density (#/m <sup>2</sup> )	perch pond density (#/m <sup>2</sup> )	pond biomass initial kg/ha	pond biomass final kg/ha	survival (%)	average initial Wt (g)	average final Wt (g)	SGR (%/day)		
3	0.00	123 ± 19.5 <sup>a</sup>	229 ± 149 <sup>a</sup>	13.8 ± 8.7 <sup>a</sup>	4.1 ± 0.65 <sup>a</sup>	61.8 ± 12.9 <sup>a</sup>	0.73 ± 0.06 <sup>a</sup>		
3	0.18	123 ± 19.5 <sup>a</sup>	380 ± 35 <sup>a</sup>	27.5 ± 5.5 <sup>a</sup>	4.1 ± 0.65 <sup>a</sup>	48.4 ± 5.9 <sup>a</sup>	0.68 ± 0.03 <sup>a</sup>		
3	0.36	123 ± 19.5 <sup>a</sup>	374 ± 16 <sup>a</sup>	31.3 ± 1.0 <sup>a</sup>	4.1 ± 0.65 <sup>a</sup>	39.8 ± 1.4 <sup>a</sup>	0.63 ± 0.00 <sup>a</sup>		
Storer (2005)		Chapter 7		T7:1 - January-July		T7:2 - March-November			
marron density (#/m <sup>2</sup> )	perch pond density (#/m <sup>2</sup> )	pond biomass initial kg/ha	pond biomass final kg/ha	survival (%)	average initial Wt (g)	average final Wt (g)	SGR Overall (%/day)	SGR T2: Nov (%/day)	
0.07	0.00	49.7 ± 0.28 <sup>a</sup>	56.9 ± 7.3 <sup>a</sup>	82 ± 11.3 <sup>a</sup>	71.6 ± 0.5 <sup>a</sup>	100.5 ± 4.1 <sup>a</sup>	0.39 ± 0.02 <sup>a</sup>		T7:1
0.07	0.14	49.4 ± 0.14 <sup>a</sup>	65.4 ± 0.9 <sup>a</sup>	80 ± 0.1 <sup>a</sup>	71.2 ± 0.1 <sup>a</sup>	117.8 ± 1.6 <sup>b</sup>	0.58 ± 0.01 <sup>c</sup>		
0.07	0.28	49.9 ± 0.14 <sup>a</sup>	48.5 ± 13.2 <sup>a</sup>	65 ± 24.1 <sup>a</sup>	71.8 ± 0.3 <sup>a</sup>	107.2 ± 1.2 <sup>ab</sup>	0.46 ± 0.00 <sup>b</sup>		
0.83	0.00	682.8 ± 5.5 <sup>a</sup>	246.4 ± 49.6 <sup>a</sup>	30.7 ± 5.9 <sup>a</sup>	81.9 ± 0.7 <sup>a</sup>	96.3 ± 8.4 <sup>a</sup>	0.08 ± 0.6 <sup>a</sup>	-0.25 ± 0.2 <sup>a</sup>	T7:2
0.83	0.28	684.6 ± 1.0 <sup>a</sup>	330.8 ± 0.0 <sup>b</sup>	53.3 ± 0.0 <sup>b</sup>	82.2 ± 0.1 <sup>a</sup>	129.1 ± 0.0 <sup>b</sup>	0.21 ± 0.0 <sup>b</sup>	1.11 ± 0.0 <sup>b</sup>	
0.83	0.56	682.7 ± 3.5 <sup>a</sup>	463.3 ± 102.4 <sup>c</sup>	40.5 ± 8.2 <sup>b</sup>	82.0 ± 0.5 <sup>a</sup>	136.9 ± 0.9 <sup>c</sup>	0.24 ± 0.0 <sup>b</sup>	0.96 ± 0.0 <sup>b</sup>	

Although growth rates from trials reported in Chapter 7 were low, due to off-season production, the specific growth rates of marron recorded in November in T7:2, where temperatures were reaching optimal levels, are more in line with commercial requirements (Table 9.1). Previous trials examining marron monoculture have returned

specific growth rates between 0.99%/day and 1.2%/day under optimal conditions of temperature (Morrissy et al. 1995a, Whisson 1995b, Whisson 2000), compared with 0.96-1.11%/day recorded in November in T7:2. In addition, average water temperature across all ponds in November was  $20.5 \pm 0.1^\circ\text{C}$ , which was still below optimal growth conditions, at around  $24^\circ\text{C}$  for marron (Morrissy 1990). This suggests that growth rates of marron may increase further in polyculture with silver perch, exceeding rates experienced in previous monoculture studies. Although results in November were only reflected in one data point, the result was consistent across all ponds.

The advantages of polyculture on crayfish production has previously been documented (Tuten and Avault 1981, Rouse and Stickney 1982, Pillay 1993, Saunders and O'Sullivan 1998). In many cases the growth benefits observed in crayfish cultured with fish have been attributed to synergism between species, with benefits including: improved nutrient cycling (Riise and Roos 1997, Liu and Cai 1998, RIRDC 2002b), soil enhancement (RIRDC 2002b), and nitrogen fixing (RIRDC 2002b, Langdon, Evans and Demetropoulos 2004). In all field studies reported in this thesis, or by Whisson (2000), no negative aspects were identified pertaining to marron production with caged perch. Based on the increased yields of crayfish seen in trials reported, the incorporation of caged silver perch in marron farms is recommended, regardless of whether silver perch are grown commercially. That is, the benefit to marron production per se exceed the costs associated with silver perch and cages.

Low survival of marron was experienced in all trials, including monoculture treatments (Table 9.1), which suggests an overriding factor was responsible. In Chapter 7, high mortality rates were predominantly associated with external predation, with carcasses often found above water line. In light of perimeter fencing (preventing access to land-bound predators) and analysis of injuries sustained by marron mortalities, avian predators are believed to be accountable for the majority of deaths, in both monoculture and caged-silver perch treatments. In marron pond culture, the benefits of bird netting cannot be understated, with survival rates of marron commonly reported above 85% where avian predation is not evident (Villarreal 1988, Bennison and Morrissy 1991, Whisson 1995a).

### 9.1.2 Density interrelationships associated with silver perch production

The foundation study into density interrelationships between silver perch held in cages was conducted by Whisson (2000), where cage densities of 17.4/m<sup>3</sup>, 52.2/m<sup>3</sup>, 87.0/m<sup>3</sup> and 121.7/m<sup>3</sup> were examined. Results from this study detailed specific growth rates of 1.76±0.01%/day, 1.37±0.01%/day, 1.33±0.03%/day and 1.04±0.07%/day, respectively. These results clearly showed a direct negative relationship between density and growth of silver perch, based on production of silver perch in small circular cages (diameter 1.5 m, mesh size 6 mm<sup>2</sup>, depth 0.75 m).

A number of factors may contribute to negative density relationships demonstrated by caged silver perch, these factors may be associated with system density - such as impacts on water quality, or localised density (cage density) - such as competition for feed, injury from contact with other fish or the cage structure, and hierarchy-related stressors from overcrowding. Field trials in Chapter 7 were designed to address some of these factors, where silver perch densities were manipulated by both cage density and pond density (multiple cages), using large cages (Plate 3.6).

#### 9.1.2.1 Density of silver perch in grow-out cages

Whisson (2000) reported reduced SGR and final weight of caged silver perch, compared to free-range culture ( $P < 0.01$ ), and a negative correlation between growth and cage density. Based on these results, Whisson (2000) recommended further examination of densities effects alongside manipulation of system variables, in an attempt to optimise cage culture environment. Production of silver perch held in grow-out cages in T7:1 and T7:2, with comparison to the trial conducted by Whisson (2000), provides some insight into factors affecting growth of silver perch in cages. Results are summarised in Table 9.2, with cage biomass listed for each trial associated with the following stocking densities: 100/cage - 6.84/m<sup>3</sup>, 180/cage - 12.3/m<sup>3</sup>, 200/cage - 13.7/m<sup>3</sup> and, 360/cage - 24.7/m<sup>3</sup>. Although cage densities of silver perch were reduced in trials in this thesis, compared with maximum tested by Whisson (2000), cage biomass was significantly higher due to larger stocking size of silver perch (Table 9.2).

**Table 9.2** Production of silver perch held in large floating cages at a range of stocking densities. Results from T7:1 and T7:2, and by Whisson (2000, Chapter 8).

<b>Whisson (2000)</b>	<b>Chapter 8</b>		<b>November-July</b>			
	initial cage biomass (kg/m <sup>3</sup> )	final cage biomass (kg/m <sup>3</sup> )	survival (%)	average initial Wt (g)	average final Wt (g)	SGR (%/day)
180/cage	0.30 ± 0.01 <sup>a</sup>	1.88 ± 0.05 <sup>a</sup>	91.7 ± 1.8 <sup>a</sup>	12.3 ± 1.03 <sup>a</sup>	151.5 ± 5.2 <sup>a</sup>	0.96 ± 0.01 <sup>a</sup>
360/cage	0.61 ± 0.03 <sup>b</sup>	3.19 ± 0.14 <sup>b</sup>	93.1 ± 2.1 <sup>a</sup>	12.3 ± 1.04 <sup>a</sup>	95.9 ± 6.5 <sup>b</sup>	0.85 ± 0.03 <sup>b</sup>
<b>Storer (2005)</b>	<b>Chapter 7</b>		<b>T7:1 - January-July</b>	<b>T7:2 - March-November</b>		
	initial cage biomass (kg/m <sup>3</sup> )	final cage biomass (kg/m <sup>3</sup> )	survival (%)	average initial Wt (g)	average final Wt (g)	SGR trial 2: Nov (%/day)
100/cage (T1)	1.36 ± 0.00 <sup>a</sup>	1.92 ± 0.01 <sup>a</sup>	98 ± 2.0 <sup>a</sup>	200.1 ± 0.2 <sup>a</sup>	286.2 ± 4.3 <sup>a</sup>	0.18 ± 0.021 <sup>a</sup>
200/cage (T1)	2.73 ± 0.01 <sup>b</sup>	3.66 ± 0.36 <sup>b</sup>	96.75 ± 1.8 <sup>a</sup>	198.8 ± 0.6 <sup>a</sup>	276.5 ± 24.9 <sup>a</sup>	0.16 ± 0.031 <sup>a</sup>
100/cage (T2)	1.26 ± 0.01 <sup>a</sup>	2.59 ± 0.08 <sup>a</sup>	84.3 ± 0.0 <sup>a</sup>	183.3 ± 0.8 <sup>a</sup>	378.3 ± 11.8 <sup>a</sup>	0.68 ± 0.00 <sup>a</sup>
200/cage (T2)	2.52 ± 0.01 <sup>b</sup>	5.06 ± 0.24 <sup>b</sup>	95.75 ± 5.3 <sup>a</sup>	184.7 ± 0.6 <sup>a</sup>	370.5 ± 15.2 <sup>a</sup>	0.68 ± 0.00 <sup>a</sup>

In all trials, survival was comparable to industry standards for silver perch monocultures (> 90%, Rowland 1994, Rowland et al. 1994c, Rowland et al. 1995), which provides evidence that basic cage conditions (water quality and nutrition) were adequate.

Comparisons of cage production of silver perch to free-range data was not made, as production in trials in Chapter 7 was not carried out during optimal growth periods, and therefore any differences could be attributed to climate. However, results failed to demonstrate any density effects over the ranges tested, with production comparisons (SGR and final average weight) between the two densities tested (100/cage and 200/cage), similar in both trials. A number of contributing factors may provide some explanation of these results. Growth rates reported in this thesis, especially T7:2, were non-linear due to being conducted over the off-season. Relatively lower growth rates over this period, compared to results from Whisson (2000), would relate to reduced time, or capacity, to established density effects, as the growth-density relationship for silver perch is a typical inverse function (Rowland et al. 1994, Rowland 1994c, Rowland et al. 1995). Similarly, silver perch in T7:1 and T7:2 were stocked at an advanced size (~200g), with the coefficient of variation (cv) for T7:1 = 22.9, and for T7:2 = 19.9 (T7:2), compared with data from Whisson (2000) for fish of similar size (~150g) at cv (%) = 41.56. That is, silver perch were of more uniform size in T7:1 and T7:2, compared to Whisson (2000). This

stocking strategy would be equivalent to mid-season grading under optimal conditions, which has previously been shown to reduce density-effects (Huguenin 1997). The use of cage shelters in T7:2 could also play a role in negating density effects, through reduced stress and increased nutrition. The role of cage shelters is discussed in Section 9.1.6.

### 9.1.2.2 Cage density versus pond density

In the previous section, cage densities were examined to determine if growth depression experienced by silver perch in cages were related to overcrowding. The problem of overcrowding has previously been suggested as a cause of reduced silver perch growth in cages (Whisson 2000), however this was not apparent in field trials conducted. Another potential influence on growth of caged perch is total system load (i.e. total pond biomass). This was tested through the addition of multiple cages in T7:2, with two cages each stocked with silver perch at the same density as in the previous trial, effectively doubling pond density. This stocking regime also allowed comparison to Whisson (2000), as pond densities and total biomass were in excess of those previously examined. Maximum pond density in T7:2 was 0.56 silver perch/m<sup>2</sup>, initial biomass of 513.1 kg/ha and final biomass at 986.2 kg/ha; compared to Whisson (2000) with a maximum pond density of 0.36/m<sup>2</sup>, initial biomass of 61.5 kg/ha, and final biomass of 446.8 kg/ha.

No density effects with increased pond biomass (200/pond versus 400/pond) were recorded within T7:2, and no density effects between T7:1 and T7:2 containing the same cage treatment densities were apparent. This may indicate that density has a greater ecological role in growth inhibition than biomass, and as such growth-density effects on production may be attenuated by splitting pond biomass into multiple reduced-density cages. As many of the factors associated with the effect of overcrowding on growth (food competition, stress and injury) would be addressed with multiple lower density cages, increased production is explicable. As pond densities in Chapter 7 were the highest trialed for marron-perch polysystems, and no density effects were apparent between treatments, this would suggest that pond carrying capacity was not reached under the experimental conditions. Any conclusions must account for the culture occurring in less than optimal conditions, however, growth rates recorded in all ponds in the final data point, where conditions were conducive to production, does provide further support for increasing pond densities further.

### 9.1.3 Optimal stocking densities

Results from both marron and perch indicate that optimal densities of both species are in excess of those trialed. However, it is possible that given optimal conditions, increased biomass of fish and marron may have produced minor density effects. In addition, results must be taken in light of reduced survival of marron in both trials, which reduces overall system loads - although due to the relatively low waste output from marron (compared with perch) this is not believed to be a major contributing factor.

### 9.1.4 Market-sized silver perch in one growth season?

Stocking size of silver perch was increased from fingerlings (<15g) in the previous trial conducted by Whisson (2000), to advanced juveniles (approx. 185g) in trials reported in Chapter 7. The introduction of advanced silver perch helped determine whether the initial increase in cage biomass would compound negative density effects previously reported (Whisson 2000) or whether, given inhibited growth of perch in cages, silver perch could obtain market size in one growth season. As growth of silver perch did not appear influenced by the densities examined in Chapter 7, preliminary evidence supports the option of cage stocking advanced fingerlings under polyculture conditions. In addition, the use of advanced fingerlings demonstrated potential production benefits associated with lower final population variation compared to introduction of juveniles (Whisson 2000), which relates to a greater proportion of the population reaching market size in a given time (reduced runts). This finding reiterates the need for continual grading of caged fish, regardless of stocking size.

The required stocking size of caged silver perch to achieve market weight in one growth season is difficult to predict as field trials in this thesis were not conducted during optimal conditions, however inferences can be made based on growth data recorded for silver perch in November, where temperature were close to optimum. Based on an average growth of silver perch between October and November (30 days) of  $66.43 \pm 5.8g$ , and conservatively assuming that growth would remain stable between September and April, silver perch would need to be stocked at around 100g to reach market size (500g) in one season. At this stocking size, average size of silver perch should be >560g at the end of the April, which should allow for more than 80% of stock over 500g, based on population distribution assessments made in November. This speculation is based on the understanding that many factors will influence results, and requires further examination .



### 9.1.5 Habitat complexity in ponds

The role of habitat complexity on interrelationships between crayfish and potential finfish predators was assessed in laboratory and field studies in Chapter 6 (T6:1, T6:2), where the addition of shelter resulted in significantly increased survival of marron ( $P < 0.05$ ). This concurs with many authors studying the affects of shelter in reducing predation (Stein and Magnusson 1976, Rincon et al. 2002, Naranjo-Paramo et al. 2004). However, where shelter was employed in T6:2, growth rates of marron were reduced. This result may have been due to high mortalities influencing population distribution, however, as marron were observed remaining in shelter in response to predators in T6:1 reduced growth may be a function of inhibited foraging. Other studies examining crayfish response to predators have previously described reduced foraging (Hazlett 1994a, Bouwma and Hazlett 2001, Gherardi et al. 2002). These results should not limit production of marron with caged perch, as laboratory investigations suggest that marron do not respond with avoidance tactics to cues associated with fish in cages.

The use of shelter in the field trials carried out in Chapter 7 was not investigated directly, however a number of outcomes are worthy of discussion. Analysis of marron carcasses discovered in all field trials indicated bird predation, with injuries consistent with avian attack, and dead animals almost always found out of water. Previous studies involving freshwater crayfish (*Cherax* species) cultured in ponds have shown highly susceptibility to avian predators, such as cormorants (Jones and Ruscoe 1996). In addition, a high percentage of the marron mortalities recovered were moulting or immediate post-moult crayfish. This suggests that either birds targeted the softer shelled marron, or more likely, that moulting marron were inhabiting shallow bank regions to escape cannibalism, and were therefore more exposed to avian predators. These observations imply that shelter complexity or density was insufficient in preventing bird predation. Although bird-netting would appear to be the only way to totally protect stock, the introduction of shelters along pond banks in T7:2 demonstrated encouraging results, with a clear decline in the number of marron carcasses found in and around ponds. It is assumed that the exposed shallow bank-regions of ponds would also contribute to the number of moult-deaths in marron ponds, regardless of bird-netting, due to increased stress levels of marron in this vulnerable area. It is suggested that even with pond netting, shelter placed along edges will increase marron survival during moulting, as stress is reduced as animals are less exposed to predation or cannibalism.

### 9.1.6 Habitat complexity in cages

The use of habitat within silver perch cages in T7:2 was investigated following significant increases in silver perch growth where shelter was provided in free-range systems in T6:2. It was hypothesised that silver perch in this trial gained benefit from reduced stress due to refuge from avian predation and/or nutritional benefit from epiphytic growth on shelters. Increased epiphyte growth on submerged materials and the associated advantages due to exploitation by fish as food, has previously been shown (Masser 1988).

The addition of cage shelters appeared to reduce feeding neophobia of silver perch, with more rapid initiation of feeding responses, and increased duration of feeding compared to previous trials where cage shelters were not used (T7:1). Similarly, silver perch held with shelter did not demonstrate startle responses to external disturbances, which are a common reaction when workers move around ponds. It is difficult to draw conclusions from these observations, as feeding and general behaviour of silver perch was not quantified. However, more conclusive evidence was apparent in feed conversion ratios (FCR) of silver perch. FCR of silver perch between October and November was between 1.81 and 2.15 (increase in weight of fish (kg) per kg of feed). These FCR data were higher than previously recorded for caged silver perch culture, where upper levels of between 1.24 and 1.48 have been reported (Rowland 1994b, Whisson 2000). The increased FCR of silver perch where cage shelters were provided may suggest increased amounts of supplemental feed. As high levels of filamentous algae were observed attached to cage shelters, along with associated invertebrates assemblages recorded within cages, both of which are natural feed for silver perch (Grant 1987, Barlow et al. 1986), this is supported. In addition, SGR of silver perch in T7:2 (approx. 0.7%/day, November), where cage shelters were provided, was much higher than in T7:1 (maximum of  $0.18 \pm 0.02\%$ /day), where no shelter was provided (temperature of both trials was approximately 20°C over period where FCR was calculated).

The use of shelter in production cages is rarely reported, but where used is has been reported to reduce effects from crowding (Deady et al. 1995, Flemming and Hone 1996). The role of shelter in negating stress from potential predation has also been shown (Appelberg et al. 1993, Baker and Montgomery 2001, Lass 2001), which may explain increased feeding responses of silver perch in T7:2. Continued investigation into cage shelters in silver perch culture is clearly required, however any studies must consider the

potential adverse effects shelters may have on water circulation through cages, as water quality problems associated with poor circulation have been identified (Masser 1988).

### **9.1.7 Off-season production**

During winter months in south-west Western Australia water temperatures are generally below 15°C. As this falls well below optimal conditions for marron (Morrissy 1995) and silver perch (Rowland and Barlow 1991), growth in these periods is often negligible, with both species even reported to lose weight in some instances as they use reserves to maintain homeostasis (Morrissy et al. 1995a, Whisson 2000, Storer et al. 2004a).

Although assessment of off-season production in this thesis was not an original aim, it was worth investigating in light of potential benefits to species that come with combined culture, which may relay to production improvements during off season. Results from Chapter 7 showed no identifiable benefits from polyculture during winter months, with SGR and FCR of both marron and silver perch displaying low to negative production. Based on growth data during winter (marron - Figure 7.3, silver perch - 7.8), stocking of both marron and silver perch would appear to be most profitable around July-August for silver perch, and September-October for marron, allowing a period of acclimatisation before temperatures begin to reach appropriate levels for growth. This finding concurs with results from partial budget analysis conducted by Whisson (2000).

## **9.2 Impact of polyculture on marron-silver perch production**

The theme underpinning all investigations reported in this thesis pertains to the capacity of polyculture to increase the production of marron in ponds, and achieve greater overall system yields for marron farmers. If multiple species can be grown in combination, without direct conflict or niche interference, then logically overall production will benefit from business advantages such as risk spreading (diversified income streams) and increased profitability compared to monoculture (resource sharing). However, the most impressive benefits from polyculture often come when species complement each other, resulting in synergistic advantages, increasing the profitability of one or more of the component species - either by reducing the amount of artificial feed required (due to nutrient cycling), and/or increased growth of species compared to their respective monoculture.

### 9.2.1 Impacts on survival

Survival of silver perch was high in all field trials in this thesis (Table 9.3), with levels comparable to optimal levels previously reported (Rowland 1994, Rowland et al. 1994c, Rowland et al. 1995). However, marron survival displayed high variability in ponds trials reported in this thesis (T7:1,T7:2), and those used for comparison in Table 9.3. The low overall survival was not found to be correlated with tested variables (marron or silver perch density), and showed no significant difference between monoculture and polyculture treatments in trials described in Table 9.3, with one exception: in T7:2, survival was significantly improved in polyculture ponds compared with monoculture. In all trials, low survival of marron was attributed mainly to avian predators, which may explained increased survivability of marron in polyculture ponds in T7:2 - due to fish cages providing increased protection from birds.

**Table 9.3** Survival of marron and caged silver perch in trials reported in this thesis, compared to previous studies conducted by Whisson (2000).

		Monoculture	Low density polyculture	High density polyculture
<b>T7:1</b> <b>Chapter 7</b>	Marron (%)	82 ± 11.3 <sup>a</sup>	80 ± 0.1 <sup>a</sup>	65 ± 24.1 <sup>a</sup>
	Silver perch (%)	N/A	98 ± 2.01 <sup>a</sup>	96.8 ± 1.8 <sup>a</sup>
<b>T7:2</b> <b>Chapter 7</b>	Marron (%)	30.7 ± 5.9 <sup>a</sup>	53.3 <sup>b</sup>	40.5 ± 8.2 <sup>b</sup>
	Silver perch (%)	N/A	84.5	95.8 ± 5.3
<b>Whisson (2000)</b> <b>Chapter 5</b>	Marron (%)	68.4 ± 9.1 <sup>a</sup>	75.6 ± 2.3 <sup>a</sup>	70.1 ± 9.2 <sup>a</sup>
	Silver perch (%)	N/A	94.2 ± 0.8 <sup>a</sup>	93.9 ± 1.6 <sup>a</sup>
<b>Whisson (2000)</b> <b>Chapter 8</b>	Marron (%)	13.8 ± 8.7 <sup>a</sup>	27.5 ± 5.5 <sup>a</sup>	31.3 ± 1.0 <sup>a</sup>
	Silver perch (%)	N/A	91.7 ± 1.8 <sup>a</sup>	93.1 ± 2.1 <sup>a</sup>

Significant differences exist where different superscripts are denoted along the same row .

### 9.2.2 Impacts on marron yields

Marron displayed significantly faster growth rates when stocked with silver perch in T7:1 and T7:2, resulting in significant increases in pond yield in T7:2 (Table 9.4). The increased growth rates of polycultured marron in all field studies in this thesis, compared to monocultures, demonstrates improved system ecology where multiple species are grown

together. Improvements in production due to polyculture have previously been shown (e. g. Scott et al. 1988, Wahab et al. 1995, Whisson 2000); for example, red swamp crayfish (*P. clarkii*) pond yields were almost doubled compared to monoculture when channel catfish (*I. punctatus*) were introduced into cages within crayfish ponds (Konikoff 1976). The ecological benefits that appear to be harnessed by crayfish within these systems have previously been discussed. Cohen (1984) suggested that increases in yields were due in part to a recycling process occurring within the system. Rouse et al. (1987) cited re-distribution of food and water quality improvements as likely polyculture benefits. In respect to marron-perch polycultures, Whisson (2000) suggested that silver perch only partially digest feed, leaving highly nutritious faecal pellet for benthic dwellers. This concurs with Yashouv (1971), who hypothesised that rich faecal pellets produced by some fish species could result in improved yields of omnivorous species, such as crayfish.

**Table 9.4** Marron pond production: monoculture *versus* polyculture with caged silver perch. Results from this thesis are compared with previous trials investigating marron-perch culture (Whisson 2000).

	Pond density of marron (/m <sup>2</sup> )	Production (kg/ha± standard error)		
		Monoculture	Low density polyculture	High density polyculture
<b>T7:1</b> <b>Chapter 7</b> (ponds - 0.072 ha)	0.07	<b>56.9 ± 7.3<sup>a</sup></b>	<b>65.4 ± 0.9<sup>a</sup></b>	<b>48.5 ± 13.2<sup>a</sup></b>
Pond density of silver perch (/m <sup>2</sup> ) = 0.14 and 0.28				
<b>T7:2</b> <b>Chapter 7</b> (ponds - 0.072 ha)	0.83	<b>246.4 ± 49.6<sup>a</sup></b>	<b>330.8<sup>b</sup></b>	<b>463.3 ± 102.4<sup>c</sup></b>
Pond density of silver perch (/m <sup>2</sup> ) = 0.28 and 0.56				
<b>Whisson (2000)</b> <b>Chapter 5</b> (ponds - 0.024 ha)	2.00	<b>1432 ± 137<sup>a</sup></b>	<b>1986 ± 18<sup>a</sup></b>	<b>1736 ± 148<sup>a</sup></b>
Pond density of silver perch (/m <sup>2</sup> ) = 0.25 and 0.50				
<b>Whisson (2000)</b> <b>Chapter 8</b> (ponds - 0.024 ha)	3.00	<b>229 ± 149<sup>a</sup></b>	<b>380 ± 35<sup>a</sup></b>	<b>374 ± 16<sup>a</sup></b>
Pond density of silver perch (/m <sup>2</sup> ) = 0.18 and 0.36				

Significant differences exist where different superscripts are denoted along the same row .

Another potential ecological benefit from combining silver perch in marron ponds may be related to removal of crayfish competitors/predators. One observation made in all field studies in this thesis, was the reduction of tadpoles and dragonfly nymphs in ponds where silver perch were held, even when in cages. As has previously been discussed (Section

6.2.4.4), both dragonfly nymphs and tadpoles display overlaps in niche occupation with marron. Tadpoles compete with marron of all sizes for feed (Parker 1996), such as artificial pellets, which would not only reduce growth of marron but will reduce profitability to farmers due to lost feed. Dragonfly nymphs will predate on marron at hatchling-juvenile stages (Bird 1995, Jones 1995), and most likely target eggs on females. Methods of controlling these pest species requires investigation, for example: a small number of silver perch released free-range into marron ponds as biological controls may provide more benefits than disadvantages.

### 9.2.3 Impacts of polyculture on system yields

In all studies examining marron polyculture with caged silver perch (using grow-out cages), the combination of species resulted in significant increases in system yields compared to marron monoculture (Figure 9.1). These results are supportive of numerous other studies demonstrating significantly higher yields from polyculture (e.g. Perry and Tarver 1987, Brummet and Alon 1994, Wahab et al. 1995, Jones and Ruscoe 1996, Whisson 2000).

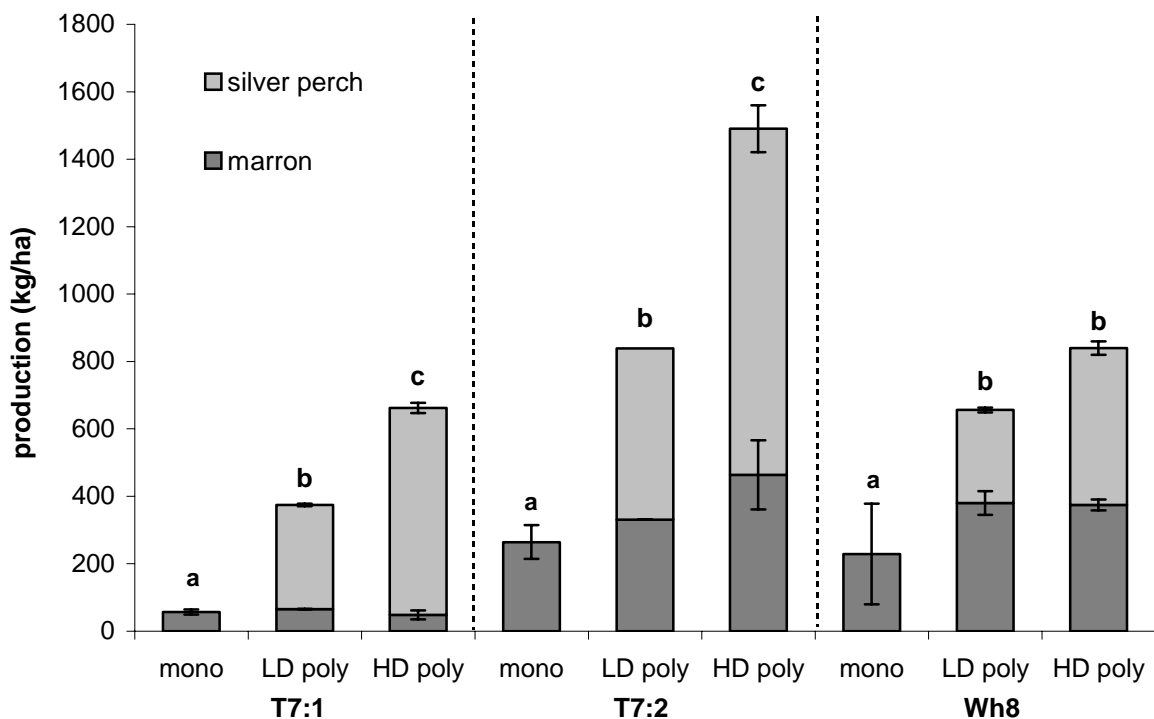


Figure 9.1 System yields from marron and silver perch production experiments: monoculture *versus* polyculture

### **9.3 Mine lake aquaculture**

The three preliminary trials conducted at the Collie Aquafarm (T6:2,T7:1,T7:2) demonstrated that experimental ponds could sustain a level of growth and survival comparable to industry standards, for both marron and silver perch. This demonstrates that the acid water treatment system (Section 3.1.2.2), was successful in providing water capable of sustaining aquatic life and more importantly, aquaculture. Assuming that problems encountered with aluminium are controlled, future studies should investigate increased pond densities in order to determine maximum profitability, and therefore commercial viability, of aquaculture as a beneficial end use for mine lakes.

## 9.4 Summary: research questions addressed

### Study area one: Interspecific chemical communication

- Do marron detect and respond to food odour? **YES**
- Are marron able to detect novel chemical signals (pheromones) from silver perch? **YES**
- Is foraging or other behaviour influenced by chemical detection of silver perch? **NO**
- Does response of marron to chemical cues from silver perch and food vary depending on crayfish size and age. **NO**

### Study area two: Multiple exteroceptive cues

- Do marron detect visual cues from silver perch? **YES**
- Do marron demonstrate a cumulative or varied response to multiple information cues (visual and chemical)? **ASSUMED, but inconclusive**
- Do marron differentiate exteroceptive cues regarding food and potential predation risk? **YES**
- Is foraging influenced by the detection of chemical and/or visual cues from silver perch? **NO**
- How does general behaviour and avoidance strategies compare between marron and invasive crayfish species? **No significant differences, other than increased dominance displayed by marron**
- Does the presence of exteroceptive cues from silver perch influence interaction behaviour between marron and other species of crayfish? **NO**
- Is individual and interaction behaviour between marron and other crayfish species effected by diurnal changes in conditions? **YES - only as function of increased activity of crayfish**

### Study area three: Interaction responses to novel cues

- What are the results of interaction between marron and a novel predatory fish, Murray cod? **Ineffective avoidance strategies result in high predation of marron**
- What impacts do shelter and light intensity have on interaction with Murray cod? **High mortality under all conditions, although shelter reduced predation rates on marron**
- Do marron exhibit innate avoidance strategies in response to Murray cod? **NO**
- Do marron display recognition and learned responses to the presence of Murray cod? and are inducible defences effective? **YES**

### Study area four: System variables

- How does stocking regime of marron effect population dynamics, growth and survival of marron in ponds? **No density effects were apparent**
- How does stocking regime of silver perch in cages effect population dynamics, growth and survival of silver perch in ponds? **No density effects on either species,**
- Does stocking advanced fingerlings have the potential to produce market sized fish in one season? **Yes**



- How does shelter complexity affect marron production in polyculture in ponds with caged silver perch? **Increased survival of marron**
- Does manipulation of cage culture dynamics (shelter) effect silver perch condition? **Increased foraging and assumed benefits to growth and stress reduction**
- Does polyculture provide any off-season benefits in growth or survival of marron or silver perch? **Inconclusive**

## 9.5 Conclusions

Attempting to understand the way species detect, interpret and react to the range of biotic and abiotic factors in their environment in order to drive management is an approach to aquaculture not previously conducted in Western Australia. Altering system variables can greatly influence interaction in multi-species systems and therefore affect productivity. However, as the effects of changing system dynamics are not ubiquitous between species combinations and between systems, management often requires a site-specific and species-specific approach. Historically, the development of management strategies that optimise production are arrived at by trial and error which, especially with complex aquatic polycultures, can take significant time. If researchers understand the way target species receive and act on information pertaining to a range of ecological events, more educated manipulation of variables would be possible - significantly reducing time taken to improve production.

Polyculture has clearly been shown as a way of improving marron production yields, total pond yields and profitability. Several system variables appear to improve polyculture production of marron and silver perch, including cage shelters, appropriate placement of pond shelters, stocking regime, and multiple lower-density cages for silver perch (*versus* single high density systems). The importance of ecological approaches to understanding interaction within multi-species systems cannot be understated. The complex interrelationships between species and the natural and artificial variables require interaction-based analysis, where multi-factor algorithms can be utilised to allow comparison of many variables at the same time, incorporating spatial and temporal variations in a range of production variables and system conditions. The many biotic and abiotic conditions influencing interactions within polysystems necessitates a multidisciplinary approach in order to optimise production.

## 9.6 Recommendations

Laboratory behavioural studies:

- The water source used to hold animals should follow a standard preparation (i.e. chlorination, and subsequent dechlorination) to remove any chemical cues that may be present, allowing closer comparison between trials.
- Due to high standard errors in behavioural responses of crayfish seen in this thesis, it is recommended that where only one crayfish is examined per replicant, the minimum replicant number be increased to twelve.
- Behavioural protocols require adaptation for each species tested, as small differences in behaviour of crayfish species (i.e. 'leg sway' in marron) can influence data analysis.
- Future laboratory studies should examine the role of experience in crayfish responses to predators, where wild-stock responses (system with predator) could be compared to farm-stock (no predators). Variations in avoidance responses between individuals within species should be examined through genetic assessment, to determine whether animals with greater fitness in the presence of predators can be selected for.

Field trials:

Optimal stocking densities in the duoculture of marron and silver perch requires investigation to determine viability of this diversification option. Production must be examined during the optimal growth season, with bird-netted ponds. Given these conditions, it is recommended that the medium silver perch density trialed in this thesis (100/cage and 2 cages) be used as the base level, increasing densities in additional treatments.

A number of key factors affecting polyculture production were outlined in Section 9.5, requiring further elucidation (i.e. interaction ecology between component species, shelter complexity and management - including crayfish pond habitat and cage shelters for fish, stocking regime), however, some additional elements warrant mention. Although increased turbidity did not advantage crayfish survivorship in trials in this thesis, this is still believed to be a key production element due to its relationship with pond productivity and activity levels of crayfish. As polyculture system load increases, turbidity will become progressively more important and it is therefore recommended that additional polyculture species that would target phytoplankton in ponds be investigated (e.g. mullet, *Mugil cephalus*). Further, additional finfish require evaluation for cage culture with marron - to determine whether

marron growth advantages seen with silver perch would occur with other species (e.g. freshwater cobbler, *Tandanus bostocki*). Finally, as it was hypothesised that access to supplemental feed by silver perch, associated with epiphytes on cage shelters, led to increased growth - it is recommended that future investigations target feed quality for caged fish.

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## ***Appendices***

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### ***Appendix A***

Water quality - all trials

### ***Appendix B***

Summary data tables for T4:1 and T5:2

### ***Appendix C***

Feed compositions - silver perch pellets

### ***Appendix D***

Feed compositions - marron pellets

### ***Appendix E***

Dye tests on tanks to determine speed of diffusion for injected solutions

## Appendix A Water quality data - all investigations

### Chapter 4 Chemical communication

Behavioural responses of marron (*Cherax tenuimanus*) presented with silver perch (*Bidyanus bidyanus*) culture water

Water quality parameters	29-Jan (03)	30-Jan (03)	31-Jan (03)
	day 1 - introduction (±SD)	test day 1 (±SD)	Test day 2 (±SD)
Temperature (°C)	19.84 (0.09)	19.8 (0.00)	19.9 (0.04)
pH	7.12 (0.01)	7.09 (0.01)	7.06 (0.01)
Salinity (ppk)	0.23 (0.01)	0.23 (0.00)	0.22 (0.00)
Conductivity (mS)	0.53 (0.00)	0.53 (0.00)	0.53 (0.00)
Dissolved oxygen (mg/L)	8.23 (0.02)	8.22 (0.01)	8.20 (0.02)
Ammonia (NH <sub>3</sub> ) (mg/L)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Average data from 24 experimental aquaria (25L)			

### Chapter 5 Visual and chemical cues

Responses of marron to visual and chemical cues from silver perch (T5:1)

Water quality parameters	31-Mar (03)	1-Apr (03)	2-Apr (03)
	day 1 - introduction (±SD)	test day 1 (±SD)	Test day 2 (±SD)
Temperature (°C)	19.90 (0.07)	19.89 (0.04)	19.78 (0.08)
pH	7.09 (0.10)	7.07 (0.06)	7.04 (0.03)
Salinity (ppk)	0.23 (0.01)	0.23 (0.01)	0.22 (0.01)
Conductivity (mS)	0.53 (0.01)	0.53 (0.01)	0.53 (0.00)
Dissolved oxygen (mg/L)	8.16 (0.06)	8.13 (0.08)	8.19 (0.06)
Ammonia (NH <sub>3</sub> ) (mg/L)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Average data from 24 experimental aquaria (25L)			

## Chapter 5 Visual and chemical cues

Responses of marron to visual and chemical cues in cohabitation with the congeneric crayfish, yabby, *Cherax albidus* (T5:2)

Water quality parameters	12-Dec (03)	13-Dec (03)
	test day 1 ( $\pm$ SD)	Test day 2 ( $\pm$ SD)
Temperature ( $^{\circ}$ C)	20.13 (0.06)	20.01 (0.10)
pH	7.01 (0.08)	7.01 (0.12)
Salinity (ppk)	0.22 (0.01)	0.23 (0.02)
Conductivity (mS)	0.53 (0.05)	0.53 (0.02)
Dissolved oxygen (mg/L)	8.20 (0.00)	8.21 (0.06)
Total Ammonia (mg/L)	0.00 (0.00)	0.00 (0.001)
Nitrite (mg/L)	0.00 (0.00)	0.00 (0.00)
Nitrate (mg/L)	0.00 (0.00)	0.00 (0.00)

Average data from 25 experimental aquaria (250L)

## Chapter 6 Predator-prey interactions

Predator-prey interactions between Murray cod (*Maccullochella peelii peelii*) and marron (*Cherax tenuimanus*) in the laboratory

Water quality parameters	27-Apr to 11-May (04)
	Average all tanks for duration of trial ( $\pm$ SD)
Temperature ( $^{\circ}$ C)	18.15 (0.08)
pH	7.11 (0.15)
Salinity (ppk)	0.23 (0.03)
Conductivity (mS)	0.53 (0.02)
Dissolved oxygen (mg/L)	7.4 (0.03)
Ammonia (NH <sub>3</sub> ) (mg/L)	0.001 (0.0015)

Data from 16 experimental aquaria (250L), over 14 days

## Chapter 6 Predator-prey interactions

Predator-prey interactions: between silver perch (*Bidyanus bidyanus*) and marron (*Cherax tenuimanus*) in the field

### MONTHLY AVERAGE OF ALL PONDS

Water quality parameters	December (±SE)	January (±SE)	February (±SE)	March (±SE)
Temperature (°C)	24.23 (0.09)	24.3 (0.05)	22.68 (0.09)	22.23 (0.09)
pH	7.56 (0.03)	7.72 (0.03)	7.44 (0.09)	7.36 (0.11)
Salinity (ppk)	0.67 (0.00)	0.80 (0.01)	0.88 (0.01)	0.90 (0.01)
Conductivity (mS)	1.42 (0.04)	1.60 (0.02)	1.64 (0.01)	1.79 (0.02)
Dissolved oxygen (mg/L)	7.68 (0.03)	7.47 (0.05)	7.65 (0.06)	7.60 (0.08)
Ammonia (NH <sub>3</sub> ) (mg/L)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Alkalinity (mg/L)	52.1 (2.99)	X	X	41.67 (3.81)
Turbidity (visible depth/cm)	>50	48 (0.06)	41 (1.6)	38 (2.9)

Average data from six aquaculture ponds (0.072 ha), measured between 1500-1700

### POND AVERAGE OVER TRIAL DURATION

Water quality parameters	Pond 1 (±SD)	Pond 2 (±SD)	Pond 3 (±SD)	Pond 4 (±SD)	Pond 5 (±SD)	Pond 6 (±SD)
Temperature (°C)	23.59 (1.72)	23.45 (1.75)	23.53 (1.86)	23.33 (1.73)	23.61 (1.73)	23.80 (1.7)
pH	7.32 (0.52)	7.43 (0.48)	7.53 (0.31)	7.65 (0.24)	7.67 (0.24)	7.68 (0.25)
Salinity (ppk)	0.81 (0.1)	0.79 (0.1)	0.80 (0.1)	0.80 (0.1)	0.77 (0.09)	0.78 (0.1)
Conductivity (mS)	1.60 (0.18)	1.58 (0.19)	1.58 (0.18)	1.58 (0.19)	1.53 (0.15)	1.62 (0.5)
Dissolved oxygen (mg/L)	7.42 (0.4)	7.64 (0.3)	7.57 (0.4)	7.70 (0.3)	7.60 (0.33)	7.56 (0.4)
Ammonia (NH <sub>3</sub> ) (mg/L)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)	0.00 (0)
Alkalinity (mg/L)	45.37 (1.67)	42.17 (4.66)	46.88 (3.11)	45.33 (1.98)	43.73 (2.66)	41.22 (3.6)
Turbidity (visible depth/cm)	45 (2.1)	42 (5.4)	44 (2.9)	42 (4.1)	43 (4.3)	47 (1.2)

Average data between December and March in all ponds, measured between 1500-1700

### Chapter 7 Polyculture of marron and caged silver perch in the field

Effects of silver perch density in cages on polyculture performance of both species (pilot study) (T7:1)

Water quality parameters	Dec (±SE)	Jan (±SE)	Feb (±SE)	Mar (±SE)	Apr (±SE)	May (±SE)	Jun (±SE)	Jul (±SE)
Temperature (°C)	22.8 (0.8)	23.38 (0.9)	21.78 (1.51)	21.77 (0.86)	19.67 (0.63)	15.85 (0.52)	14.9 (0.45)	13.76 (0.48)
pH	7.36 (0.1)	7.45 (0.2)	8.73 (0.5)	8.12 (0.2)	7.81 (0.2)	7.42 (0.2)	7.62 (0.2)	7.61 (0.2)
Salinity (ppk)	0.54 (0.03)	0.58 (0.03)	1.29 (1.47)	0.68 (0.02)	0.62 (0.02)	0.52 (0.02)	0.5 (0.03)	0.5 (0.03)
Conductivity (mS)	no data	1.3 (0.06)	1.39 (0.11)	1.44 (0.02)	no data	1.07 (0.0)	1.0 (0.03)	no data
Diss. oxygen (mg/L)	10.44 (0.11)	10.34 (0.09)	10.14 (0.73)	10.32 (0.15)	10.42 (0.15)	10.48 (0.11)	9.96 (0.15)	10.51 (0.12)
Ammonia (NH <sub>3</sub> )(mg/L)	0.00 (0.0)	0.00 (0.0)	0.00 (0.0)	0.00 (0.0)	0.00 (0.0)	0.00 (0.0)	0.00 (0.0)	0.00 (0.0)

Turbidity (visible depth/cm)

48 (1.1) 48 (0.9) 45 (1.1) 28 (4.3) 27 (4.0) 22 (3.1) 26 (2.5) 19 (1.3)

Average data from six aquaculture ponds (0.072 ha), measured between 1500-1700

### Chapter 7 Polyculture of marron and caged silver perch in the field

Effects of increased pond densities and cage shelters on polyculture production of marron and silver perch (T7:2)

Water quality parameters	Mar-April (±SE)	May-June (±SE)	July-Aug (±SE)	Sept-Oct (±SE)	November (±SE)
Temperature (°C)	21.5 (0.14)	14.69 (0.06)	12.36 (0.07)	16.88 (0.04)	20.48 (0.12)
pH	7.64 (0.09)	7.06 (0.19)	7.82 (0.12)	7.99 (0.06)	7.57 (0.05)
Salinity (ppk)	0.68 (0.01)	0.43 (0.01)	0.49 (0.01)	0.48 (0.01)	0.57 (0.01)
Conductivity (mS)	1.19 (0.01)	0.87 (0.01)	1.01 (0.01)	1.13 (0.07)	1.17 (0.01)
Dissolved oxygen (mg/L)	8.58 (0.08)	9.57 (0.05)	10.01 (0.07)	8.99 (0.06)	8.13 (0.11)
Ammonia (NH <sub>3</sub> ) (mg/L)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Alkalinity (mg/L) (SD only)	41.67 (5.59)	no data	22.33 (6.98)	41.67 (8.52)	no data
Turbidity (visible depth/cm)	39 (5.6)	41 (4.1)	32 (1.9)	28 (4.2)	22 (5.9)

Average data from six aquaculture ponds (0.072 ha), measured between 1500-1700

**Appendix B** Summary tables for behavioural recordings**Chapter 4** **Chemical communication**

Table I Mean values (s.e.) of the reaction time (s), behaviours and body posture (%) in the presence of two different odours (FOOD, F+CW = food and silver perch culture water)

Table II Summary table - results from Chapter 4

**Chapter 5** **Visual and Chemical cues**

Table III T5:1: Mean values (s.e.) of the reaction time (s), behaviours and body posture (%) in the presence of two different odours (FOOD, F+P = food and silver perch pheromones)

Table IV Summary table - results from T5:1

Table Va T5:2: Reaction time, behaviours and body posture of *C. tenuimanus* presented with visual and/or chemical cues from *B. bidyanus*

Table Vb T5:2: Reaction time, behaviours and body posture of *C. albidus* presented with visual and/or chemical cues from *B. bidyanus*

Table VI T5:2: Summary of interaction response of crayfish in control treatments for each test.

Table VII T5:2: Summary of response of crayfish to exteroceptive cues from silver perch.

**Table III** Mean values (s.e.) of the reaction time (s), behaviours and body posture (%) in the presence of two different odours (FOOD, F+PCW = food + perch culture water)

Observation	Odour solution	Small Marron						Medium Marron						Large Marron													
		Control		Test		Magnitude of Change		Control		Test		Magnitude of Change		Control		Test		Magnitude of Change		Control		Test		Magnitude of Change		Direction of Change	t
		AVG	SE	AVG	SE	AVG	SE	AVG	SE	AVG	SE	AVG	SE	AVG	SE	AVG	SE	AVG	SE	AVG	SE	AVG	SE	AVG	SE		
Reaction Time	FOOD	233.57	49.26	81.43	36.85	152.14	50.44	0.030	-	245.63	45.44	101.25	46.64	144.38	53.18	0.030	-	238.13	39.32	90.00	34.37	148.13	41.02	0.009	-		
	F+PCW	287.14	26.06	98.57	35.82	188.57	37.48	0.003	-	219.28	38.55	105.00	45.88	146.25	40.66	0.196	-	307.50	6.50	59.17	14.89	248.33	19.74	0.000	-		
In Shelter	FOOD	14.29	13.36	14.29	13.36	0.00	0.00	0	-	50.60	18.68	55.36	17.59	19.05	12.98	0.756	+	12.50	12.50	12.50	12.50	0.00	0.00				
	F+PCW	57.14	18.90	42.18	17.67	14.97	11.92	0.285	-	23.21	14.01	36.31	16.07	13.10	7.01	0.104	+	17.46	14.31	16.67	14.43	0.79	0.69		0.363		
Locomotion	FOOD	11.56	6.14	47.62	11.38	36.05	11.54	0.027	+	4.76	4.12	22.02	10.41	17.26	8.24	0.075	+	9.52	6.97	32.74	10.82	23.21	9.11	0.038	+		
	F+PCW	10.88	7.64	36.05	13.32	34.69	11.93	0.168	+	33.93	11.57	14.88	6.20	29.76	11.09	0.218	-	27.78	13.69	34.13	11.92	12.70	5.18	0.450	+		
General feeding movements	FOOD	10.88	6.28	24.49	11.60	17.69	10.86	0.318	+	1.19	1.19	17.26	6.03	16.07	6.36	0.039	+	2.38	2.38	20.24	10.25	17.86	8.33	0.069	+		
	F+PCW	1.36	1.27	25.85	11.74	24.49	11.27	0.088	+	0.00	0.00	15.48	7.62	15.48	7.62	0.082	+	0.00	0.00	0.79	0.69	0.79	0.69	0.363	+		
Antennule Flicking	FOOD	35.37	15.94	42.86	14.45	11.56	5.57	0.324	+	80.36	13.48	78.57	10.80	12.50	5.69	0.815	-	60.71	12.03	56.55	15.02	22.02	8.63	0.736	-		
	F+PCW	98.64	1.27	100.00	0.00	1.36	1.27	0.356	+	86.31	12.39	73.21	16.02	13.10	12.43	0.327	-	80.16	14.02	84.92	12.25	4.76	2.61	0.175	+		
Antennae Movement	FOOD	8.84	5.87	35.37	12.44	26.53	11.20	0.069	+	5.95	5.30	23.21	9.88	17.26	7.63	0.058	+	10.71	8.09	16.67	8.82	11.90	5.83	0.424	+		
	F+PCW	7.48	7.00	24.49	10.76	31.97	10.55	0.323	+	7.86	14.17	14.88	6.33	16.09	13.38	0.839	-	24.60	14.34	27.78	11.24	11.11	4.35	0.666	+		
Lowered posture	FOOD	22.45	14.24	10.88	10.18	11.56	7.77	0.213	-	25.00	16.37	25.00	16.37	0.00	0.00			50.00	18.90	48.21	18.30	1.79	1.79	0.351	-		
	F+PCW	28.57	17.25	8.16	7.64	20.41	13.63	0.211	-	0.00	0.00	1.19	1.19	1.19	1.19	0.351	+	33.33	18.26	36.51	17.58	3.17	2.75	0.363	+		
Intermediate Posture	FOOD	19.73	13.48	25.85	13.81	17.01	8.24	0.596	+	37.50	18.30	42.86	16.74	14.88	10.55	0.663	+	33.33	16.67	36.90	15.79	3.57	2.34	0.170	+		
	F+PCW	28.57	17.25	17.69	6.85	35.37	12.96	0.597	-	44.05	16.97	51.79	14.18	26.79	8.95	0.576	+	34.13	16.37	3.17	1.74	30.95	15.71	0.149	-		
Raised Posture	FOOD	57.82	18.61	63.27	16.97	21.77	13.71	0.760	+	37.50	18.30	32.14	15.55	14.88	10.55	0.663	-	16.67	12.60	14.88	10.93	1.79	1.79	0.351	-		
	F+PCW	42.86	18.90	74.15	12.85	31.29	14.11	0.083	+	55.95	16.97	47.02	13.95	25.60	8.53	0.497	-	32.54	16.13	60.32	16.93	30.95	15.71	0.206	+		
Cleaning	FOOD	2.72	1.64	3.40	2.11	6.12	2.11	0.846	+	0.00	0.00	0.60	0.60	0.60	0.60	0.351	+	0.60	0.60	0.00	0.00	0.60	0.60	0.351	-		
	F+PCW	0.68	0.64	2.04	1.32	2.72	1.32	0.457	+	2.98	2.37	3.57	3.57	5.36	3.54	0.888	+	8.73	5.26	2.38	0.92	7.94	4.60	0.318	-		
Climbing	FOOD	0.68	0.64	6.12	3.03	5.44	3.14	0.156	+	12.50	12.50	5.36	2.45	15.48	10.98	0.575	-	7.74	4.40	5.95	4.29	1.79	1.25	0.197	-		
	F+PCW	1.36	0.82	21.77	13.67	20.41	13.63	0.211	+	20.83	12.79	18.45	13.05	9.52	6.49	0.756	-	19.84	11.88	26.19	10.47	9.52	4.39	0.337	+		

Magnitude of change is the difference in mean values between control and test. Direction of change: (-) lower or (+) higher with test solution than with control water; empty cell = no change. Control water and test solution were compared by paired t-test (t).

**Table II** Summary table - significant results from Chapter 4

Summary of behavioural responses of marron to control and test solutions. Statistical differences accompanying results are indicated by \* =  $P < 0.05$ , \*\* =  $P < 0.01$ , <sup>NS</sup> = non-significant ( $P < 0.1$ ).

<b>Size-class response to control water</b>	<i>signif.</i>
Note: high population variations (standard errors) within size classes	
Shelter rarely utilised by large marron	<i>NS</i>
<b>Sex-related differences in response to control water</b>	
LM: Low posture preferred by males v intermediate posture by females	**
MM: females sheltered more than males	<i>NS</i>
<b>Control water v test solutions</b>	
Reaction time: faster for all crayfish sizes to both test solutions	*/**
Locomotion Increased in response to test solutions for all crayfish sizes ( <i>NS</i> for F+PCW responses)	*
Feeding: Increased in response to test solutions (only significant in MM and food solution)	*
<b>Comparison between test solutions</b>	
LM reacted faster responding to F+PCW than food solution	*
LM displayed inhibited feeding with F+PCW ( $P < 0.1$ )	<i>NS</i>
MM reduce locomotion in F+PCW	*
<b>Comparison between size-classes</b>	
SM and MM used shelter frequently more than LM in response to F+PCW	*
<b>Overall Trends</b>	
SM sustained feeding, locomotion, antennule flicking, antennae movement and raised posture longer in response to test solutions than MM and LM	<i>N/A</i>
LM reacted faster to F+PCW (*), with less pronounced changes to locomotion, feeding and antennule flicking, than in response to food solution alone	<i>N/A</i>



**Table III** Mean values (s.e.) of the reaction time (s), behaviours and body posture (%) in the presence of two different odours (FOOD, F+PCW = food + perch culture water)

Observation	Odour solution	Marron Monoculture						Marron + Empty Bag						Marron + Bag with silver perch																
		Control	Test	Magnitude of Change	Direction of Change	t	Control	Test	Magnitude of Change	Direction of Change	t	Control	Test	Magnitude of Change	Direction of Change	t														
		AVG	SE	AVG	SE	AVG	SE	AVG	SE	AVG	SE	AVG	SE	AVG	SE	AVG	SE	AVG	SE	AVG	SE	AVG	SE	AVG	SE	AVG	SE	AVG	SE	t
Reaction Time	FOOD	178.13	51.76	99.38	41.27	138.75	47.33	-	0.259	228.75	43.06	69.38	35.74	159.38	43.63	-	0.008	275.63	27.62	88.13	20.13	187.50	28.21	-	0.000					
	F+PCW	277.50	37.50	88.13	34.42	196.88	41.41	-	0.005	229.29	46.71	109.29	33.50	132.86	40.78	-	0.051	226.88	46.01	127.50	43.08	106.88	40.93	-	0.056					
In Shelter	FOOD	12.50	12.50	17.26	12.72	4.76	4.76	+	0.351	33.33	16.66	32.14	16.37	15.46	10.16	-	0.922	27.98	15.98	37.50	18.30	9.53	9.53	+	0.351					
	F+PCW	12.50	12.50	0.00	0.00	12.50	12.50	-	0.351	41.50	18.33	37.41	17.10	4.08	3.82	-	0.356	0.00	0.00	12.50	12.50	12.50	12.50	+	0.351					
Locomotion	FOOD	2.38	1.56	31.56	10.49	29.18	10.93	+	0.032	7.74	4.21	16.07	8.53	9.52	4.41	+	0.122	21.43	12.60	26.20	10.46	22.62	6.84	+	0.672					
	F+PCW	32.15	15.55	44.65	15.35	12.50	8.14	+	0.169	2.04	1.32	26.53	10.32	24.49	9.54	+	0.053	22.02	14.02	36.34	11.42	25.02	8.63	+	0.257					
General feeding movements	FOOD	0.00	0.00	21.44	8.05	21.44	8.05	+	0.032	0.60	0.60	14.30	7.37	13.70	7.50	+	0.110	2.39	2.39	17.85	10.05	15.47	10.13	+	0.171					
	F+PCW	0.00	0.00	18.46	6.20	18.46	6.20	+	0.021	2.04	1.32	30.60	12.67	28.56	11.70	+	0.063	1.19	1.19	21.44	11.28	22.63	11.02	+	0.126					
Antennule Flicking	FOOD	9.52	5.01	41.68	10.86	38.10	11.60	+	0.054	14.88	12.29	34.54	11.89	19.65	6.45	+	0.019	52.38	15.42	50.60	10.61	19.62	5.65	-	0.854					
	F+PCW	9.53	5.40	36.32	12.07	26.79	11.80	+	0.057	20.41	13.14	53.07	13.52	32.66	11.69	+	0.040	32.15	15.11	49.60	13.62	33.73	12.74	+	0.333					
Antennae Movement	FOOD	3.57	1.96	29.17	9.95	26.79	10.49	+	0.051	8.33	4.65	26.79	14.67	18.46	10.35	+	0.118	25.58	12.26	36.30	7.99	19.04	4.76	+	0.202					
	F+PCW	33.94	15.01	42.09	14.60	9.70	5.88	+	0.231	1.36	0.82	32.64	11.31	31.28	10.99	+	0.037	31.55	14.05	56.56	13.12	32.14	13.32	+	0.147					
Lowered posture	FOOD	0.00	0.00	0.00	0.00	0.00	0.00		0	0.00	0.00	0.00	0.00	0.00	0.00		0	12.50	12.50	12.50	12.50	0.00	0.00	+	0					
	F+PCW	0.00	0.00	0.00	0.00	0.00	0.00		0	0.00	0.00	2.04	1.91	2.04	1.91	+	0.356	35.13	17.26	25.00	16.37	10.13	10.13	-	0.351					
Intermediate Posture	FOOD	80.93	12.17	65.49	15.86	30.91	13.26	-	0.386	49.40	16.59	37.50	18.30	11.90	8.25	-	0.192	16.68	12.21	7.74	7.74	8.94	4.97	-	0.115					
	F+PCW	37.50	18.30	50.59	16.76	20.24	12.43	+	0.372	53.06	17.91	35.39	13.88	17.68	10.41	-	0.163	7.15	3.93	7.15	5.40	2.83	1.77	-	0.999					
Raised Posture	FOOD	19.05	12.17	34.53	15.86	30.96	13.25	+	0.384	50.60	16.59	62.50	18.30	11.91	8.25	+	0.192	70.84	15.68	79.76	13.73	8.93	4.96	+	0.115					
	F+PCW	62.50	18.30	49.41	16.76	20.24	12.43	-	0.372	46.94	17.91	62.59	14.66	17.50	10.44	+	0.229	57.74	17.23	67.85	15.68	13.69	10.47	+	0.390					
Cleaning	FOOD	0.00	0.00	2.98	2.00	2.98	2.00	+	0.180	1.19	0.78	0.00	0.00	1.19	0.78		0.170	4.77	3.60	2.38	1.27	5.21	2.92	-	0.529					
	F+PCW	0.00	0.00	4.17	3.54	4.17	3.54	+	0.277	2.72	2.55	1.36	0.82	2.72	1.91	-	0.568	1.79	1.79	0.60	0.60	2.38	1.80	-	0.563					
Climbing	FOOD	0.60	0.60	5.96	5.31	6.55	5.25	+	0.357	0.00	0.00	1.19	1.19	1.19	1.19	+	0.351	9.52	8.86	10.72	5.53	8.33	3.89	+	0.817					
	F+PCW	30.36	15.61	24.42	12.16	14.30	7.03	-	0.511	0.00	0.00	2.04	1.32	2.04	1.32	+	0.200	11.91	6.24	16.66	8.34	9.53	5.97	+	0.503					

Magnitude of change is the difference in mean values between control and test. Direction of change: (-) lower or (+) higher with test solution than with control water; empty cell = no change. Control water and test solution were compared by paired t-test (t).

**Table IV** Summary table - significant results from T5:1

Summary of behavioural responses of marron to control and test solutions. Statistical differences accompanying results are indicated by \* =  $P < 0.05$ , \*\* =  $P < 0.01$ , <sup>NS</sup> = non-significant ( $P < 0.1$ ).

<b>General responses to control water</b>	significance
Marron held in aquaria containing fish in bags showed a number of significant differences in background behaviours to other groups:	
— Increased antennule flicking compared to monoculture treatment	**
— Increased antennae movement compared to marron with empty bags in aquaria	*
— Chose low posture more frequently compared to both groups	*
— Chose intermediate posture less frequently than both groups	*
— Increased climbing compared to marron with empty bags in aquaria	*
No significant differences were recorded in behaviour between 'Monoculture' and 'Marron with empty bag' treatments	<b>NS</b>
<b>Sex-related differences in response to control water</b>	
No significant difference found	<i>N/A</i>
<b>Control water v test solutions</b>	
Reaction Time - faster for all groups in response to both test solution	
— significant for: MONO and F+PCW, MBAG and FOOD, MSP for FOOD	*
Locomotion - increased for all groups in response to test solutions	
— significant for: MONO and FOOD, MONO and F+PCW	*
Feeding activity - increased for all groups in response to test solutions	
— significant for: MONO and FOOD	*
Antennule flicking - increased for all groups in response to test solutions	
— significant for: MBAG and FOOD, MBAG and F+PCW	*
Antennae movement - increased for all groups in response to test solutions	
— significant for: MBAG and F+PCW	*
<b>Comparison between test solutions</b>	
No significant differences found	<i>N/A</i>
<b>Comparison between treatments for each test solution</b>	
No significant differences found	<i>N/A</i>

Abbreviations for treatments are MONO - monoculture, MBAG - marron with empty bag, and MSP - marron with silver perch in bag, FOOD - food solution, F+PCW - food with perch conditioned water.

**Table Va** Data represent differences in reaction time, behaviours and body posture of *C. tenuimanus* presented with visual and/or chemical cues from *B. bidyanus*

Behaviour observations	Treatment	Marron ( <i>C. tenuimanus</i> )												
		%Time spent in behaviour		v Visual Treatment		v Chemical Treatment		v Vis/Chem Treatment		v Single sex Treatment				
		Mean	± S.E											
Reaction Time (sec)	Control	286.50	28.50	0.000	***	0.000	***	0.000	***	0.000	***			
	Visual	54.00	29.26									0.963	0.920	0.873
	Chemical	78.00	39.55									0.571	0.493	
	Vis/Chem	24.00	4.00									1.000		
	SingleSex	19.50	3.20											
In Shelter	Control	20.00%	13.33	0.807		0.800		1.000		0.972				
	Visual	3.33%	3.33									0.195	0.807	0.989
	Chemical	42.86%	15.18									0.800	0.428	
	Vis/Chem	20.00%	13.33										0.972	
	SingleSex	10.00%	10.00											
Locomotion	Control	10.48%	5.93	1.000		1.000		0.821		0.781				
	Visual	13.33%	6.76									0.977	0.947	
	Chemical	14.29%	4.97									0.950	0.913	
	Vis/Chem	22.38%	5.55									1.000		
	SingleSex	24.76%	7.51										1.000	
Low Posture	Control	48.57%	14.53	1.000		0.987		0.897		0.967				
	Visual	46.19%	14.02									0.998	0.957	0.994
	Chemical	30.48%	12.64									1.000	1.000	
	Vis/Chem	29.52%	12.31										1.000	
	SingleSex	28.10%	12.65											
Intermediate posture	Control	16.67%	10.05	1.000		0.982		1.000		0.998				
	Visual	15.71%	8.58									0.888	0.979	0.950
	Chemical	33.33%	13.49									1.000	1.000	
	Vis/Chem	29.05%	10.52										1.000	
	SingleSex	31.43%	11.75											
Raised Posture	Control	10.48%	7.47	0.992		0.782		0.549		0.439				
	Visual	20.00%	10.64									0.999	0.984	0.980
	Chemical	31.43%	12.96									1.000	1.000	
	Vis/Chem	37.62%	12.77										1.000	
	SingleSex	39.05%	11.17											
Cleaning	Control	4.29%	2.88	1.000	***	0.984		1.000		1.000				
	Visual	2.38%	1.91									1.000	1.000	1.000
	Chemical	1.43%	1.43									0.973	0.997	
	Vis/Chem	3.81%	1.98									1.000		
	SingleSex	3.33%	2.25										1.000	
Antennae Movement	Control	5.71%	2.11	0.347		0.533		0.033	*	0.007	**			
	Visual	30.95%	9.13									0.998	0.783	0.443
	Chemical	27.62%	7.27									0.593	0.274	
	Vis/Chem	41.43%	11.75										0.980	
	SingleSex	53.33%	8.21											
Antennule Flicking	Control	38.10%	8.03	0.194		0.001	**	0.030	*	0.004	***			
	Visual	69.52%	8.49									0.312	0.918	0.513
	Chemical	89.05%	6.31									0.803	0.997	
	Vis/Chem	73.81%	11.63										0.943	
	SingleSex	89.52%	2.91											
Climbing	Control	0.96%	0.96	0.857		0.750		0.872		0.172				
	Visual	16.67%	10.27									1.000	1.000	0.704
	Chemical	20.48%	11.56									0.999	0.820	
	Vis/Chem	15.71%	10.95										0.684	
	SingleSex	37.62%	13.19											
Approaches	Control	3.81%	3.31	0.634		0.634		0.853		0.752				
	Visual	0.48%	0.48									1.000	0.995	1.000
	Chemical	0.48%	0.48									0.995	1.000	
	Vis/Chem	1.43%	1.43										1.000	
	SingleSex	0.95%	0.95											
Aggressor	Control	12.86%	9.42	0.294		0.326		0.360		0.433				
	Visual	0.48%	0.48									1.000	1.000	0.999
	Chemical	0.95%	0.95									1.000	1.000	
	Vis/Chem	1.43%	1.43										1.000	
	SingleSex	2.38%	1.63											
Non Aggressive interaction	Control	0.00%	0.00	0.999		1.000		0.802		0.059				
	Visual	0.48%	0.48									0.999	0.920	0.110
	Chemical	0.00%	0.00									0.802	0.059	
	Vis/Chem	1.90%	1.45										0.466	
	SingleSex	4.76%	2.24											

'Control' had no fish cues and 'single sex' was in presence of both visual and chemical stimuli. Analysis of variance and post-hoc (Equal variances - Tukey's (reported), Bonferroni, Sheffe; Non-equal variances - Dunnett's T3 (reported) and Tamhane) were used to determine differences between treatments for each behaviour. \*P<0.05, \*\* P<0.01, \*\*\*P<0.001

**Table Vb** Data represent differences in reaction time, behaviours and body posture of *C. albidus* presented with visual and/or chemical cues from *B. bidyanus*

Behaviour observations	Treatment	Yabbie ( <i>C. albidus</i> )							
		% Time spent in behaviour		v Visual Treatment	v Chemical Treatment	v Vis/Chem Treatment	v Single sex Treatment		
		Means	± S.E.						
Reaction Time (sec)	Control	255.00	40.00	0.000 ***	0.014 *	0.000 ***	0.000 ***	0.000 ***	
	Visual	51.00	29.51						
	Chemical	115.50	43.76						
	Vis/Chem	18.00	2.00						
	SingleSex	21.00	2.44						
In Shelter	Control	10.95%	9.94	0.998	1.000	1.000	1.000		
	Visual	5.24%	5.24						
	Chemical	9.52%	9.52						
	Vis/Chem	10.00%	10.00						
	SingleSex	10.00%	10.00						
Locomotion	Control	10.95%	3.55	0.074	1.000	0.878	0.464		
	Visual	36.71%	7.65						
	Chemical	11.43%	4.03						
	Vis/Chem	19.52%	7.22						
	SingleSex	26.19%	8.47						
Low Posture	Control	40.48%	15.00	0.358	0.285	0.678	0.306		
	Visual	17.62%	6.70						
	Chemical	72.38%	11.94						
	Vis/Chem	25.24%	11.02						
	SingleSex	15.71%	5.41						
Intermediate posture	Control	48.57%	13.33	1.000	0.662	1.000	1.000		
	Visual	59.05%	9.23						
	Chemical	18.10%	10.01						
	Vis/Chem	50.48%	11.47						
	SingleSex	57.14%	10.55						
Raised Posture	Control	1.90%	1.90	0.466	0.978	0.962	0.364		
	Visual	16.67%	9.29						
	Chemical	7.62%	6.07						
	Vis/Chem	9.06%	3.65						
	SingleSex	20.48%	8.16						
Cleaning	Control	4.76%	15.06	0.900	0.602	0.688	0.769		
	Visual	1.90%	6.02						
	Chemical	0.00%	0.00						
	Vis/Chem	0.48%	1.51						
	SingleSex	0.95%	3.01						
Antennae Movement	Control	14.76%	7.76	0.246	1.000	0.768	0.762		
	Visual	43.81%	8.33						
	Chemical	14.29%	7.68						
	Vis/Chem	32.86%	8.05						
	SingleSex	31.90%	6.55						
Antennule Flicking	Control	49.05%	10.91	0.551	0.011 *	0.865	0.439		
	Visual	75.24%	7.34						
	Chemical	92.86%	2.58						
	Vis/Chem	69.05%	10.68						
	SingleSex	76.67%	8.62						
Climbing	Control	0.00%	0.00	0.970	1.000	1.000	0.137		
	Visual	1.90%	1.45						
	Chemical	0.48%	0.48						
	Vis/Chem	0.00%	0.00						
	SingleSex	7.14%	4.45						
Approaches	Control	2.86%	2.86	0.955	0.954	0.637	0.883		
	Visual	1.43%	1.02						
	Chemical	1.43%	0.73						
	Vis/Chem	0.00%	0.00						
	SingleSex	0.95%	0.95						
Aggressor	Control	1.43%	1.43	1.000	1.000	0.961	0.999		
	Visual	1.90%	1.90						
	Chemical	1.43%	1.02						
	Vis/Chem	0.00%	0.00						
	SingleSex	0.48%	0.48						
Non Aggressive interaction	Control	0.00%	0.00	1.000	0.479	0.999	0.999		
	Visual	0.48%	0.48						
	Chemical	9.05%	8.53						
	Vis/Chem	1.43%	1.02						
	SingleSex	1.43%	1.02						

'Control' had no fish cues and 'single sex' was in presence of both visual and chemical stimuli. Analysis of variance and post-hoc (Equal variances - Tukey's (reported), Bonferroni, Sheffe; Non-equal variances - Dunnett's T3 (reported) and Tamhane) were used to determine differences between treatments for each behaviour. \*P<0.05, \*\* P<0.01, \*\*\*P<0.001

**Table VI** Summary of interaction response of crayfish in control treatments for each time period: 1. following introduction of crayfish; 2. following introduction of silver perch; 3. nocturnal behaviour. (T5:2).

<b>Interaction between <i>C. tenuimanus</i> and <i>C. albidus</i> (no fish cues)</b>	
Time period 1	
5-minute test	No significant differences between species, sex, blocks or days
2-hour test	<i>C. tenuimanus</i> dominant in interactions, and displayed increased use of shelter and screen
Time period 2	
5-minute test	No significant differences between species, sex, blocks or days
2-hour test	<i>C. tenuimanus</i> dominant, with increased use of screen
Time period 3	
2-hour test	<i>C. tenuimanus</i> dominant, increased use of screen and evicted <i>C. albidus</i> from shelter
<b>Comparisons between control behaviour over time periods</b>	
5-minute test (TP1 vs. TP2)	Locomotion, antennae movement and NAI's increased in TP1 for both species  Number of approaches by <i>C. albidus</i> and raised poster in <i>C. tenuimanus</i> in TP1
2-hour test (TP 1-3)	Number of aggressive encounters and NAI's reduced in TP2 and TP3  <i>C. tenuimanus</i> dominant species in all TP's, with aggression in <i>C. albidus</i> rarely seen in TP 2 and TP3  Shelter use highest in TP2, with <i>C. tenuimanus</i> acquiring shelter more often than <i>C. albidus</i> in all TP's (sig. In TP1 and TP2). <i>C. tenuimanus</i> evicted <i>C. albidus</i> from shelter in TP3, no eviction by <i>C. albidus</i> in any TP's  <i>C. tenuimanus</i> climbed on screen more than <i>C. albidus</i> in all TP's and mostly in TP2

Statistical differences accompanying results are indicated by \* =  $P < 0.05$ , \*\* =  $P < 0.01$ , <sup>NS</sup> = non-significant ( $P < 0.1$ ). TP refers to time period, NAI - non-aggressive interaction

**Table VII** Summary of response of crayfish to exteroceptive cues from silver perch (time period 2), results from T5:2

Reaction time and behaviour of crayfish in response to silver perch in time period 2	
5-minute test	<p>Reaction to all fish cues significantly faster than control for both species</p> <p><u>Trend 1</u>: Increased antennae use in response to all fish cues for both species (except between control and T3 for <i>C. albidus</i> - no difference)</p> <p><u>Trend 2</u>: Increased antennule movements in response to all fish cues for species</p> <p><u>Trend 3</u>: Increased climbing in perch treatments in <i>C. tenuimanus</i></p>
15-minute test	Less aggressive encounters in response to test solutions ( <i>NS</i> )
Behaviour of crayfish in response to <b>chemical cues alone (T3)</b>	
5-minute test (TP2)	<p><i>C. tenuimanus</i> used antennules more than in control</p> <p><i>C. albidus</i> chose low posture compared to T2, T\$ and T%, and used antennules more than in control</p> <p><i>C. albidus</i> chose low posture more than <i>C. tenuimanus</i></p>
2-hour test (TP2 vs. TP3)	<p>Only treatment to not observe aggressive interactions (TP2)</p> <p>Highest shelter rate for <i>C. tenuimanus</i> and lowest for <i>C. albidus</i> (TP2)</p> <p>No difference between T3 and other treatments in TP3</p>
Behaviour of crayfish in response to <b>visual cues alone (T2)</b>	
5-minute test (TP2)	<p>No sig. differences were seen between treatments, however, shelter use reduced markedly compared to control (T1), T3 and T4.</p> <p><i>C. tenuimanus</i> moved less and showed greater use of intermediate posture than <i>C. albidus</i>.</p>
2-hour test (TP2 vs. TP3)	No significant differences reported in TP2 or TP3 between treatments
Behaviour of crayfish in response to <b>combined cues (T4/T5)</b>	
5-minute test (TP2)	<p>Reaction times fastest with multiple cues for both species (T4/T5) (<i>NS</i>)</p> <p>Less use of low posture compared to chemical cues alone for <i>C. albidus</i></p> <p>Increased use of antennules and antennae compared with control for <i>C. tenuimanus</i> within T4/T5</p>
2-hour test (TP2 vs. TP3)	No diffs between T4 and T5, or between these and other treatments
Comparison of treatment responses between day and night time	
2-hour test (TP2 vs. TP3)	Reduction in shelter use and climbing at night, increased eviction of <i>C. albidus</i> by <i>C. tenuimanus</i> , and increased aggressive encounters ( <i>C. tenuimanus</i> dominant) at night compared to directly after introduction of silver perch ( <i>NS</i> )

Statistical differences accompanying results are indicated by \* =  $P < 0.05$ , \*\* =  $P < 0.01$ , <sup>NS</sup> = non-significant ( $P < 0.1$ ). *NS* - Non-significant results, TP - time period, Tx - treatment + No.

### Appendix C Silver perch pellet feed formulation

Table IV Formulation and biochemical composition of commercial silver perch pellets used for all experiments (Glen Forrest Stockfeeders Pty Ltd)

<b>Ingredients</b>	<b>%</b>
Fish meal	27.0
Soybean meal	20.0
Blood meal	2.0
Corn gluten meal	4.0
Wheat	28.4
Sorghum	11.0
Millrun	2.0
Cod liver oil	1.0
Di-calcium phosphate	2.0
Vitamin/mineral premix	2.5
L-methionine	0.15
<b>Proximate composition</b>	<b>%</b>
Crude protein	35.6
Crude fat	5.5
Linoleic series fatty acids	1.1
Fibre	4.4
Carbohydrate	52.1
	<b>g/Kg</b>
Total methionine	7.4
Total lysine	22.6

**Appendix D** Marron pellet feed formulation

Table V Formulation and biochemical composition of commercial marron pellets used for all experiments (Wesfeeds Pty Ltd)

Protein	23%
Fat	6%
Crude Fibre	8.3%
Calcium	2.9%
Phosphorous	1.0%
Salt	0.3%
Metabolisable energy	9.9 MJ/kg
Vitamin A	1700 IU/kg
Vitamin E	10 mg/kg
Nicotinic acid	33 mg/kg
Folic acid	0.8 mg/kg
Thiamine	2.5 mg/kg
Copper	0.8 mg/kg
Vitamin D	250 IU/kg
Vitamin K	0.3 mg/kg
Calcium pantothenate	21 mg/kg
Riboflavin	3 mg/kg
Biotin	125 mg/kg
Choline	170 mg/kg
Iodine	0.1 mg/kg
Iron	2 mg/kg
anganese	10 mg/kg
Zinc	4 mg/kg



## Appendix E

### Dye test

In T4:1 and T5:1 the ability for crayfish to detect odours from both food and fish culture water was tested through injection of cues by syringe into each 54L experimental aquaria.

To determine the rate of diffusion of injected material throughout the system, a dye test was performed. This test involved injection of equal volume of food dye into ten separate aquaria (these systems were not used for experiments) and recording the time taken for the colour to reach all parts of the aquarium. This test was repeated twice with each aquaria, therefore the test was carried out a total of 30 times.

### Results

The diffusion rate of dye throughout aquaria was consistent for all test systems, the following results were recorded.

**Table A** Total diffusion time of coloured dye in 54L aquaria

Dye test No.	Diffusion time	Dye test No.	Diffusion time	Dye test No.	Diffusion time
1	15	11	14	21	19
2	13	12	15	22	18
3	14	13	14	23	15
4	17	14	11	24	17
5	14	15	14	25	12
6	14	16	15	26	17
7	15	17	18	27	14
8	12	18	18	28	19
9	15	19	14	29	15
10	15	20	13	30	15

Total diffusion of liquid throughout aquaria was achieved in  $15.03 \pm 2.00$  s after infection, across all aquaria. Diffusion time was less than 20 s for all aquaria tested.

This test was repeated for experiments in T5:2, using 250L aquaria, where time taken for dye to move from 1 compartment of aquarium to completely fill the second compartment was recorded. The results were as follows:

**Table B** Total diffusion time of coloured dye in 250L aquaria

Dye test No.	Diffusion time	Dye test No.	Diffusion time	Dye test No.	Diffusion time
1	28	11	29	21	23
2	29	12	29	22	21
3	28	13	29	23	26
4	27	14	28	24	28
5	23	15	28	25	25
6	28	16	29	26	24
7	26	17	26	27	25
8	24	18	26	28	25
9	25	19	25	29	28
10	29	20	24	30	21

Total diffusion of liquid throughout aquaria was achieved in  $26.2 \pm 2.4$  s after infection, across all aquaria. Diffusion time was less than 30 s for all aquaria tested.