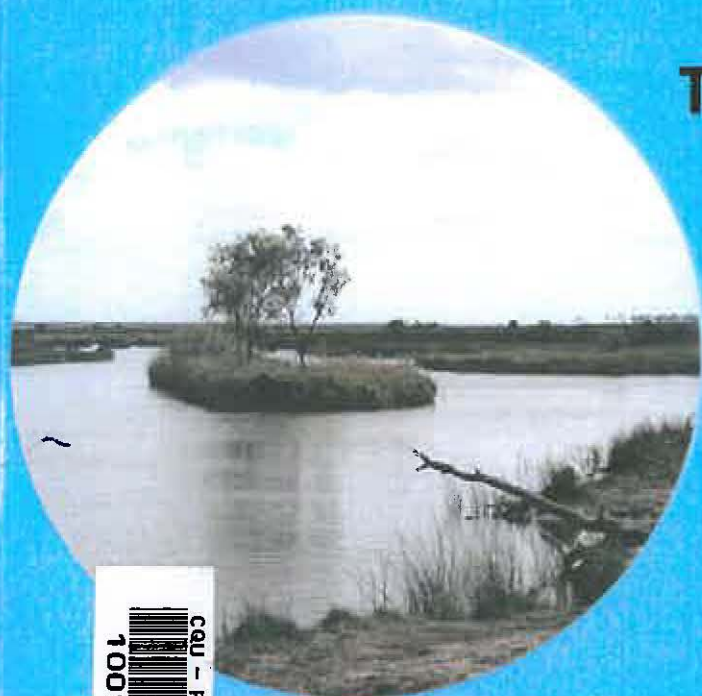




Cooperative Research Centre for Coastal Zone, Estuary & Waterway Management

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The contribution of floodplain wetland pools to the ecological functioning of the Fitzroy River estuary

**Marcus Sheaves, John Collins,
Wayne Houston, Pat Dale,
Andrew Revill, Ross Johnston,
Katya Abrantes**

June, 2006

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**CRC for Coastal Zone
Estuary & Waterway Management**





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Cooperative Research Centre for Coastal Zone, Estuary and Waterway Management

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Executive summary

Coastal wetlands function as links between terrestrial and marine ecosystems throughout the world. They have vibrant and diverse flora and fauna, they are crucial habitats for fish and invertebrates, often providing critical nursery grounds, and they are major contributors of nutrients to coastal systems. However, our present understanding of estuarine floodplain wetlands is limited, particularly in tropical and subtropical areas. This lack of understanding, together with their extensive ecological importance and their value to so many user groups, makes detailed understanding of estuarine floodplain wetlands an important research priority.

The delta of the Fitzroy River in Central Queensland has extensive wetlands clustered around its large estuary system. Except during flooding, the aquatic environment of the wetlands is restricted to a number of semi-permanent pools of varying types and sizes, which are recognised as important nursery habitats for marine fish such as barramundi. Unfortunately, the way these habitats provide for juvenile fish, and how juvenile fish interact with other animals and plants associated with the pools (as prey or predators), is unknown. Similarly, there is no knowledge of how aquatic animals are influenced by the type of pool environment (e.g. marine or freshwater influenced), or how the compositions and fates of pool inhabitants are influenced by the degree and regularity of connection to other habitats.

Thus the current project aims to extend, broaden and refine our understanding by investigating the influence of connectivity on the faunal dynamics and food webs of the Fitzroy estuarine floodplain wetland pools.

The current study was conducted during a drought period, with no substantial wet season flows during the project. This has two consequences: (1) the study is limited to wetland pools, with little ability to generalise the results to the whole wetland, and (2) the results of the study are not necessarily representative of the situation during wet years.

Methods

The project studied a variety of wetland pools, ranging from completely fresh pools to hypersaline pools, from pools regularly connected to other habitats to those isolated throughout the study, of sizes ranging from a few hundred metres long to pools a number of kilometres in length, and pools in settings ranging from natural forest to rural. A broad variety of sampling techniques was employed to gain a detailed understanding of the organisms inhabiting the pools, and the patterns of biological connectivity among the pools. Data were collected on abundances, biomasses and stable isotope compositions (measures of position in the food chain) of fish and invertebrates; on fish sizes, biochemical condition (as a measure of health), diets and spatial distributions; on patterns of abundance of waterbirds; and on the physical environments of the pools and their patterns of connectivities.

Results

Connectivity

The physical environment of the Fitzroy estuarine floodplain wetland pools and the extent of their physical connectivities are governed by rainfall and flooding regimes, the length and nature of the connecting channels, whether the pools have direct connections to the marine environment, and tidal anomalies that modify potential tidal connections.

Some pools are only connected to each other and to the main estuary system during major floods, at intervals of years to tens of years. These isolated freshwater pools can only provide productive habitats for aquatic fauna (including a nursery-ground function for marine species) if they are large enough to retain adequate water to support the aquatic assemblage until the next physical connection event occurs. If connections don't occur frequently enough the pools dry out, with the last stages of drying out characterised by fish kills as the shallow water becomes hot, muddy and inhospitable.

A second group of pools are connected a number of times a year by local rainfall. These pools occur as components of defined creek systems, and their regular connection allows passage to both upstream and downstream movements of fauna. This is important in allowing recolonisation of pools that have dried out, in providing access to marine spawning species moving upstream into nursery or feeding habitats, and in allowing freshwater species to recolonise brackish pools where conditions may be unsuitable for reproduction. These species (such as the

freshwater bony bream) can be dominant components of the community of brackish pools.

A third group of pools is never threatened with drying out because they are reasonably deep and have regular connections to the marine environment on high spring tides. These pools have a fauna dominated by marine species. Although there are many spring tides during the year with predicted heights great enough to produce connections, in many cases expected connections do not result or connections occur when predicted tides are below 'normal' connection levels. This is due to tidal anomalies; the modification of tidal heights caused by factors like increases in air pressure depressing water levels or strong winds blowing down long river reaches slowing the progress of tidal currents.

A final group of pools are shallow and only connected during a few of the largest tides each year. These pools are not part of stream systems, and like the isolated freshwater pools, saw very little freshwater input during the study. As a result these pools dried out quickly, but because they contained salt water, evaporation quickly produced very hypersaline conditions, making them inhospitable to most species long before they dried out.

The timing of connections is crucial for the successful use of the pools as nurseries for marine fish. Marine fish generally spawn at particular times of the year. Their larvae live and grow in the upper levels of estuarine and coastal waters for only a few weeks before they need to move into appropriate juvenile habitats (termed recruitment). Consequently, they are available to enter pools for only part of the year, so if physical connections do not occur at these times, no biological connection can result.

While fish rely on aquatic connections to facilitate their movements between pools, and to and from the estuary, fish-eating waterbirds do not suffer this restriction. Waterbirds are able to fly between pools, producing biological connections independent of physical connections. This action of birds connecting pools across the whole floodplain has far-reaching consequences for both the birds and the fish they feed on. Predatory birds are particularly effective at feeding on fish when water depths become very shallow (around 1 m or less). Being able to fly between pools that reach these shallow depths at different times, means the birds are regularly able to find abundant supplies of fish that are easy to catch. In this way, as a connected unit, the wetland pools support large populations of waterbirds.

At the same time, the movement of birds to feed in pools at times when the fish become vulnerable has a considerable impact on patterns of mortality of fish in

Chapter 1 Introduction

Marcus Sheaves

Littoral wetlands occur adjacent to marine coasts and estuaries throughout the world, and function as links between terrestrial and marine ecosystems (Levin *et al.* 2001). These wetlands comprise temporarily flooded lowlands, 'swampy' palustrine habitats (Kingsford & Norman 2002), and permanent and semi-permanent pools, lakes and lagoons (Allanson & Whitfield 1983). Littoral wetlands have vibrant and diverse flora and fauna, and are crucial habitats for fish (Brown *et al.* 2005, Noble *et al.* 2004), birds (Kingsford & Norman 2002, Noble *et al.* 2004) and invertebrates (Castellanos & Rozas 2001). In particular, they are often critical nursery grounds for fish and invertebrates (Secor & Rooker 2005), and major contributors of nutrients and pollutants to coastal systems (Caddy 2000).

Littoral wetlands are of substantial value to commercial, traditional and recreational fishers, both in terms of the exploitable fish stocks they contain (Barbier & Strand 1998, Paterson & Whitfield 2000, Ley *et al.* 2002) and their nursery-ground value (Secor & Rooker 2005). Above and beyond their fisheries values, littoral wetlands are highly valued by many elements of the community. They often have considerable traditional value (Anon 2004), are used substantially by a diversity of groups including birdwatchers and eco-tour operators, and are highly valued by a diversity of members of the community (e.g. artists and photographers) for their aesthetic beauty (Anon 2005). Additionally, the dwindling area of littoral wetlands confers considerable conservation value on them (Barbier *et al.* 2002).

The nursery-ground function of littoral wetlands

Littoral wetlands are widely recognised as nursery grounds for a variety of fish (Russell & Garrett 1988, Laffaille *et al.* 2000) and crustaceans (Achuthankutty 1988, Sheridan & Hays 2003), but nursery-ground value is incompletely understood (Sheaves 2001, 2005). While relatively few fish that use wetlands are obligatory users (Secor & Rooker 2005), many species are advantaged by their use as juvenile habitats. Advantages flowing from abundant food supplies (Javonillo *et al.* 1997) and/or reduced predation (Paterson & Whitfield 2000) lead to enhanced storage pools of energy and genetic material. These ultimately lead to more productive and less variable adult stocks than would otherwise be the

case (Kraus & Secor 2005). The importance of the utilisation of nursery habitats to marine fish populations is underlined by the fact that, across a broad range of ecosystems, patterns of abundance of juveniles in nursery habitats is a reliable predictor of abundance of adults in adult habitats in subsequent years (Kraus & Secor 2005). Conversely, however, adult abundance is generally a poor predictor of juvenile abundance, emphasising that factors influencing the entry to and successful use of juvenile habitats are more important to future spawning stocks than are previous patterns of spawning.

Species that utilise temporary littoral wetlands are themselves special. They can be seen in one sense as generalists, able to thrive in and utilise a diversity of conditions (Gelwick *et al.* 2001), and in another as specialists, that require great phenotypic plasticity (Ray 2005) to prosper under a diversity of environmental regimes.

A crucial factor in nursery-ground value is the availability of suitable habitat. Although some organisms are habitat specialists (Davis *et al.* 1995, Nagelkerken & Van der Velde 2002), many can utilise a variety of habitats (Ray 2005). However, even these species require habitat type and condition to be within acceptable ranges (Halpern 2004). Even in open systems, the condition and extent of necessary habitats vary greatly between years, and may become critically restricted (Niklitschek & Secor 2005). The situation is even more variable for closed systems, where the inability to move to a new area means that the loss of a particular habitat from the system can have far reaching effects for a variety of species (Bloomfield & Gillanders 2005).

As well as nursery-ground value varying in space and time (Kraus & Secor 2005), utilisation of habitats by juveniles is also variable (Able 2005). This reflects the interaction of larval supply and habitat availability in determining location-specific juvenile abundance (Brown *et al.* 2005). Consequently, the degree of connectivity and integrity of connections among habitats, and between wetland units and sources of larval supply, is of overriding importance to nursery-ground value because both habitat availability and larval supply are determined by connectivity (Chabrierie *et al.* 2001, McCormick-Ray 2005). Larval and juvenile aquatic and marine animals can not occupy a habitat that is not connected to a source of supply, no matter how potentially favourable that habitat is. In fact, larvae and/or juveniles cannot be supplied to a habitat without connection at the specific time when the larvae and/or juveniles are available (Brown *et al.* 2005).

The importance of habitat availability and the needs for appropriate connectivity to enable habitat occupancy are obvious. Just as obvious is that the widespread occurrence of habitat modification (Ferrer Montano 1994, Vose & Bell 1994,

Blaber 1999) and restriction and removal of connectivity (Hyland 2002, Kraus & Secor 2005) has the potential for substantial impacts on the distribution and dynamics of fish and other fauna (Noble *et al.* 2004). Conversely, land management plans that restore connectivity and rehabilitate habitats are important in protecting biodiversity and restoring whole-of-ecosystem function (De Freese 1995). Additionally, restoring connectivity can advantage endangered species (Tanner *et al.* 2002) and lead to expanded diversity of life-history variation (Bottom *et al.* 2005), leading ultimately to more resilient ecosystems (D'Eon *et al.* 2002). Ensuring that ecosystem resilience is maximised is a pressing issue, given speed of habitat and connectivity loss and modification is accelerating in response to human-induced climate change and sea-level increase (Kingsford & Norman 2002).

The relationship between waterbird populations and the nursery-ground function of littoral wetlands

Piscivorous birds benefit from foraging over large areas (Alexander 2002) and depend on access to wetlands that are healthy fish habitats (Noble *et al.* 2004). In fact, many waterbirds respond to newly generated wetland habitats to feed and/or breed (Kingsford & Norman 2002), then disperse or die as wetlands dry up. Predatory birds are advantaged by cycles of filling and drying of wetland pools, with birds moving to take advantage of pools (Timms 2001) as they become shallow enough for effective feeding (Roshier *et al.* 2002). This advantage to piscivorous birds feeds back to influence nursery-ground value, with predatory birds visiting substantial mortality on small and juvenile fish in wetlands (Whitfield & Blaber 1978, Miranda & Collazo 1997). In view of the importance of wetlands to waterbirds, their loss is a major threat to bird populations (Kingsford & Norman 2002), and their numbers and diversity are closely linked to wetland health (Kingsford 1999).

Littoral wetlands and nutrients and pollutants

Because most pathways of transport of nutrients and pollutants pass through them, littoral wetlands play a crucial role in the movement of nutrients between catchments and the sea. Understanding this role is particularly important in the current climate of increasing loads of suspended sediments, nutrients and pollutants (Brodie & Mitchell 2005). Depending largely on the strength of flow (Brodie & Mitchell 2005) (e.g. wet season versus dry season), a variable

proportion of the nutrients and pollutants generated in the catchment are trapped in wetlands (Thimdee *et al.* 2003). There they may be stored for long periods (Boto *et al.* 1989, Alongi *et al.* 2000a, Thimdee *et al.* 2003), modified (Davis *et al.* 2001a), controlled (Davis *et al.* 2001b) or passed rapidly onwards (Brodie & Mitchell 2005). For instance, large quantities of nutrients may be converted to mangrove biomass and trapped in mangrove forests (Cebrian 2002) or pollutants removed from water and stored in wetland plants such as reeds (Hosoi *et al.* 1998).

At the same time, wetlands themselves generate large amounts of organic carbon (Jennerjahn & Ittekkot 2002, Alongi *et al.* 2004), and can be substantial contributors of nutrients and pollutants to coastal systems (Machiwa & Hallberg 2002, Caddy 2000). Depending on the type of wetland (Clarke 1985, Mohammed *et al.* 2001) and its geographical setting (Alongi *et al.* 2000a, Dittmar & Lara 2001) this carbon may be retained in the wetland by recycling (Cebrian 2002) or passed onwards (Alongi *et al.* 1998). Thus littoral wetlands can trap nutrients and pollutants and/or slow, modify or promote their flows between ecosystems.

The movement of nutrients and pollutants through wetlands is generally thought of in terms of physical transport as dissolved or particulate material (Thimdee *et al.* 2003, Brodie & Mitchell 2005). However, wetland organisms play crucial roles in nutrient recycling (Alongi *et al.* 2000b), nutrient accumulation (Alongi *et al.* 2000a, Cebrian 2002), nutrient regeneration (Dham *et al.* 2002), and nutrient transport (Javonillo *et al.* 1997, Deegan 1993), which may be as great as that of physical processes (Deegan 1993). Our incomplete understanding of these biologically mediated flows is a reflection of our general lack of recognition of the importance of biological connectivities (Sheaves 2005).

Fitzroy estuarine floodplain wetland pools

The Fitzroy River is the largest coastal river system in central and southern Queensland, draining a catchment of more than 140 000 square kilometres. It has an estuary about 65 km in length, with its upper boundary defined by a barrage, constructed in 1970 to prevent ingress of saltwater to areas further upstream (Kowarsky & Ross 1981). The barrage is located at the city of Rockhampton, the major centre in the region.

At the mouth of the estuary is an extensive delta system surrounded by a broad floodplain (Figure 2.1). Interspersed across the floodplain are a variety of wetland pools that are the focus for this study. For the purposes of this study this

particular subset of littoral wetlands is termed 'Fitzroy estuarine floodplain wetland pools' (see Chapter 2 for definitions). These pools present a range of degrees of connectivity to each other and to the Fitzroy estuary proper (see Chapters 2 and 3). During major floods the floodplain may become covered with water, producing an extensive area of nursery habitat for fish and crustaceans. Once the floodwaters recede the floodplain wetlands contract, with the pools representing persistent remnants of this wetland.

Littoral wetlands are recognised as important nursery habitats for juveniles of the commercially and recreationally important fish, the barramundi, *Lates calcarifer* (Russell & Garratt 1983, 1985, 1988), prompting a series of studies into the importance of Fitzroy estuarine floodplain wetland pools to this species (Sawynok 1998, Infofish 2005, Sawynok & Platten 2005).

User needs

In the last five years there has been a shift from centralised management of natural resources and environments of river catchments in Queensland, to management at a local level. In 2000 the Fitzroy Basin Association (FBA), the community organisation charged with coordinating this management in the Fitzroy region, produced a strategy for sustainability (FBA 2000). The strategy identified river health and water quality as key regional issues, with a key objective of developing planning and management measures to protect fisheries habitats and ensure the maintenance of fish passage through the Fitzroy River system.

In response to the strategy, a number of studies were implemented to understand the use of habitats in the system by recreationally and commercially important species, principally barramundi. These studies include habitat utilisation by barramundi and evaluation of relative habitat quality (Infofish 2005), barramundi spawning and recruitment (Sawynok & Platten 2005), and establishing the relationship between freshwater flows and barramundi production (Robins *et al.* 2005, project in progress). These first two projects, supported by the Coastal CRC, identified Fitzroy estuarine floodplain wetland pools as crucial habitats for barramundi. The latter project, a major Coastal CRC subproject, has linked barramundi recruitment pulses with freshwater flow events, implicating wetlands as important in underpinning fisheries production. These studies also build on the studies of the use of ponded pastures in the region by barramundi (Hyland 2002). While these studies represent a broad range of necessary work relating to the barramundi themselves, there is very little understanding of the functioning of the Fitzroy estuarine floodplain wetland pools in particular or indeed littoral wetlands in general. In particular, there is essentially no understanding of the faunal

dynamics of littoral wetland pools or of the trophic webs supporting nursery-ground function and productivity.

Aims

At present our understanding estuarine floodplain wetlands is limited, particularly in tropical and subtropical areas. Most previous research in coastal northern Australia has focussed on purely estuarine (e.g. Blaber *et al.* 1989, Sheaves 2001) or freshwater (e.g. Pusey *et al.* 2000) systems and then mainly on moving waters. This lack of understanding, along with their extensive ecological importance and their value to so many user groups, makes detailed understanding of estuarine floodplain wetland pools an important research priority. Thus the current project aims to extend and broaden our understanding by investigating the faunal dynamics and food webs of Fitzroy estuarine floodplain wetland pools, and the influence of connectivity on faunal dynamics and food webs.

The project particularly investigates the nature and connectivity of Fitzroy wetland pools (Chapter 3), the influence of connectivity on densities (Chapter 4) and biomasses (Chapter 5) of fish, the densities of invertebrates (Chapter 6), the diets of fish (Chapter 7), stable isotope profiles of fauna and flora (Chapter 8), the structure of food webs (Chapter 9), the health and condition of fish (Chapter 10), the spatial distribution of fish within pools (Chapter 11), and the spatial and temporal abundance of waterbirds (Chapter 12).

The current study was conducted during a drought period, with no substantial wet season flows during the project. This has two consequences: (1) the study is limited to wetland pools, with little ability to generalise the results to the whole wetland, and (2) the results of the study are not necessarily representative of the situation during wet years.

Chapter 2 The physical nature of Fitzroy floodplain wetland pools

Marcus Sheaves and Ross Johnston

Summary

Floodplain wetland pools were defined as water bodies on the floodplain of the Fitzroy River, adjacent to and intermittently connected with the Fitzroy River estuary or other major estuarine channels forming the Fitzroy River delta.

Study pools were selected to cover the Fitzroy floodplain as representatively as possible.

Pool environments ranged from entirely freshwater, through low salinity brackish and fully marine, to hypersaline.

Pools varied in the periodicity of connection to the marine environment and to upstream fresh waters.

Pools varied in the duration they retained water.

Some pools were isolated while others comprised upstream series within stream systems.

Study sites

Pool definition

For the purposes of these studies, 'estuarine floodplain wetland pools' are defined as: *Water bodies on a coastal floodplain, adjacent to and intermittently connected with an estuary or estuarine system.*

Fitzroy estuarine floodplain wetland pools are specifically defined as: *Water bodies on the floodplain of the Fitzroy River, adjacent to and intermittently connected to the Fitzroy River estuary or other major estuarine channels forming the Fitzroy River delta.* For brevity this will usually be shortened to 'floodplain wetland pools' or simply 'wetland pools' throughout this report, except where clarity demands the full title.

To comply with the definition of the pools' locations as 'adjacent to the estuary', the investigation was limited to pools downstream of the Fitzroy River barrage, which marks the upper limit of the estuary. Defining pools as 'intermittently connected' led to the inclusion of pools from those only cut off from the estuary at low tide through to freshwater pools with no tidal connection.

Because only one highly connected marine pool could be found directly adjacent to the Fitzroy River delta, the study was extended to include Munduran Creek. Although not part of the Fitzroy River delta, Munduran Creek enters the mid section of The Narrows, which connects the Fitzroy River delta with Port Curtis. Munduran Creek also includes a number of freshwater pools, so, as well as providing spatial replication of a highly connected marine pool, including Munduran Creek provided the opportunity to study a connected series of pools ranging from marine to fully fresh in the one system.

Selection criteria

The primary aim was to select sites comprising a broad representation of pool types and levels of physical connectivity. Ideally, the pools selected would include:

- Multiple pools in individual streams forming upstream series
- Pools with a broad range of salinity profiles
- Pools with different levels of physical connectivity
- Pools that retain water for different durations
- Multiple pools of each type to provide spatial replication of pool type
- A spread of pools that covers the floodplain representatively
- Pools that could be accessed reliably, considering physical impediments to access (road conditions, stream depth etc.) and willingness of owners
- Pools without major human-constructed impediments (dams, bund walls etc.) likely to reduce effective connections under normal circumstances.

Site selection

Potential study sites were identified from aerial imagery and topographic maps. Sites were inspected and evaluated during a two-week field trip in November 2003. Local knowledge and site advice were provided by Bob Packett from the Queensland Department of Natural Resources and Water (NRW) and Bill Sawynok from Infofish.

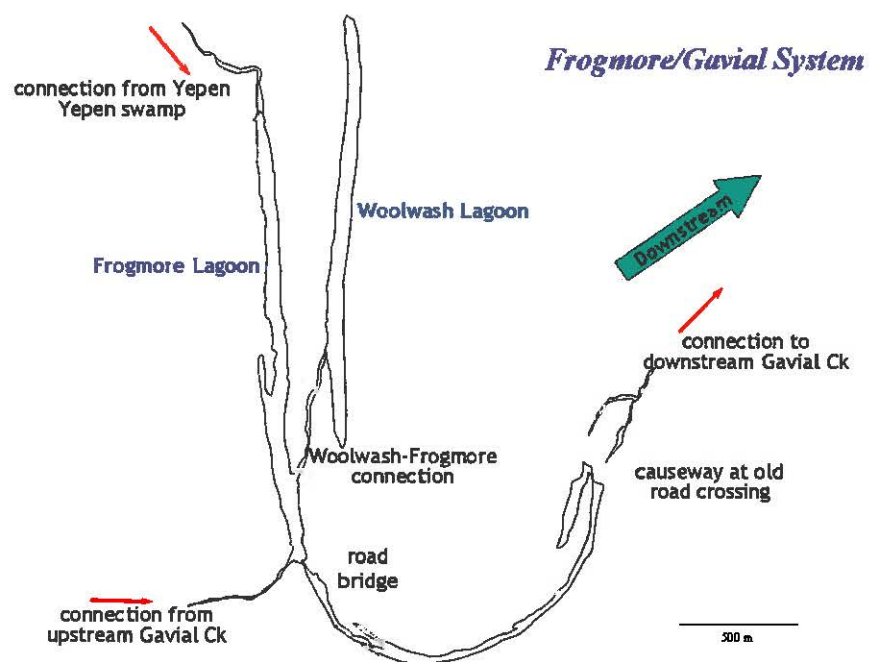
Study sites chosen

Although aerial imagery (Figure 2.1) and topographic maps suggested many potential sites, on-ground surveys showed that most sites were unsuitable under criterion 8 (above). Unreliable accessibility (criterion 7) eliminated many other potential sites, while others, such as Big German Jack's lagoon, held no water or were inhospitable to life (extreme salinity and/or temperature) at the beginning of the study. Initially, five primary sites were selected: Frogmore lagoon (Figures 2.1 and 2.2), Twelve Mile Creek brackish pool (Figures 2.1 and 2.3), Twelve Mile Creek upstream fresh pool (Figures 2.1 and 2.3), Munduran Creek brackish pool

(sampled from February 2004 to May 2005) (Figures 2.1 and 2.4), and Munduran Creek downstream freshwater pool (Figures 2.1 and 2.4).



Figure 2.1. Locations of the Fitzroy estuarine floodplain wetland pools studied



Figure[B1] 2.2. Outline map of Frogmore and Woolwash lagoons

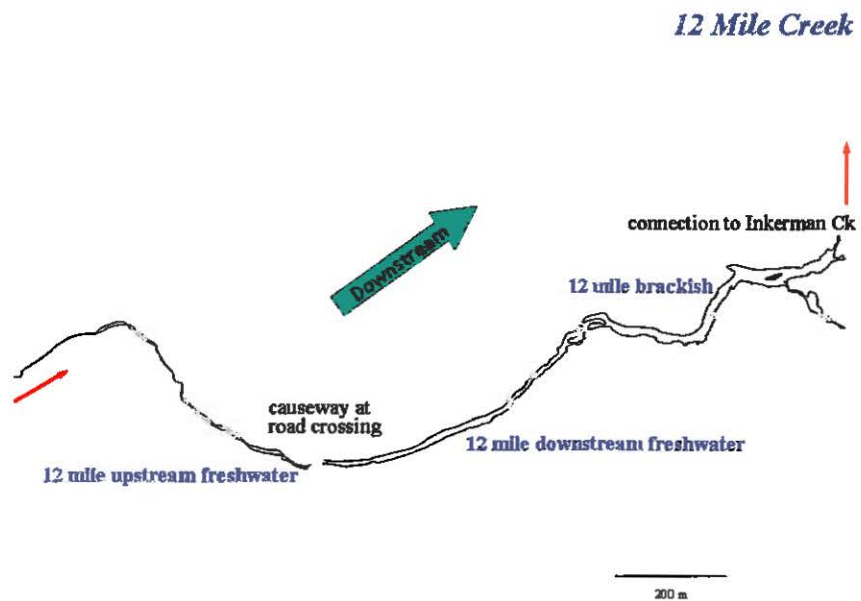


Figure 2.3. Outline map of the Twelve Mile Creek system

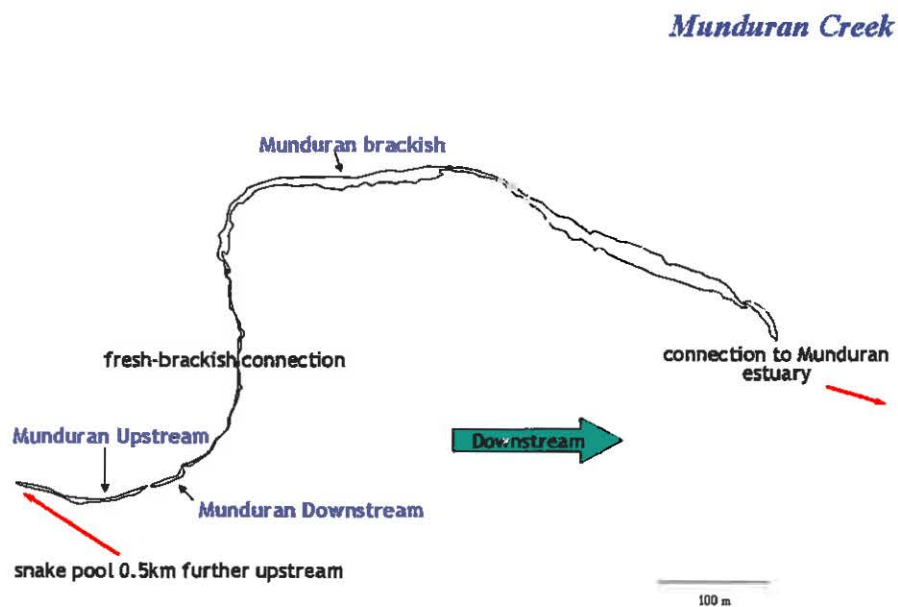


Figure 2.4. Outline map of the Munduran Creek system

Subsequent to the initial sampling trip in February 2004, during which sampling protocols were tested and refined, six additional sites were added. These were; Munduran upstream freshwater pool (Figures 2.1 and 2.4), Gonong Creek brackish pool (Figures 2.1 and 2.5) and Twelve Mile Creek downstream freshwater pool (Figures 2.1 and 2.3) (sampled from May 2004 onwards), Big German Jack's lagoon (Figures 2.1 and 2.6), Little German Jack's lagoon (Figures 2.1 and 2.6) (sampled from November 2004 onwards), and Woolwash lagoon (Figures 2.1 and 2.2) (sampled during August 2004, February 2005 and May 2005).

To extend the range of stable isotope data, samples were collected from two additional sites during December 2004: Black's lagoon, a large freshwater pool on Raglan Creek in the south-east of the Fitzroy floodplain (Figure 2.1) and Munduran 'snake pool', upstream of Munduran Creek upstream pool (Figures 2.1 and 2.4).

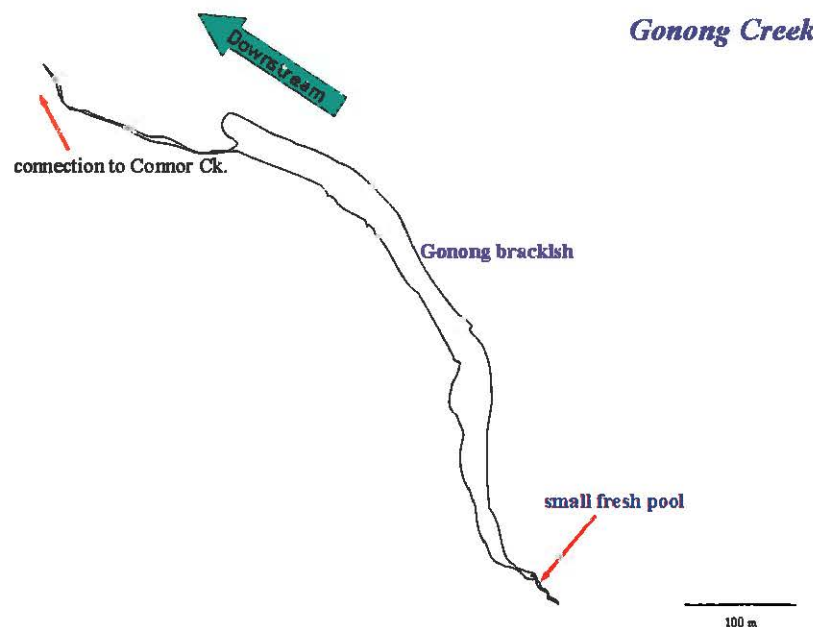


Figure 2.5. Outline map of the Gonong Creek system

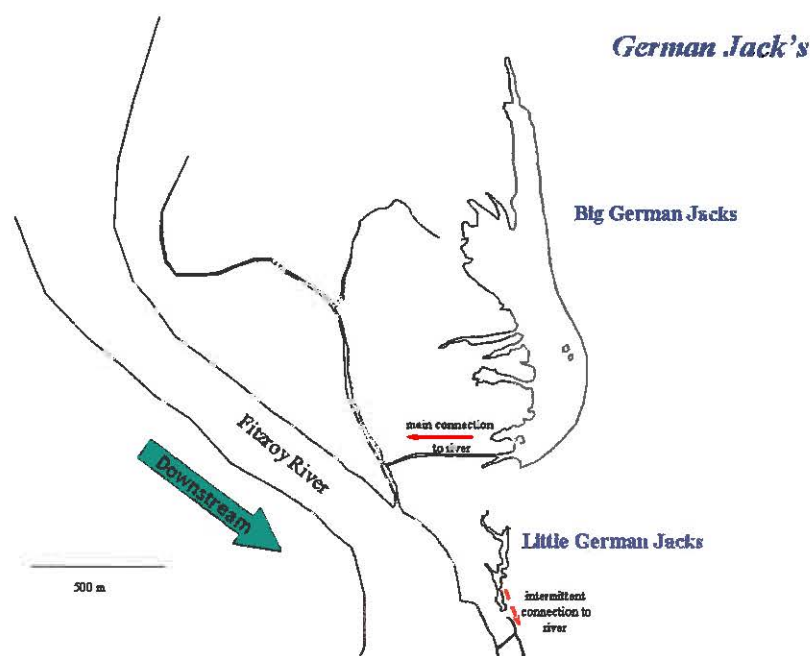


Figure 2.6. Outline map of the German Jack's lagoon system

Pool descriptions

Descriptions of the pools' settings and habitat types were developed from in-field observations. Records of patterns of stream flow, kept by government agencies, did not provide the detail needed to define regularity of connection at the level of individual wetland pools. As a consequence, information from local landholders and other key stakeholders was married with observations from the research team and the local knowledge of Bob Packett (NRW) and Bill Sawynok (Infotish), to develop an approximate classification of regularity of connection for each study site (Table 2.1). No definitive detail on regularity of tidal connection to the Fitzroy River estuary is provided here because empirical studies showed a low level of concordance between actual connections and predicted tidal heights. This issue is covered in detail in Chapter 3.

Table 2.1. Summary of the nature of the major Fitzroy wetland study sites

	Surrounding habitat type	Dominant setting	Regularity of connection		Maximum depth (m)
			Fresh	Marine	
Twelve Mile Creek brackish	1,4	Pasture	Sub-annual (local rainfall + stream flow)	c.a. 2 periods annually (extreme tides)	4.3
Twelve Mile Creek fresh downstream	1,5	Pasture	Sub-annual (local rainfall + stream flow)	Nil	3.0
Twelve Mile Creek fresh upstream	1,6	Pasture	Sub-annual (local rainfall + stream flow)	Nil	4.0
Frogmore lagoon	1,6	Pasture	5–10 years (major floods)	Nil	4.7
Woolwash lagoon	1,6	Pasture	5–10 years (major floods)	Nil	2.8
Gonong Creek brackish	2,3,5,6	National park	Sub-annual (local rainfall + stream flow)	Regularly on spring tides	2.1
Munduran Creek brackish	2,3,5,6	State forest	Sub-annual (local rainfall + stream flow)	regularly on spring tides	1.8
Munduran Creek downstream and upstream	3,6	State forest	Sub-annual (local rainfall + stream flow)	Nil	2.1
Big German Jack's lagoon	1,2,3,5	Pasture	Sub-annual (local rainfall)	c.a. 4 periods annually (large tides)	0.7
Little German Jack's lagoon	2,7	Saltmarsh	Sub-annual (local rainfall)	c.a. 2 periods annually (extreme tides)	0.5

Habitat types:	1: pasture	3: scrub	5: forest	7: salt marsh
	2: mangrove	4: saltpan	6: scattered trees	

Frogmore and Woolwash lagoons

Frogmore and Woolwash lagoons are freshwater pools situated ~3 km from the upper Fitzroy estuary (Figure 2.2). At their maximum non-flood levels, both pools are ~2 km in length and, for most of their lengths, approximately 80 m wide. During the study period the maximum depths of Frogmore and Woolwash lagoons were 4.7 m and 2.8 m respectively (Table 2.1). Both pools have moderately sloping cross-sectional profiles (Figure 2.7).

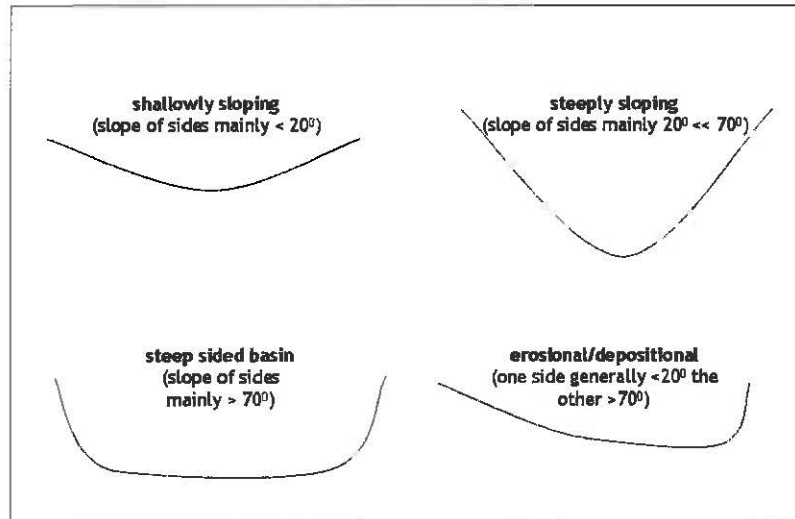


Figure 2.7. Diagrammatic representation of pool cross-sectional profiles

The pools are usually separate entities but are connected via a narrow channel during major flooding (Figure 2.2). Both pools form upstream connections to Yeppen Yeppen swamp during major floods, but more often receive water from the Scrubby Creek/Ti-tree Swamp system, or their downstream connection to the Gavial Creek system, a side-branch of the Fitzroy River. Even this connection is intermittent, with no connection to Gavial Creek during the study period. Information from local landholders suggests the pools only connect to Gavial Creek with a periodicity of around 5–10 years (Table 2.1).

Both Frogmore and Woolwash lagoons are situated in extensively cleared pastoral land, with cattle grazing to the pool edges. However, while Frogmore is completely surrounded by grazing land, Woolwash is bordered by a sealed road on its eastern side. The vegetation surrounding the pools consists mainly of grasses and small sedges interspersed with large *Eucalyptus* and *Melaleuca* trees. Neither pool contains any macroscopic aquatic vegetation.

Twelve Mile Creek

Twelve Mile Creek is situated to the south of Casuarina Creek, a major estuarine component of the Fitzroy River delta (Figure 2.1), and connects to the upper reaches of Inkerman Creek, another estuarine component of the Fitzroy delta. During the study period, Twelve Mile Creek flowed two to four times a year as a result of local rainfall in its catchment. Substantial flow from these events persisted for no more than a week on any occasion. Between these times,

Twelve Mile Creek contracted to a series of separate pools, the lower three of which were used as study sites (Figure 2.3).

The most downstream pool (Twelve Mile brackish) is bordered on its northern side by pasture and on its southern side by a habitat reclamation area (previously grazed land from which cattle are now excluded). There are few mature trees adjacent to the pool, although a number of saplings are established in the reclamation area. Salt couch, *Sporobolus virginicus*, and sedges line the bank but there is no macroscopic aquatic vegetation. Twelve Mile brackish is situated on the landward edge of a saltpan adjacent to Inkerman Creek and, during the highest spring tides, is connected to Inkerman Creek across ~2½ km of saltpan. When full, the pool is ~800 m in length and 10–15 m wide for most of its length, with a maximum depth of 4.3 m (Table 2.1). The occasional connections to Inkerman Creek maintained hyposaline conditions in the pool throughout the study.

The pool immediately upstream of Twelve Mile brackish (Twelve Mile downstream) is separated from the brackish pool by a low concrete weir (30 cm above the normal 'full' level of the brackish pool) that prevents egress of salt water, but which is quickly overtopped during freshwater stream flow. The Twelve Mile downstream pool is ~1 km long and 5–7 m wide for most of its length, and had a maximum depth of 3 m during the study. The pool is bordered by pasture on its northern bank, and *Eucalyptus* forest on its southern bank (Table 2.1), and contained extensive areas of water lilies, *Nymphaea* spp., and the invasive aquatic plant, *Cabomba caroliniana*.

Immediately upstream of Twelve Mile downstream, and separated by a causeway, is the second Twelve Mile Creek freshwater study site (Twelve Mile upstream). Twelve Mile upstream is ~330 m in length, 2–5 m wide and had a maximum depth of 4 m during the study (Table 2.1). The pool is bordered by pasture on its southern side and by pasture with scattered *Eucalyptus* trees on its northern bank, and, like Twelve Mile downstream, contained extensive areas of water lilies, *Nymphaea* spp., and the invasive aquatic plant, *Cabomba caroliniana*.

Munduran Creek

Munduran Creek is situated to the south of the Fitzroy River delta (Figure 2.1) and flows into the Narrows, the body of water connecting the Fitzroy River estuary with Port Curtis. The upstream section of the Munduran Creek estuary contains a series of lateral rock bars forming natural impoundments, the most upstream of which is only overtopped by the highest spring tides (Figure 2.4). The pool formed

by this natural barrier (Munduran saline) is ~350 m long, ~18 m in width at its widest point, and has a maximum depth of 1.8 m. Munduran saline is surrounded by state forest (lightly grazed) and has a narrow mangrove border (primarily *Aegiceras corniculatum*, *Rhizophora stylosa*, and *Avicennia marina*) interspersed with grasses and *Eucalyptus* woodland (Table 2.1). Except during streamflow events (2–5 times per year), the upper end of the pool is separated from freshwater sections of Munduran Creek by a further rock bar and a lightly forested dry stream channel. Munduran saline has an erosional/depositional cross-sectional profile (Figure 2.7).

Except during streamflow events, the freshwater section of Munduran comprises a series of pools surrounded by *Eucalyptus* woodland. When full of water, the most downstream of these (Munduran downstream) fills the stream channel, and is ~60 m in length and ~20 m in width. It has gently sloping sides and a maximum depth of 2.1 m. Munduran fresh has extensive areas of aquatic vegetation, principally water lilies, *Nymphaea* spp. Munduran downstream has a shallowly sloping cross-sectional profile (Figure 2.7). Munduran upstream is similar but of greater length (120 m) with an erosional/depositional cross-sectional profile (Figure 2.7).

A further 0.5 km upstream is the 'snake pool'. The snake pool is a steep-sided, freshwater pool, about 300 m in length and 10 m in width and surrounded by native woodland designated as state forest. Snake pool has a steep-sided basin cross-sectional profile (Figure 2.7).

Gonong Creek

Gonong Creek is at the upstream extremity of Connor Creek, the southernmost major estuarine branch of the Fitzroy delta (Figure 2.1). At the upstream end of the Gonong Creek estuary is a pool (Gonong saline) separated from the estuary proper by a cobble and gravel bar about 50 m long. As with Munduran saline, Gonong saline is only connected with the estuary by the highest spring tides (Figure 2.5). The pool is ~450 m long, ~20 m in width at its widest point and has a maximum depth of 2.1 m. It is bordered on its eastern side by national park and on its western side by a forestry plantation (Table 2.1). Gonong saline has an intermittent mangrove border (primarily *Aegiceras corniculatum*, *Rhizophora stylosa*, and *Avicennia marina*), interspersed with native grasses. Except during streamflow events (2–5 times per year), the upper end of the pool is separated from freshwater sections of Gonong Creek by further gravel and rubble bars. There are no substantial permanent freshwater pools in Gonong Creek. Gonong saline has an erosional/depositional cross-sectional profile (Figure 2.7).

German Jack's lagoons

The German Jack's wetland comprises two lagoons adjacent to the northern bank of the middle Fitzroy estuary (Figure 2.1). Neither lagoon has a connection to a defined freshwater stream. The lagoons only receive substantial inputs of freshwater during major flooding of the Fitzroy River. Both lagoons are connected with the Fitzroy River estuary only on the few largest tides of the year. Neither pool contains permanent aquatic macrophytes.

The larger lagoon (Big German Jack's) is bordered on its eastern side by *Eucalyptus* woodland that is used as pasture for cattle and on its western side by salt marsh, dominated by the salt couch, *Sporobilis virginicus*. When full, it is ~2 km in length, ~150 m wide and ~0.7 m maximum depth. The major connection with the Fitzroy River estuary is through a shallow channel, roughly 500 m in length, leading to an unnamed side branch of the Fitzroy River (Figure 2.6). Big German Jack's has a shallowly sloping cross-sectional profile (Figure 2.7).

The smaller lagoon (Little German Jack's) is surrounded by *Sporobilis virginicus* salt marsh. It contains scattered mangroves (mainly *Avicennia marina* with a few *Rhizophora stylosa*), particularly around its southern end. When full, Little German Jack's is ~400 m in length, ~20 m in width and ~0.5 m in depth. On the highest spring tides, water flows from a small channel adjacent to the southern end of Little German Jack's, through about 15 m of salt marsh and then into the pool (Figure 2.6). Under particularly high tidal conditions, water sheet flow enters the south-eastern side of Little German Jack's directly from the Fitzroy River which is only about 30 m from the pool at this point. Although very shallow in depth, in the main, Little German Jack's has a steep-sided basin cross-sectional profile (Figure 2.7).

Chapter 3 Dynamics of the physical environment of Fitzroy wetland pools

Marcus Sheaves and Ross Johnston

Summary

The study was conducted to gain an understanding of the physical environment of the Fitzroy wetland pools and the physical connectivities between them. This provides a basis for developing a understanding of biological connectivity.

Measurements of water quality parameters, pool and connection depths, and analyses of aerial photography were used to investigate the pool environments and connectivities.

The pools represent a spectrum of pool types from completely fresh to hypersaline. They also range widely in their extent and periodicity of connectivity, from pools connected a number of times a year to pools isolated for many years. The physical environment of the pools and the extent of connectivity are governed by rainfall and flooding regimes, the length and nature of the connecting channels, whether the pools have direct connections to the marine environment, and tidal anomalies that modify potential tidal connections.

The complexity of physical connectivity needs to be factored in to our understanding if we are to successfully manage the effects of future climate and sea-level changes.

Introduction

The nature of the Fitzroy wetland pools investigated during the study was outlined in Chapter 2. This chapter documents changes in the physical environment of the pools from February 2004 until May 2005 to examine the nature and extent of physical connectivity between the pools and between the pools and the Fitzroy River estuary.

At the beginning of the study, the physical environments of the pools and the nature and extent of connectivity between them was completely unknown. As a consequence, it was necessary to undertake a descriptive study as a basis for understanding the physical and biological connectivity between the pools and for understanding the pools' roles in supporting their biota. The empirical understanding gained provides the context for understanding biological connectivity (Chapter 4). It is also used to generate specific questions for more detailed investigations (Chapter 13) and to develop and test specific conceptual models (Chapter 13).

Methods

Nine pools—Twelve Mile brackish, downstream and upstream; Munduran saline and downstream; Gonong saline; Little German Jack's; Frogmore; and Woolwash—were selected for detailed physical sampling.

The salinity, temperature, pH, turbidity and depth of each pool were measured on each sampling occasion (February 2004, May 2004, July 2004, November 2004, February 2005 and May 2005), except when equipment failure prevented measurements. An additional trip, to collect physical data, was conducted in December 2004 to match with predicted extreme high tides (5.5 m at Port Alma, 12–14 December [AHS Seafarer Tides 2004]). Because pools could only be visited every four months, the regular cleaning required to ensure continuous data loggers work effectively was not feasible. Consequently, point sampling was used rather than continuous data logging. This approach was considered adequate for the purposes of gaining a broad, initial understanding of the physical nature of each of the pools and of connections between them. As a result, firm information is only available for each sampling occasion, and an understanding of conditions between those times relies on interpolation. Other variables such as dissolved oxygen were not measured because their high levels of temporal variability at multiple scales would render point measurements uninformative.

Measurements of water quality parameters

Salinity and temperature were measured using a TPS WP-84 conductivity/salinity/temperature meter, and pH using a TPS WP-80 pH meter. Turbidity was measured in NTU using an Analite 152 Nephelometer. This meter produced unreliable data on a number of occasions, so only reliable turbidity data are included.

Measurements of depth and pool levels

Depth profiles of each pool were recorded using a Lowrance LCX-18C sonar and mapping GPS. This information was cross-referenced to depth measurements made manually at each castnetting location, on each sampling occasion. At the beginning of the study a permanent survey peg with a height datum mark was placed on the edge of each pool. The level of each pool relative to datum level was measured on each sampling trip, using a laser level.

For each pool (except the two German Jack's pools which could not be accessed until November 2004 due to unfavourable conditions on the access road), the water level in February 2004 was defined as the 'full' level. This was an accurate description for pools in Twelve Mile Creek, Munduran Creek and Gonong Creek because heavy local storm rainfall in the southern catchments of the Fitzroy floodplain during January and February 2004 produced flow in each system, filling all the pools. Frogmore and Woolwash lagoons were disconnected from each other and from other systems throughout the study, so levels fell throughout the study period. Consequently, for these pools the 'full' level at the beginning of the study provides a relative benchmark only.

The situation in the two German Jack's pools is more complex. The only substantial inputs of water into these pools during the study period came from connections to the Fitzroy estuary. However, while the duration of these connections was sufficient to fill Little German Jack's, they were not sufficient to fill Big German Jack's. Consequently, while a 'full' level could be defined for Little German Jack's, no similar definition could be made for Big German Jack's.

Connection depths

To allow investigation of connection depths and timing between the estuary and each of the marine and brackish pools, the end of each seven-day sampling trip was set to coincide with the largest tides of the month. Simple depth recorders (Figures 3.1 and 3.2) were placed at the connection point of each pool at the beginning of each sampling trip (i.e. prior to the largest tides) and the maximum depth the tide reached, relative to the pool depth datum, measured each day.

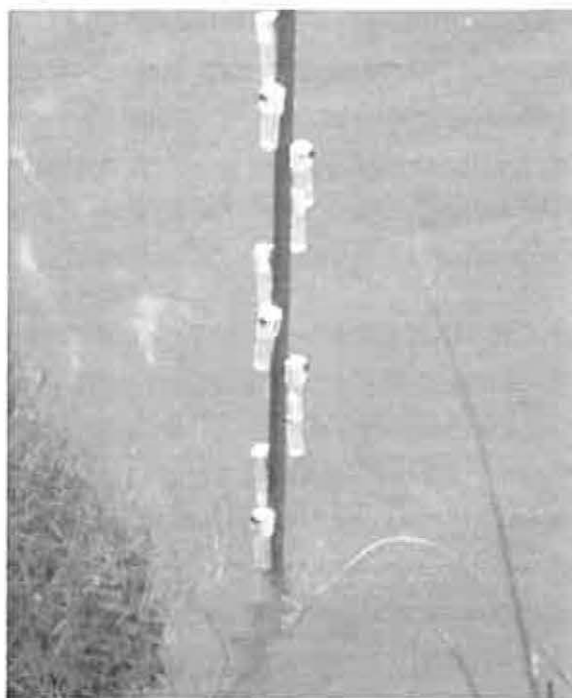


Figure 3.1. Simple depth recorder used to measure connection depth

The depth recorders consisted of 30 mm long vials attached sequentially, along the length of a 2 m stake set vertically into the edge of the pool, with the lowest vial at the pool surface. Each vial had two holes drilled into it, one hole at the mid-point of the vial to allow water to enter and one just below the lip of the lid to let air escape, so forestalling pressure build-up that might prevent water entering the lower hole. Because the vials were attached sequentially every 30 mm, connection depths were automatically recorded to the nearest 30 mm.

Experiments prior to using the depth recorders in the field showed they recorded depth accurately and were not influenced by rainfall, which was deflected away by the overhanging lid of the vial (Figure 3.2).

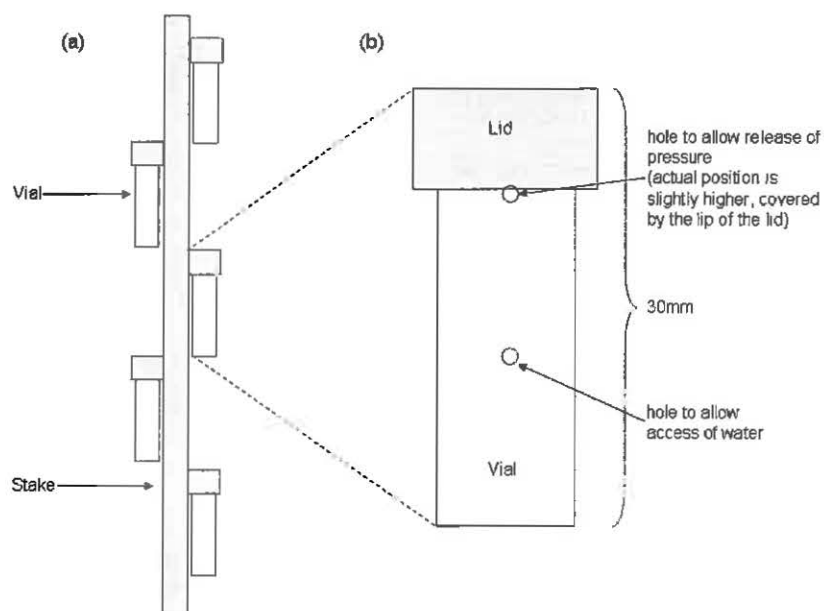


Figure 3.2. Diagrammatic representation of the design of the simple depth recorders used to measure connection depth: (a) configuration of the vials; (b): location of the holes in the vials

Results and discussion

The physical environment

Salinity

Salinities at Frogmore, Woolwash, Twelve Mile downstream, Twelve Mile upstream and Munduran fresh remained at or very close to zero throughout the study (Figure 3.3).

Small inputs of estuarine water from Inkerman Creek balanced freshwater input from local rainfall to maintain low salinities in Twelve Mile brackish (mainly 5–10 ‰, except for December 2004 when salinity fell to 0.7 ‰) until the final sampling trip in May 2005 when substantial inflow from Inkerman Creek during extremely high tides caused salinities to increase to 35 ‰ (Figure 3.3).

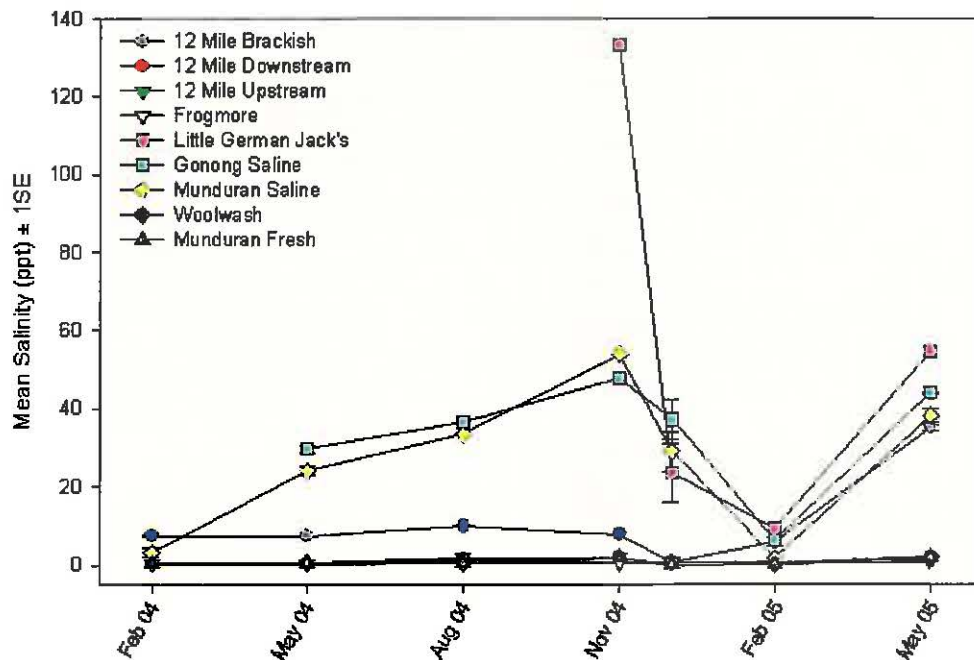


Figure 3.3. Patterns of SALINITY over time in Fitzroy estuarine floodplain wetland pools

Salinities in Munduran and Gonong saline pools tracked together throughout the study (Figure 3.3). Salinities in Munduran saline were close to zero in February 2004, following extensive local flooding. Salinities in the two pools increased continually until November 2004, due to repeated tidal connections. Local rainfall at the end of 2004 and early 2005 reduced salinities to minimums of 6 I in Gonong saline and 2 I in Munduran saline, measured in February 2005. The extreme high tides in February 2005 led to salinities increasing rapidly to around 40 I. The high salinity levels reached in the three 'brackish' pools in May 2005 seem anomalous, in that they are higher than normal seawater salinities. However, these levels simply reflect the fact that the three systems source their tidal waters from the upstream parts of dry subtropical estuaries that typically maintain elevated salinities throughout most of the year (Ian Webster pers. comm.).

When first measured in November 2004 the salinity was extremely high in Little German Jack's (130 I) (Figure 3.3). Very low water levels indicated the high salinity was due to evaporation during an extended period of disconnection from both fresh and marine water. Local rainfall in November and December 2004 filled Little German Jack's, reducing salinity to 9 I in February 2005. The extreme high tides in February 2005 led to salinities increasing rapidly to around 55 I, mirroring the changes in Munduran and Gonong saline pools.

Overall there were four distinct patterns of salinity (Figure 3.4): (1) constant freshwater salinities in the Frogmore, Woolwash, Twelve Mile downstream,

Twelve Mile upstream and Munduran fresh—the pools without direct connections to the estuary; (2) salinities fluctuating between fresh and hypersaline levels in Gonong and Munduran saline—the pools with regular connection to the estuary and regular inputs of fresh water from local flooding; (3) low salinities for the majority of the time in Twelve Mile brackish—reflecting regular inputs of fresh water from local flooding and restricted marine input from most potential marine connections due to the large distance tides have to bridge to create marine connectivity; and (4) salinities fluctuating widely and reaching extreme levels in Little German Jack—a pool with infrequent inputs of fresh (not part of a stream system, so only from local rainfall) and marine water (short connection but at a high topographic level that is only overtopped infrequently), and a very shallow depth allowing evaporation to rapidly reduce water levels and increase salinity.

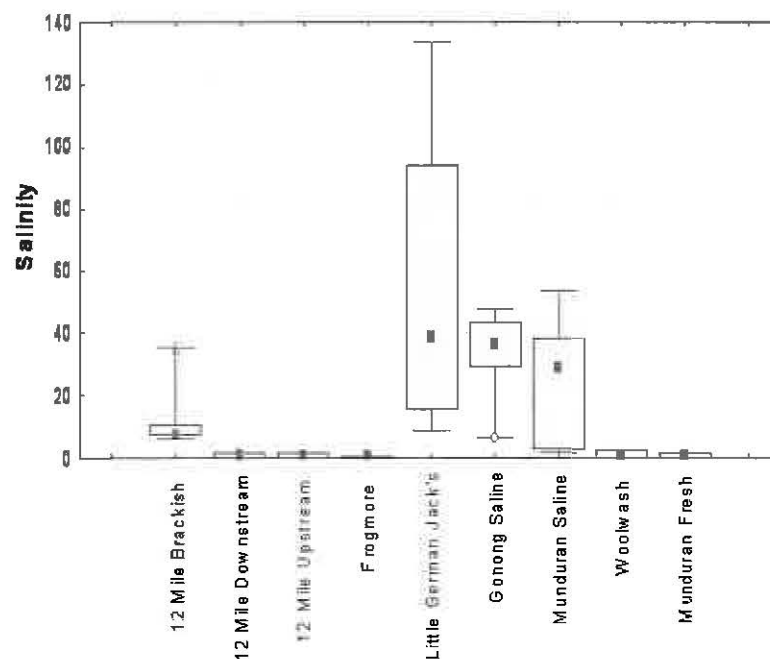


Figure 3.4. Comparison of salinity profiles of eight floodplain wetland pools
Central point = median; large box = interquartile range; whiskers = minimum–maximum range

Temperature

Despite a strong pattern of seasonal change, water temperatures varied little among sites at any time (Figure 3.5). One aspect of the seasonal pattern is noteworthy; temperatures in February and May 2005 were consistently 1–4°C higher than those in February and May 2004. Early in the study (early–mid 2004), water temperatures in the brackish sites tended to be slightly higher than in the fully fresh sites; however, differences became less distinct through the latter parts of 2004 and early 2005. Very high temperatures in Little German Jack's in November 2004 relate to a lack of inputs of fresh or marine water, leading to extremely shallow water levels (29.5 cm maximum depth) and no input of cool water to moderate temperatures.

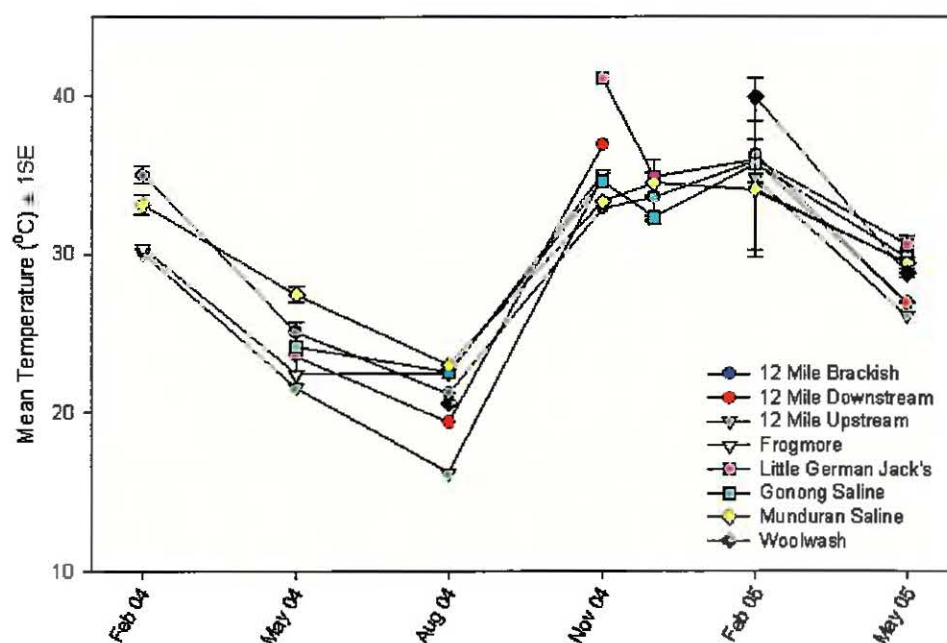


Figure 3.5. Patterns of TEMPERATURE over time in Fitzroy estuarine floodplain wetland pools

pH

A range of pH patterns appeared through time. The low salinity Twelve Mile brackish pool had constantly higher pH than the Twelve Mile upstream pool but followed the same pattern of temporal change; levels becoming more alkaline through time but with a dip in February 2005 (Figure 3.6a). The Twelve Mile downstream pools initially had similar pH to Twelve Mile brackish but changed to be similar to Twelve Mile upstream in November 2004 and February 2005, before again converging with Twelve Mile brackish in 2005.

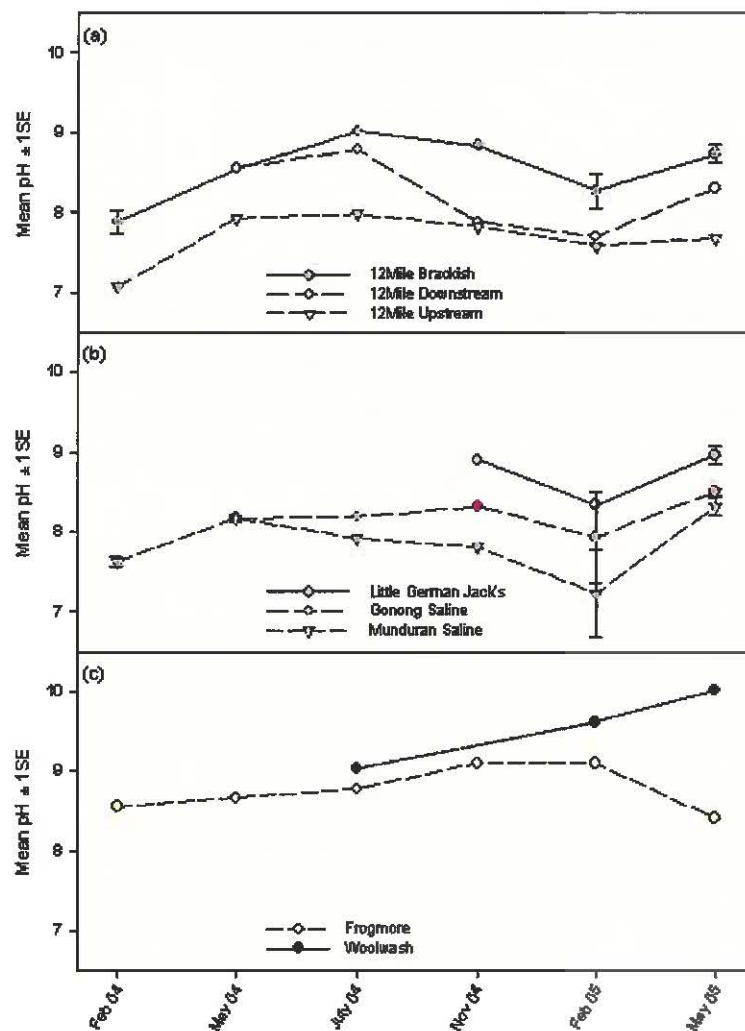


Figure 3.6. Patterns of pH over time in Fitzroy estuarine floodplain wetland pools
(a) Twelve Mile Creek pools; (b) high salinity pools; (c) freshwater lagoons

The pH levels at Gonong saline and Munduran saline (Figure 3.6b) were similar to those in Twelve Mile brackish in February 2005 and, although they increased in May 2004, the increase was less marked and not continued in July and November. While pH levels at Gonong saline remained similar through May, July

and November 2004, they became increasingly acid at Munduran saline over the period. In a similar way to Twelve Mile Creek, the pH at both Munduran saline and Gonong saline fell in February 2005 before increasing to similar to Twelve Mile brackish in May 2005. pH at the highly saline German Jack's lagoon was only measured in the last three months of the study but followed a similar pattern to that at Gonong and Munduran, but at a more alkaline level (Figure 3.6b).

The pattern at Frogmore lagoon (Figure 3.6c) was quite different to that at the other sites; starting at a more alkaline level in February 2004 and continuing to increase until February 2005 before falling in May 2005. Woolwash lagoon showed even more alkaline pH levels, but these continued to rise through to May 2005.

Turbidity

Turbidities (Figure 3.7) were low to moderate at all sites throughout the study, with highest turbidities in Twelve Mile brackish in February 2004. In-field observations suggested that turbidities were a simple reflection of the wind conditions over the days prior to sampling. The levels of turbidity were much lower than those usually found in the Fitzroy estuary (Phillip Ford pers. comm.).

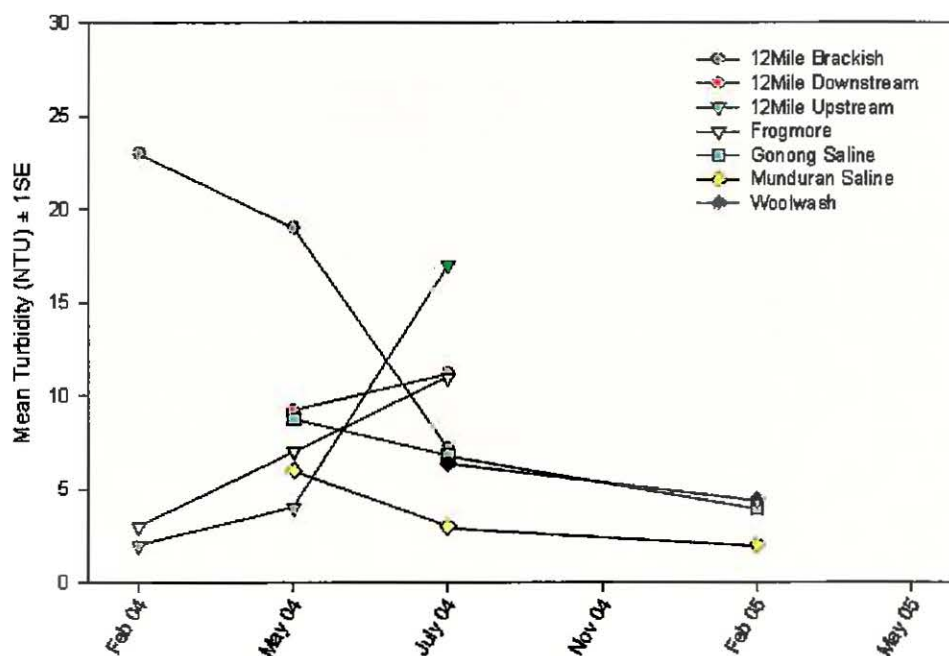


Figure 3.7. Patterns of TURBIDITY over time in Fitzroy estuarine floodplain wetland pools

Depth

The two saline pools, Gonong saline and Munduran saline, were connected to their estuaries regularly so maintained levels when disconnected that varied by only a few centimetres. Gonong saline had a maximum depth when disconnected of 2.1 m and a maximum depth when connected of 2.7 m, while Munduran saline had a maximum depth when disconnected of 1.8 m and a maximum depth when connected of 2.4 m.

Frogmore (maximum depth 4.7 m, February 2004) and Woolwash (maximum depth 2.8 m, July 2004) lagoons had no connections to other systems during the study and suffered continual declines in depth throughout the study until, by September 2005, the maximum depth of Frogmore lagoon was 1.1 m while the maximum depth of Woolwash lagoon was 0.3 m (Figure 3.8). The Twelve Mile system had substantial freshwater flows in January and February 2004 and 2005, and in December 2004. As a result, although the two Twelve Mile freshwater pools showed similar patterns of decline in depth to Frogmore and Woolwash through most of 2004, depth increased rapidly to 'full' level in December 2004.

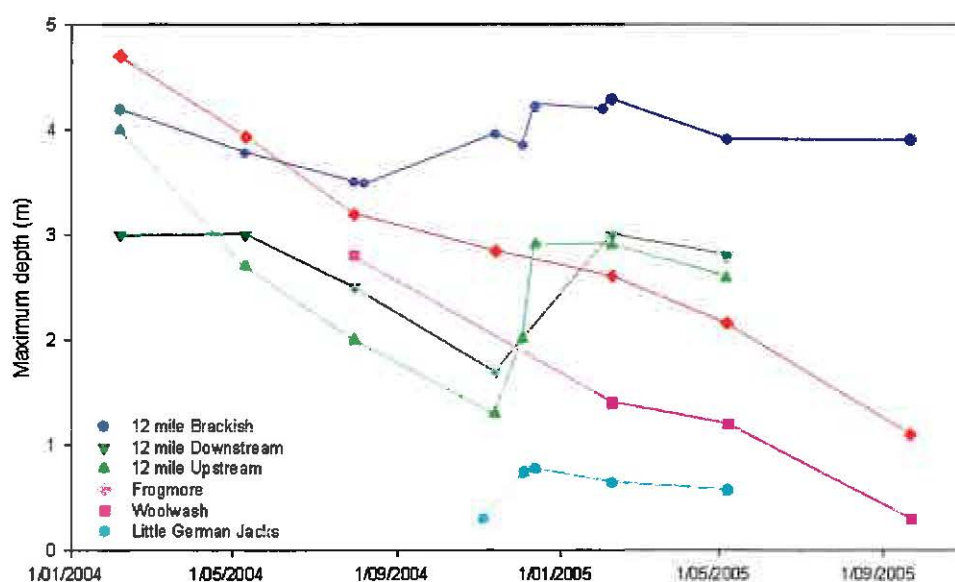


Figure 3.8. Comparison of maximum depths of six non-tidal estuarine floodplain wetland pools over time

Twelve Mile brackish followed a similar pattern, but with a slower reduction in depth and an earlier increase in level to be close to full in November 2004 (Figure 3.8). It is unclear whether this increase was due to freshwater flow or a marine connection; however, as there was a concomitant slight decrease in salinity (Figure 3.3), it seems most likely that the increase in depth was the result of very localised rainfall.

The increase in depth in Twelve Mile brackish at the end of 2004 also matched with marine connections at the times of extreme high tides. Little German Jack's (Figure 3.8) and Big German Jack's were only a few centimetres deep in November 2004, but the same storms that filled the Twelve Mile system in December also raised the levels in these pools. The depth of both pools declined throughout the rest of the study. Even though there were marine connections late in 2004 these were not extensive enough to do more than slow the rate of decline.

Access to Munduran Fresh was often difficult, so a consistent sequence of depth measurements was not possible. The pool had a maximum depth of 1.7 m in February and a minimum depth of 0.5 m in November 2004.

Physical connectivity

Fitzroy estuarine floodplain wetlands pools can be classified into five groups based on connectivity patterns: (1) infrequently connected, isolated freshwater pools; (2) regularly connected, in-stream freshwater pools; (3) pools with frequent marine and freshwater connections; (4) pools with infrequent marine and freshwater connections; and (5) pools with infrequent marine but frequent freshwater connections. Each of these is discussed below.

(1) Infrequently connected, isolated freshwater pools (Frogmore and Woolwash lagoons)

Frogmore and Woolwash lagoons are isolated systems; they are not part of a defined stream system, rather they are billabongs cut off from the Gavial and Scrubby Creek systems under all except flood situations. In addition, the two pools are in the centre of the floodplain in an area of low annual rainfall where heavy falls are infrequent (Figure 3.9).

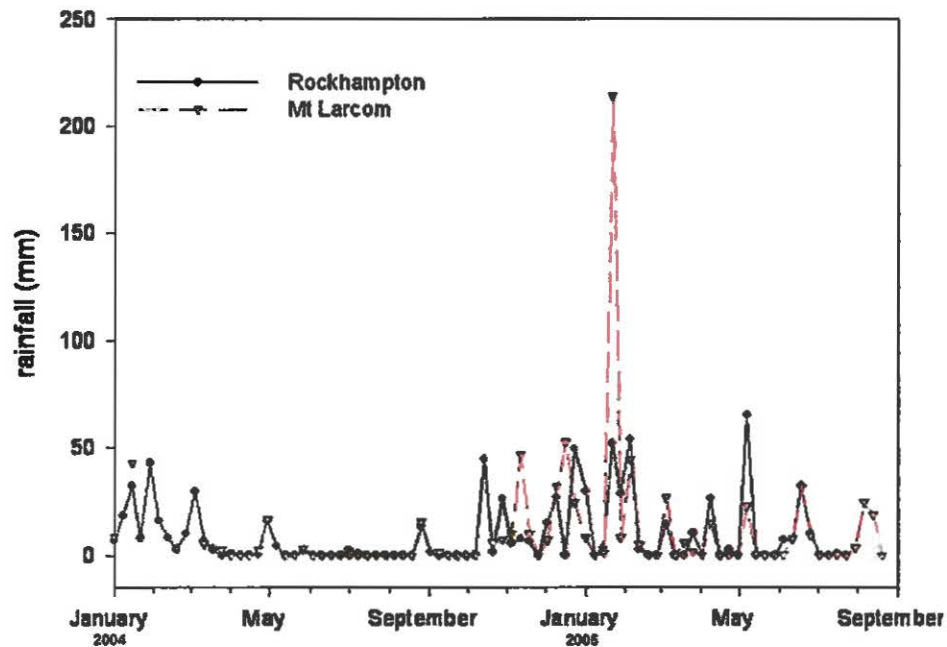


Figure 3.9. Weekly rainfall totals for Rockhampton and Mount Larcom between January 2004 and September 2005

There were no connections between Frogmore or Woolwash lagoons during the period of the study, as reflected in the continued decline in water levels (Figure 3.8). There had been connection between Woolwash lagoon and Frogmore lagoon, and between Frogmore lagoon and both upstream and downstream (estuarine) areas of Gavial Creek due to significant local rainfall and flooding in early 2003. Aerial imagery shows these connections were still in existence in late May 2003 (Figure 3.10). At this time there was considerable water in Bates lagoon, in the downstream channel of Gavial Creek. However, by November 2003, when preliminary evaluations of sites were made, Bates lagoon was greatly reduced in size with a maximum depth of around 40 cm, and Frogmore lagoon was disconnected from Gavial Creek, and Woolwash from Frogmore.

(2) Highly connected, in-stream pools
(Twelve Mile Creek freshwater pools and Munduran freshwater pool)

The two freshwater pools in Twelve Mile Creek (Twelve Mile upstream and downstream) and Munduran freshwater are in-stream pools; they are part of defined stream systems and are connected to each other and upstream areas by normal stream flows. Both systems are in the southern part of the Fitzroy floodplain and are fed by areas with higher and more regular rainfall than occurs over much of the floodplain.

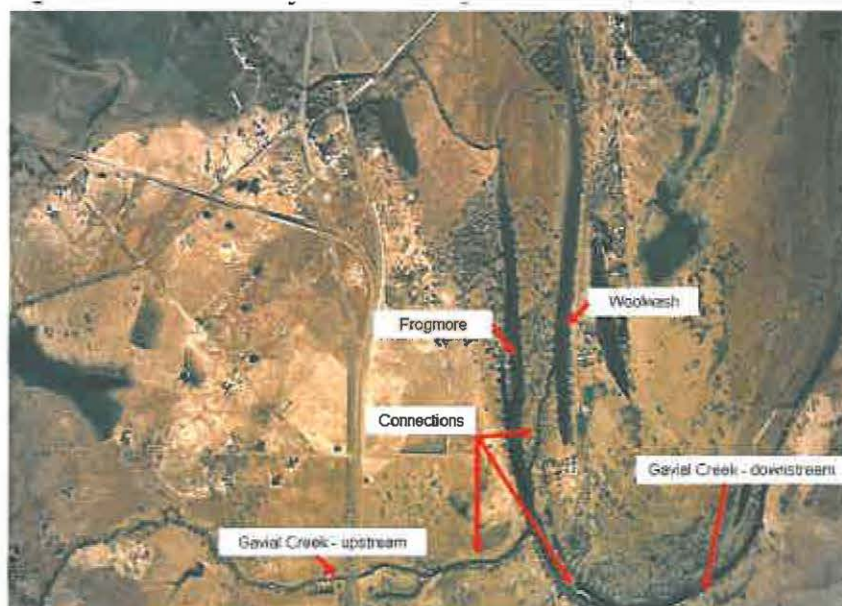


Figure 3.10. Connections between Frogmore and Woolwash lagoons and Gavial Creek, late May 2003

Substantial freshwater flows at all three sites in January, February and December 2004 and January and February 2005 resulted from heavy rainfall in their local catchments. Consequently, all three pools were connected to both upstream and downstream areas a number of times during the study, resulting in refilling of the pools and allowing the movement of fauna.

***(3) Pools with frequent marine and freshwater connections
(Gonong saline and Munduran saline)***

The 'saline' pools are immediately adjacent to the estuary of Munduran Creek (Munduran saline) and Connor Creek (Gonong saline), and separated from the estuary by a rock (Munduran) or gravel (Gonong) bar. The tide overtops these rock/gravel bars during the largest tides of most lunar cycles. Both pools are also the downstream section of freshwater drainage streams. Consequently, both pools are highly connected to both their upstream sections and to the marine environment.

Both Gonong (Figure 3.11) and Munduran (Figure 3.12) saline pools remained close to 'full' level throughout the study due to regular tidal connections and a number of freshwater flows from local rainfall.

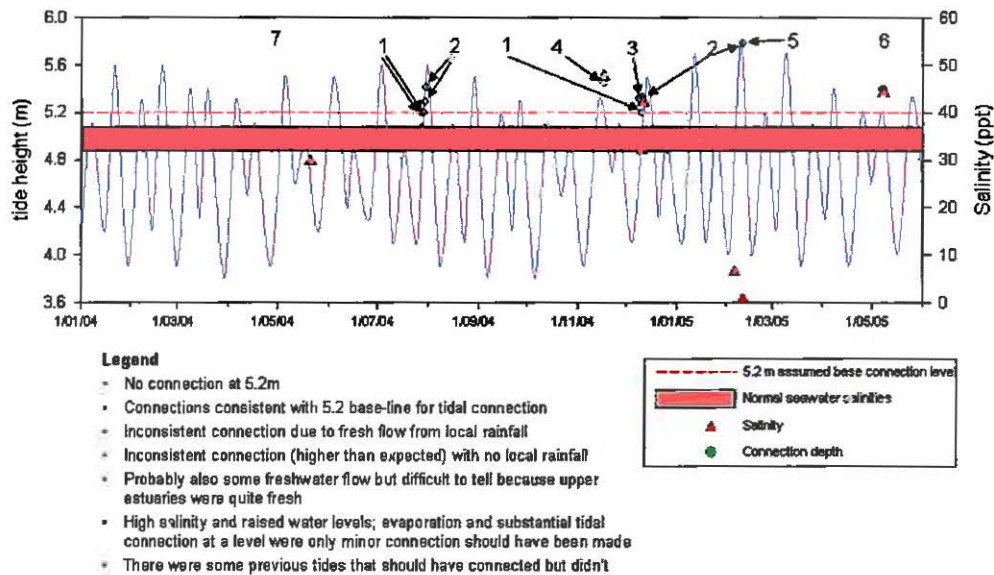


Figure 3.11. Height of water level (and salinity) of the Gonong saline pool over the study period relative to the predicted tidal tracks for Port Alma; pool water levels relate to an assumed minimum tidal connection of 5.2 m

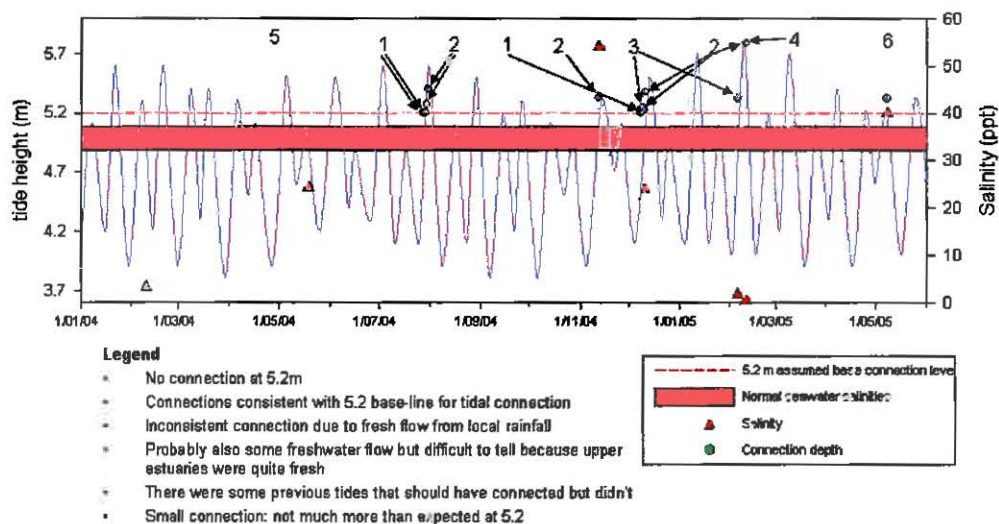
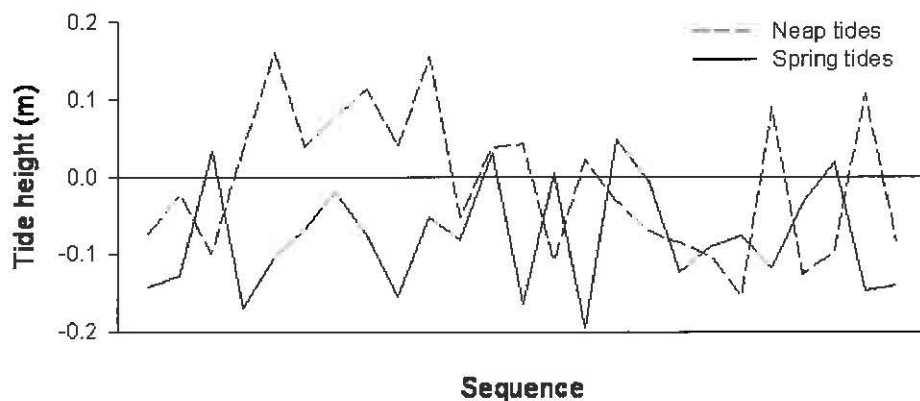


Figure 3.12. Height of water level (and salinity) of the Munduran saline pool over the study period relative to the predicted tidal tracks for Port Alma; pool water levels relate to an assumed minimum tidal connection of 5.2 m

The apparent minimum tidal height needed for connection was 5.2 m at both sites. However, a number of tides predicted to reach this level failed to produce connection. This can be explained by tidal anomalies (Ian Webster pers. comm.), resulting from variations in atmospheric pressure, wind fields and current patterns, that influence realised tidal levels.

During much of 2004 realised spring tidal levels were up to 20 cm below predicted levels at Port Alma (at the mouth of the estuary system leading to Gonong Creek) (Figure 3.13). The effects of wind fields on the long reaches of Fitzroy delta estuaries tend to exacerbate this effect, producing even greater anomalies in upstream parts. Given the length of these estuaries (Figure 2.1), substantial anomalous outcomes are probable (Ian Webster pers. comm.), explaining the unpredictable nature of marine connections to these pools.



Tidal data provided by the Technical Services Division of the Environment Protection Agency.

Figure 3.13. Sequence of differences between predicted and realised high tides at Port Alma during 2004

**(4) Pools with infrequent marine and freshwater connections
(Little German Jack's and Big German Jack's)**

The two German Jack's pools do not form part of drainage systems, so their only substantial inputs of fresh waters are during major flooding of the Fitzroy River. Consequently, their freshwater inputs mirror those of the isolated freshwater pools. Even though their shallow depths meant that small amounts of local rainfall could produce a larger change in percentage volume than in the isolated pools, only the heavy local rainfall in late 2004 and early 2005 had any influence on volume or salinity (Figure 3.14).

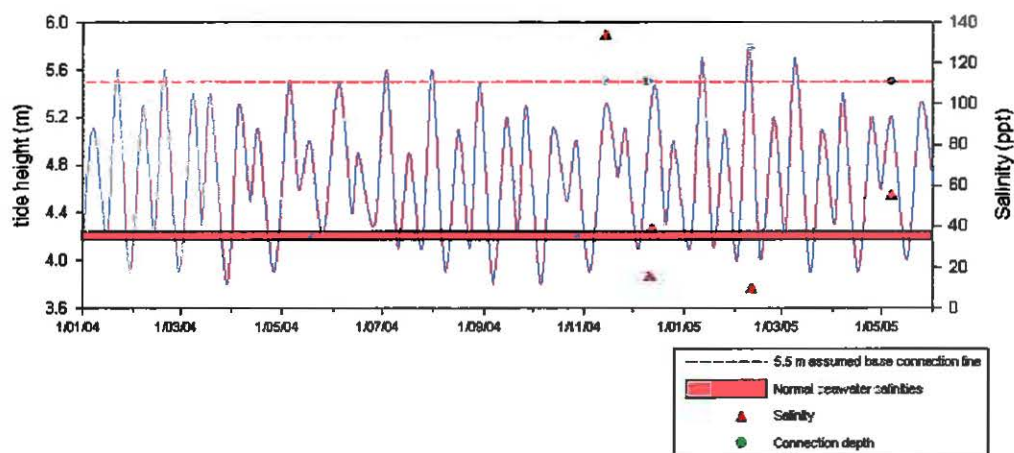


Figure 3.14. Height of water level (and salinity) of the Little German Jack's pool over the study period relative to the predicted tidal tracks for Port Alma; pool water levels relate to an assumed minimum tidal connection of 5.5 m

This change was relatively minor however, only reducing the overall rate of decline in depth in Little German Jack's (Figure 3.8) and lowering its salinity to 91 in February 2005 (Figure 3.3). Inputs of marine water to the two pools are low as they only connect to the estuary on the highest spring tides, and then for only a short period of the time. While there were a number of brief, marginal connections, only on one occasion was there sufficient inputs to fill Little German Jack's (Figure 3.14). There were no inputs of marine water sufficient to fill Big German Jack's during the study.

The differences between the pools relate to differences in both their sizes and their levels of connection to the marine environment. Little German Jack's is small (Figure 2.6) and close to the Fitzroy River. Although the tide level needed for connection through the connecting channel is high, the short connection distance plus the possibility for direct connection by sheet flow from the Fitzroy River mean that a reasonable volume of water can enter, particularly on anomalously high tides (see below). Big German Jack's is much larger (Figure 2.6) and this, together with its longer connection distance (Chapter 2), mean that the tidal influx never raised its level by more than a few centimetres at any time during the study.

A minimum tidal level (relative to tidal predictions at Port Alma) for connection of 5.5 m was calculated for Little German Jack's, although lower tides may connect—or tides at or above this level fail to connect—due to tidal anomalies (see above).

The shallow nature of the two German Jack's pools (Chapter 2), their low inputs of marine water (followed by long periods of evaporation) and their low inputs of fresh water allowed the two pools to rapidly become hot and hypersaline.

**(5) Pool with infrequent marine but frequent freshwater connections
(Twelve Mile brackish)**

The Twelve Mile brackish pool is part of the same drainage system as the two Twelve Mile fresh pools, so experienced the same regular freshwater flows. Additionally, the brackish pool was connected to the estuary of Inkerman Creek by the highest spring tides. Based on the predicted tidal heights at Port Alma (the nearest standard prediction site), and assuming the same minimum tidal level of 5.2 m calculated for the two saline pools, there should have been 19 connections during the study period (Figure 3.15a). However, the patterns of change of salinity and water level in the Twelve Mile brackish pool suggested that actual connection only occurred during four periods, at the end of 2004 and in early 2005 (Figure 3.15b).

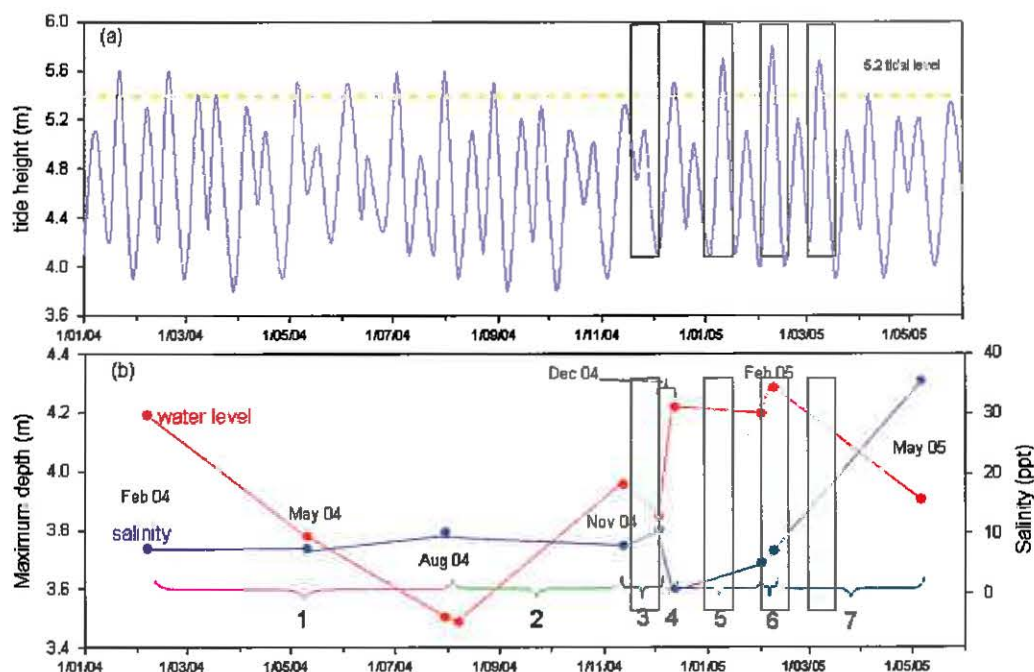


Figure 3.15. Predicted tidal tracks for Port Alma over the study period (a), and height of pool water level and salinity of the Twelve Mile brackish pool over the study period (b)
The dashed line in (a) indicates a 5.2 m predicted tidal level; the four elongated boxes indicate probable marine connections. Trips are indicated by month for data points in (b); brackets and numbers relate to periods indicated in text

The Twelve Mile brackish pool had a low salinity (7.4 ppt) and was full in February 2004, following freshwater flows in January and early February. The water level then fell consistently, while the salinity increased slowly from February 2004 to

July 2004, indicating that no marine or freshwater connections occurred (period 1, Figure 3.15a). The water level had increased in Twelve Mile brackish by November 2004 but the salinity had declined slightly, indicating freshwater inputs (period 2, Figure 3.15a). As the water levels were still falling in the two Twelve Mile Creek freshwater pools (immediately upstream of Twelve Mile brackish) at this time (Figure 3.8), the increase in depth at Twelve Mile brackish must have been due to very localised rainfall adjacent to the pool.

In the period between the November 2004 sampling trip and the additional trip to match the large tides in December 2004 (period 3, Figure 3.15a), salinity rose but the pool level fell. Although the water level fell, the increase in salinity was much sharper than during early 2004, suggesting that a small marine connection may have occurred (it is unlikely that this salinity increase was due to salt being washed from the saltpan as this would have been expected during the local rains in November). Heavy storm rains between two visits to Twelve Mile brackish during extra field trips (8 December 2004 and 11 December 2004) (period 4, Figure 3.15a), led to extensive flooding of the Twelve Mile Creek system, resulting in a sharp decline in salinity and a return of the pool to its full level.

Between December 2004 and February 2005 (period 5, Figure 3.15a), fresh inflow to Twelve Mile brackish ceased, water levels only fell marginally but salinity rose considerably suggesting further marine connections. The saltpan between Inkerman Creek and Twelve Mile brackish was dry on the first visit to Twelve Mile brackish in February 2005 (6 February 2005), indicating no recent downstream connection had occurred. However, on the second visit (9 February 2005) (period 6, Figure 3.15a), the saltpan was flooded and the salinity of the pool had increased indicating a marine connection. Water levels fell and salinity increased sharply between February and May 2005 (period 7, Figure 3.15a) suggesting no further connections, although very high tides of 5.7 m in March may have produced a further marine connection.

The unpredictability of connection at Twelve Mile brackish is partially explained by tidal anomalies. The upstream end of Inkerman Creek, which supplies marine water to Twelve Mile brackish, is even further from the entrance to the estuary at Port Alma than the top of Connor Creek from which Gonong saline receives its marine water (Figure 2.1). Consequently, tidal anomalies are likely to be even more amplified.

In addition, for marine water to reach Twelve Mile brackish it must cross about 2 km of saltpan. Thus the tide needs to remain at a sufficient level for long enough for water to flood across the saltpan before connection can occur. This is not just a simple function of distance because the water also spreads laterally

across the saltpan, increasing the volume of water necessary to produce connection and the time taken. The time taken to cross the saltpan depends in turn on the condition of the saltpan at the time of potential connection. If the saltpan is dry, a considerable amount of water will soak into the surface, and hydraulic friction will slow down water movement. These effects will be exacerbated if the saltpan has become dry enough to form cracks (Figure 3.16). Consequently, connection will occur at a much lower tidal level if the saltpan is wet or flooded from local rainfall, or if a previous tide has soaked the surface.



Figure 3.16. The cracked surface of the saltpan connecting Twelve Mile Creek to Inkerman Creek

Overall, the pattern of connectivity of Twelve Mile brackish is complex, with four drivers to consider: (a) predicted tidal height; (b) tidal anomalies that influence the actual tidal height; (c) stream flows that produce upstream and downstream connection; and (d) local rainfall that, together with flow down Twelve Mile Creek, wets the 2.5 km wide saltpan between Twelve Mile brackish and Inkerman Creek.

Conclusions

Physical connectivity between wetland pools, between wetland pools and other freshwater environments, and between wetland pools and the estuary, rely on a number of factors, many of which have not previously been recognised:

Local rainfall producing localised stream flow: In the Fitzroy this is a much more common source of connection for many pools than major flooding, and because it is more frequent is more likely to occur at an advantageous time for biological connectivity.

Tidal anomalies: Tidal anomalies can greatly alter the realised tide height, determining whether or not the tide reaches a high enough level to cause a connection.

Distance: The probability of connection due to the tide is greatly dependent on the distance the tide has to travel. This relates to long narrow channels or particularly to flow across saltpans. Flow over saltpans is influenced by the distance and how much lateral spread is involved.

Pre-existing conditions: Movement of the tide over saltpans is also modified by pre-existing conditions, such as whether the saltpan is wet or dry and whether the surface is smooth or rough (e.g. craze cracks).

The concordance of these factors is crucial in producing a physical connection. Given the complexity of the situation and the high level of chance involved in bringing a particular series of conditions together, predicting a particular connection event is extremely difficult. Despite this we now know enough to understand that the complexity of physical connectivity needs to be factored into our understanding if we are to successfully manage the effects of future climate and sea-level changes.

Chapter 4 The Influence of connectivity on patterns of composition and density of fish from Fitzroy wetland pools

Marcus Sheaves and Ross Johnston

Summary

This component of the study sets out to investigate the fish faunas of Fitzroy floodplain wetland pools, and patterns of biological connectivity.

A variety of sampling approaches were trialled, with castnet sampling proving to be the most appropriate method across the range of pools sampled.

Fitzroy estuarine floodplain wetland pools provide a diverse range of environments, harbouring diverse fish assemblages.

Patterns of connectivity determine the nature of each of the pools and the nature of their faunas.

These connectivities are determined by patterns of freshwater flow and marine connection.

Because these connectivities are greatly affected by small changes in rainfall and/or tidal height, they will be profoundly impacted by climate change.

More extreme weather patterns will lead to more infrequent and unpredictable connectivities, resulting in a greater number and variety of pools moving to the point of ecosystem collapse.

Introduction

Fish are important components of the wetland faunas of tropical and subtropical northern Australia. These wetlands are recognised as important nursery areas for many species of fish, including icon species like barramundi, *Lates calcarifer* (Sawynok 2004, Arthington *et al.* 2005). They are generally considered to benefit juvenile fish through reduced levels of predator-induced mortality and/or enhanced growth outcomes (Beck *et al.* 2001). Fish are in turn important faunal components, performing key functions in food webs and transporting substantial amounts of nutrients between wetlands and other habitats during migration (Beck *et al.* 2001, Herzka 2005). As the focus of recreational and traditional fisheries, fish stocks also contribute directly to the economic and social values of wetlands (Costanza *et al.* 1997).

The composition of the fish faunas of Australia's tropical and subtropical floodplain wetlands are poorly understood (Blaber *et al.* 1989, Sheaves 2005). As with other fish fauna, composition probably reflects physical aspects such as salinity, habitat structure and water quality (Tejerina-Garro *et al.* 1998, Saint-Paul *et al.* 2000, Levin & Stunz 2005). However, the discrete nature of wetland pools, and the obvious importance of connections between pools and other systems, suggests that the extent and history of connectivity are also likely to be influential in determining composition (Hoeinghaus *et al.* 2003, Ray 2005). The abundance, or density, of fish is likely to reflect habitat type and quality (Tejerina-Garro *et al.* 1998, Levin & Stunz 2005), but is also likely to be influenced by the extent of predation (Rodriguez & Lewis 1997) and the health of habitats (McKenna 2001).

The importance of fish in wetlands makes knowledge of their compositions, abundances and densities the basic currency for beginning to understand wetland pattern and process and relating that understanding to management. Our lack of knowledge of these simple parameters makes determining them a necessary first step towards ecosystem understanding. This component of the study sets out to determine and compare the compositions and densities of fish faunas in floodplain wetland pools adjacent to the estuarine region of the Fitzroy River delta.

Methods

Sampling was conducted in ten wetland pools: Frogmore and Woolwash lagoons; Twelve Mile brackish, and Twelve Mile downstream and upstream freshwater pools; Munduran brackish, and Munduran downstream and upstream freshwater pools; Gonong brackish; and Little German Jack's lagoon (site details, Chapter 2) (Big German Jack's was too shallow for efficient sampling by any method, and consistent high temperatures and salinities made it inhospitable for fish throughout the study.)

Table 4.1. Number of 18 mm castnet samples per site, per trip

Site	Feb 2004	Jul 2004	May 2004	Nov 2004	Feb 2005	May 2005	Sep 2005
Twelve Mile brackish	52	53	50	82	103	60	
Twelve Mile downstream		28	41	13	50	37	
Twelve Mile upstream	22	23	20	18	31	16	
Frogmore lagoon	31	206	76	120	120	60	50
Gonong saline		51	35	52	51	48	
Little German Jack's lagoon					20	50	
Munduran saline		55	44	64	72	62	
Munduran downstream		5	5	5			
Munduran upstream		4	4				
Woolwash lagoon		50			66	42	

Only three sites were sampled during the initial sampling trip in February 2004 (Table 4.1), when field techniques were being evaluated and refined. Most sites were sampled regularly over subsequent trips (February 2004 to May 2005), as long as access was possible. The only exception was Woolwash lagoon. Woolwash was initially sampled in July 2004 as a spatial replicate for the nearby Frogmore lagoon. Because of the close similarity of the fauna to that of Frogmore,

and because a considerable sampling effort was necessary to represent the fauna of such a large system, Woolwash was not sampled again until February 2005 when it became obvious that water levels in Woolwash were becoming low. Extensive faunal change had occurred in Woolwash lagoon in May 2005, so additional samples were collected from Frogmore lagoon in September 2005 when water levels had fallen below those of Woolwash in May 2005. A series of fish kills were reported in Woolwash lagoon during August and September 2005, and although there was too little water and bank conditions were too muddy to allow sampling in Woolwash in September 2005, dead fish were collected from the banks.

Sampling gear

Initially it was planned to use four gear types: gill nets, cast nets, fish traps and scoop nets, to provide as complete a picture of the fish fauna as possible. Other gear types were considered but not employed, generally because they could not be used in all pool types. These included electrofishing (only effective in very low salinity water), seine nets (need shallowly sloping banks devoid of vegetation for hauling), and fyke nets (useful for catching fish moving between shallow habitats, but of limited effectiveness in deep wetland pools). The four gear types chosen (gill, cast [6 mm & 18 mm mesh] and scoop nets, and fish traps) were all employed during the initial sampling trip; however, only 18 mm mesh cast nets were employed on subsequent trips.

Comparison of sampling gear types

No other gear types produced species not captured in the 18 mm cast nets, so added no additional information on species richness. Although *fish traps* are useful in sampling a broad range of habitats, including many inaccessible to other gears (Sheaves 1992), they were discarded because of their propensity to capture tortoises. Trapped tortoises could suffocate before traps were checked. This was considered an unacceptable risk to potentially endangered species. Cast nets also captured tortoises, but because cast nets are removed from the water immediately, tortoises could always be released unharmed.

Scoop nets were discarded because their use was restricted to edges, so they could not provide quantitative samples over the full range of habitats. The relatively thick, heavy-weight mesh needed to make *small-mesh cast nets* (6 mm mesh) robust enough for sampling meant that only small diameter nets could be used. This, together with slow sink rates due to restricted passage of water

through the small mesh, meant catches per net were relatively low. Although the small mesh net did capture fish below the lower limit of the larger mesh cast net, it added no additional species and represented larger size classes poorly. It was considered that the extra time needed to collect samples with the small mesh net could be more profitably spent collecting more replicate samples with the large mesh cast net that captured fish over a much greater range of species and sizes.

Gill nets were trialled extensively, both in trial sampling in the Townsville region and during the initial Fitzroy sampling trip. Gill nets were evaluated more extensively than alternative gear types because they were likely to capture large fish that might be poorly represented in cast nets. During the initial Fitzroy sampling trips (February and May 2004) gill nets were set in Twelve Mile brackish, Twelve Mile upstream, Frogmore and Munduran saline on the same day that castnet sampling was conducted. Two gill nets of each of 4 mesh sizes (25, 50, 100 and 200 mm) were used. All nets were 10 m in length, to allow them to be set in narrow pools without bunching up. Each net was set for three 2-hour daytime soaks and a single night-time soak. The catches from gill nets were compared to catches from 18 mm mesh cast nets (see below for sample sizes and sampling protocols).

Gill net catches were too low at Munduran saline to allow comparison to cast nets. Gill net catches from the four different gill net mesh sizes were combined for the other three sites. This was necessary because size and taxonomic structures were too restricted for each individual mesh size for a reasonable comparison.

For all three sites, 18 mm cast nets captured more species than the four gill net mesh sizes combined (Figure 4.1). Additionally, profiles of relative abundance, for the species captured by the two gear types, were very similar for both methods at the two Twelve Mile Creek sites. At Frogmore lagoon there was one discrepancy; *Nematalosa erebi* was caught in much higher relative abundance in 18 mm cast nets (Figure 4.1c). Given the similarities in relative abundance at the other two sites, that the castnet data from Frogmore lagoon are based on 150 replicate nets, and the high concentration of *N. erebi* in deep water in Frogmore lagoon (see Chapter 11), it is hard to attribute this difference to anything but undersampling of *N. erebi* by gill nets set along the edges of the lagoon.

In light of these results, gill nets were excluded from further sampling because they captured less species overall, did not appear to sample any group more efficiently than cast nets, were more taxonomically and size selective, and required the integration of four different mesh sizes to produce results comparable to the cast nets.

Similar difficulties with gill nets have been recorded in previous studies (Smith & Hindell 2005). Additionally, fish caught in gill nets are often unsuitable for dietary studies, which were an important aspect of the trophic component of this study (Chapter 7).

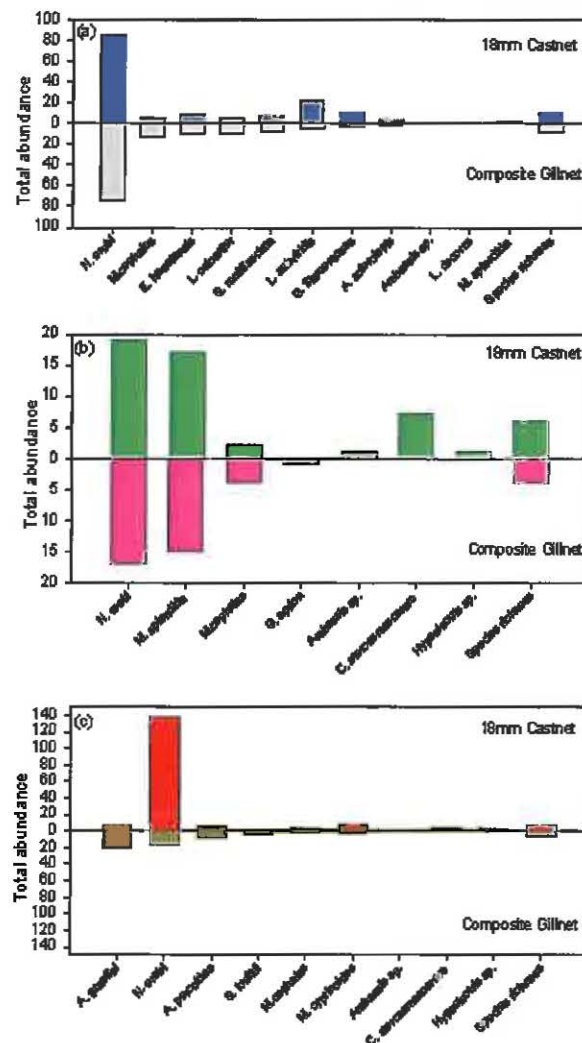


Figure 4.1. Comparison of catches between 18 mm cast net and combined gill nets from (a) Twelve Mile brackish, (b) Twelve Mile upstream and (c) Frogmore lagoon

Because gill nets need to be set for long periods of time to capture fish, any fish captured early in a net soak may digest prey already in their gut to an unrecognisable state, pass food from their gut that would otherwise be found or regurgitate food (loss through defecation and regurgitation is also exacerbated by the mechanical action of squeezing fish during removal from the net). Thus gut content of fish caught in gill nets is an unreliable measure of diet.

One further aspect makes cast nets a more desirable sampling tool; all fish not needed for laboratory studies could be released unharmed from cast nets,

whereas the need to leave gill nets in the water for extended periods, and the nature of their capture method (entangling), meant gill net consistently caused collateral mortality on non-target fish, and had the potential to kill non-target species (e.g. waterbirds and tortoises).

Cast nets were clearly the superior sampling gear of those trialled. Compared to other methods they were less taxonomically selective, produced equivalent or better representations of the fauna (richness, abundance and size structure), provided many discrete replicate samples per unit effort, were logistically simpler, produced more data per unit time, were usable across the full range of habitats available, except for those heavily vegetated with water plants or among fallen timber (no other gear was efficient in these), and eliminated collateral mortality.

Castnet sampling methods and protocols

At least 50 castnet samples (18 mm mesh) were collected from each site whenever there was sufficient area for 50 independent samples. In some cases the area available became limited as the pool dried; in other cases the presence of water lilies, *Nymphaea* spp., or the invasive aquatic weed, *Cabomba caroliniana*, reduced the area that could be sampled. Of the 43 trip x location combinations (Table 4.1), 51% had 50 or more replicate samples, with a further 30% between 20 and 50 replicate samples. Three more combinations (7%) had between 10 and 20 replicates, while only five combinations (12%) had fewer than 10 replicate samples. These samples came from the two Munduran fresh sites where dense beds of aquatic vegetation restricted available sampling area. Although data from these two sites extends the range of pools investigated, the low number of replicates means the data should be treated with caution: abundant species are likely to be represented reasonably well, but less common species may have been underrepresented, as are estimates of species richness.

For consistency, all castnet samples were collected observing the following protocols. Cast netting was conducted from a small boat fitted with an electric motor to minimise site disturbance. Castnet samples were not used if: (1) a net throw did not sample greater than an estimated (by eye) 85% of the actual net area; (2) the net became snagged on any structure; (3) it appeared that a site was disturbed during boat positioning; or (4) if the net operator's shadow encroached onto the proposed sampling area. In this way sampling biases were reduced as much as possible and/or standardised. Any variability in sampling volume (i.e. differences in the surface area of net throws), was randomly distributed throughout the study, therefore any biases would have added variability to the

data in a random manner. In theory the maximum sample area for the cast nets was 16.5 m² for the 18 mm mesh (4.29 m diameter) net and 7.4 m² for the 6 mm mesh (3.07 m diameter) net, but measurements from net throws on land indicated actual sampling area was considerably below theoretical maximum for each net though not highly variable; 18 mm net mean area = 7.35 m² (SE = 0.40, n = 50) and 6 mm net mean area = 2.9 m² (SE = 0.19, n = 50). As a result the empirical estimates of area sampled were used in subsequent analyses.

Data and statistical analyses

Raw abundances of fish per net were averaged to produce the basic data for analysis: mean numbers of each species of fish per cast net, for each wetland pool, on each sampling trip. These data were first transformed by $\log(x+1)$, to downweight the influence of very common species (allowing less common species some influence on analytical outcomes) and analysed using multivariate classification and regression trees (De'ath & Fabricius 2000, De'ath 2002). Tree selection was conducted using 10-fold cross-validation, and the 1+SE tree (the smallest tree with cross-validation error [CV error] within 1 SE of that of the tree with the minimum CV error).

Further interpretation was facilitated by displaying the data in two-dimensional space using non-metric multidimensional scaling (nMDS) based on Bray-Curtis dissimilarities. Information on the strength and nature of the correlation of species with the nMDS space was added as vectors indicating the direction of greatest increase in density of species most highly correlated with the space. The directions of these vectors was determined by regression of each species on the nMDS space, with the length of vectors reflecting the R² value for each regression, so indicating the strength of correlation with the space.

Individual nMDS ordinations were done for both the whole data set as well as for Twelve Mile Creek (because there were sufficient data for more detailed analysis and comparison of these three sites). Preceding analyses, the original data matrix for species was reduced to include only species occurring in more than 10% of samples, to remove any undue effects of rare species on the analysis (Gauch, 1982).

Results

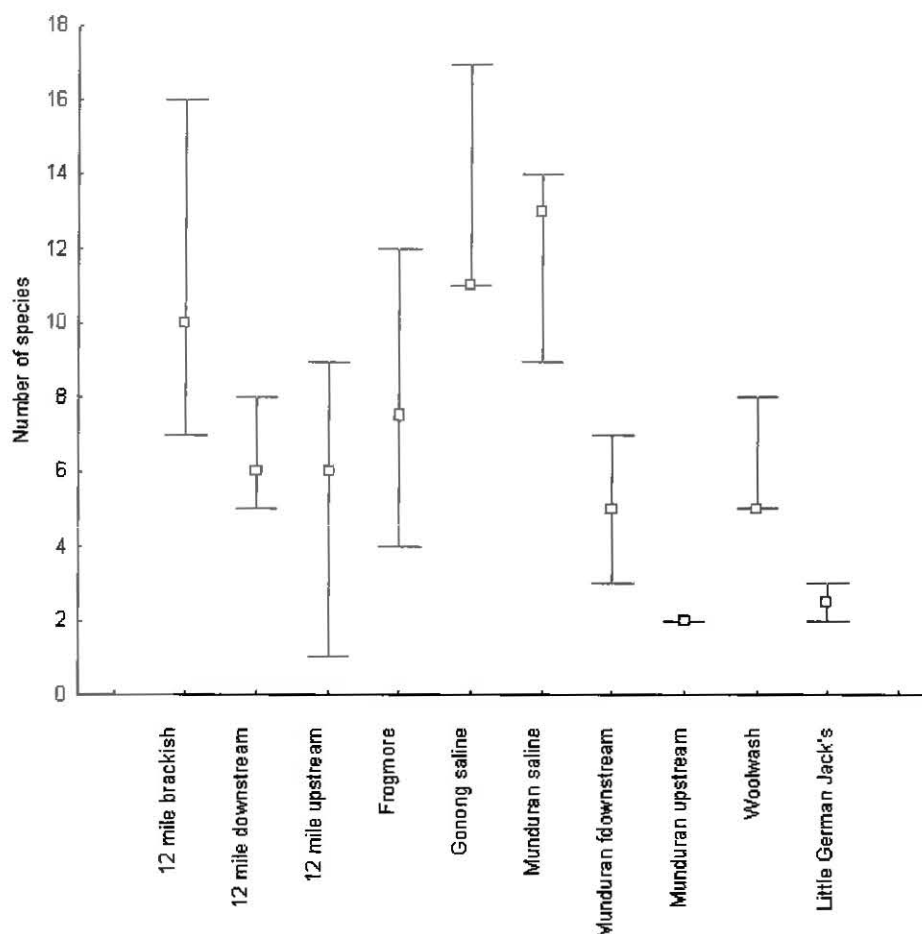
Over the course of the study, 46 species of fish were captured from the 10 Fitzroy floodplain wetland pools (Table 4.2).

Table 4.2. Total numbers and species richness of fish captured in 18 mm cast nets from 10 wetland pools

Common name	Species name	Twelve Mile brackish	Twelve Mile downstream	Twelve Mile upstream	Frogmore lagoon	Little German Jack's lagoon	Gorong saline	Munduran saline	Munduran downstream	Munduran upstream	Woolwash lagoon
Yellowfin bream	<i>Acanthopagrus australis</i>	1					4	12			
Pikey bream	<i>Acanthopagrus berda</i>							1			
Forktailed catfish	<i>Arius graeffei</i>				28						29
Glass perchlet	<i>Ambassis spp.</i>	5	11	14	7		9	15	4		6
Barred grunter	<i>Amniataba percoideus</i>				81						71
Snub-nosed garfish	<i>Arrhamphus sclerolepis</i>	13			3						
Bidyanus	<i>Bidyanus bidyanus</i>										1
Milkfish	<i>Chanos chanos</i>							2			
Fly-specked hardyhead	<i>Craterocephalus stercusmuscarum</i>		7	30	10				2	2	
Speckled longfin eel	<i>Anguilla reinhardtii</i>	3			1						
Giant herring	<i>Elops hawaiiensis</i>	18					1				
Gudgeon	<i>Unidentified Eleotrid</i>		1		1						6
Mouth almighty	<i>Glossamia aprion</i>		27	3							2
Silver biddy	<i>Gerres erythrorus</i>						11	3			
Whipfin silver biddy	<i>Gerres filamentosus</i>	14					88	128	1		
Goby	<i>Gobid sp.A</i>							1			
Goldfish	<i>Carassius auratus</i>				2						
Herring	<i>Herklotsichthys castelnaui</i>						13	16			
Carp gudgeon	<i>Hypseleotris sp.</i>	1	2	3	3						
Mangrove jack	<i>Lutjanus argentimaculatus</i>						1	3			
Barramundi	<i>Lates calcarifer</i>	17			1	3		2			
Ponyfish	<i>Leiognathus decorus</i>	23					1	14			
Ponyfish	<i>Leiognathus equulus</i>	1					11	23			
Moses perch	<i>Lutjanus russelli</i>						2				
Greenback mullet	<i>Liza subviridis</i>	69				14	214	284	3		
Spangled perch	<i>Leiopotherapon unicolor</i>	1	11	12							
Silver batfish	<i>Monodactylus argenteus</i>	1			1		1	1			
Sea mullet	<i>Mugil cephalus</i>	38	4	5	4		42	45	6	6	
Tarpon	<i>Megalops cyprinoides</i>		2	2	6		1		1		
Eastern rainbowfish	<i>Melanotaenia splendida</i>	4	13	57					10	1	
Gizzard shad	<i>Nematalosa come</i>						3	10			
Bony bream	<i>Nematalosa erebi</i>	793	396	306	1630						915
Catfish	<i>Neosilurus hyrtlii</i>				5						1
Blue-eye	<i>Pseudomugil signifer</i>						2				
Popeye mullet	<i>Rhinomugil nasutus</i>	5									
Butterfish	<i>Scatophagus argus</i>							1			
Queenfish	<i>Scomberoides commersonianus</i>	1					1				
Freshwater long tom	<i>Strongylura krefftii</i>				5						3
Rabbitfish	<i>Siganus lineatus</i>							1			
Banded scat	<i>Selenotoca multifasciata</i>	238	2			16	11	8			
Whiting	<i>Sillago sihama</i>						4	5			
Sardine	<i>Thryssa hamiltoni</i>							3			
Crescent perch	<i>Terapon jarbua</i>	5				2	8	1			
Bluespot mullet	<i>Valamugil seheli</i>	1					11	9			
Mullet	<i>Unidentified Valamugil sp.</i>	1				9	50	21			
Garfish	<i>Zenarcopterus buffonis</i>							1			
	Total species richness	22	11	9	16	5	22	25	7	3	9

Species richness

All pools had reasonably low numbers of species with a maximum total richness of 25 species at Munduran saline (Table 4.2), and the highest in any one sampling trip of 17 at Gonong saline (Figure 4.2). Lowest numbers of species were found at Munduran Upstream (although sample sizes were low there) and Little German Jack's (rarely connected and often inhospitable). Freshwater pools tended to have fewer species than brackish/saline pools. The large variation in the Twelve Mile upstream pool is probably attributable to the restriction of sampling area on some trips due to increases in aquatic vegetation. Species richness of freshwater pools increased with pool rank surface area (or volume) [Spearman's $r_s = 0.8407$, $t = 3.105$, $df = 5$, $p = 0.036$]. Species richness was even more highly correlated with the number of net samples [Spearman's $r_s = 0.9856$, $t = 11.662$, $df = 5$, $p = 0.0003$].



Figure[B2] 4.2. Means and ranges of species richnesses per sampling trip, for floodplain wetland pools

Patterns in fish composition and density

There was a major dichotomy in fish faunal composition based on the presence or absence of freshwater species (Figure 4.3), principally *N. erebi*, separating Little German Jack's, Gonong saline, Munduran saline, and the two Munduran fresh sites from Frogmore, Woolwash and the Twelve Mile Creek sites. Secondary splits segregate the Munduran fresh sites from the three saline sites and Twelve Mile brackish from the purely freshwater sites. The fauna of each pool were stable over time with only one important change: the two February samples from Twelve Mile brackish had higher densities of *N. erebi* and lower densities of *Selenotoca multifasciata* than were found during the other trips.

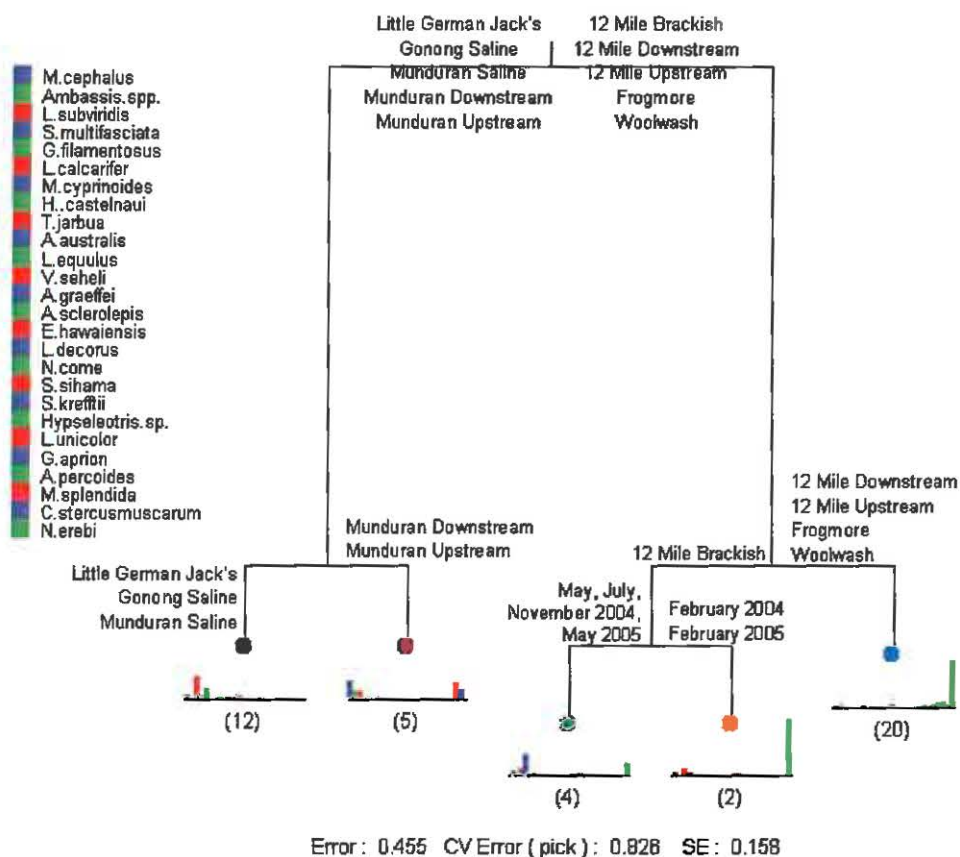


Figure 4.3. Classification and regression tree for abundance [log(1+x) transformed] of fish in Fitzroy estuarine wetland pools

Species on bar graphs ranked in decreasing abundance, marine species from left (*M. cephalus*–*S. sihama*), freshwater species from right (*N. erebi*–*S. krefftii*)

The nMDS ordination (Figure 4.4) provides a visual display of the similarities and differences in faunal composition between samples. The overall similarity within sites is clear, with only Twelve Mile brackish showing substantial changes between samples. The tight groupings of the Munduran and Gonong saline sites, the two Munduran fresh sites, the two German Jack's samples, and Frogmore, Woolwash and the Twelve Mile Creek fresh sites are obvious. As expected from the tree analysis, these four groups are well separated from each other.

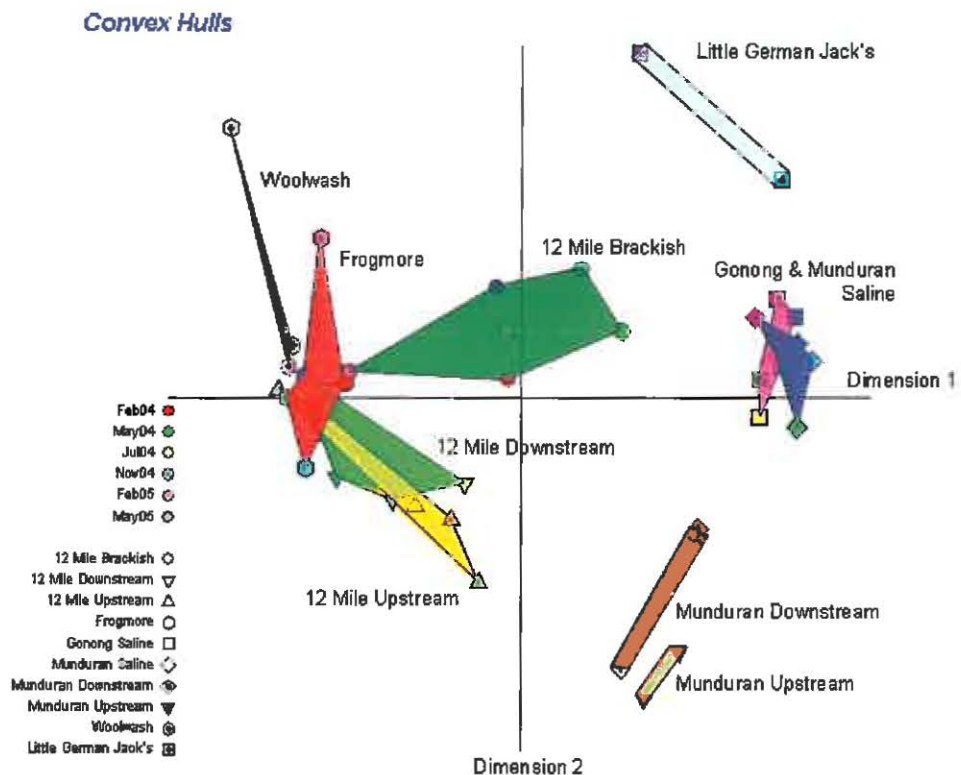


Figure 4.4. Comparison of density per net, from 12 mm mesh cast nets, for fish from Fitzroy estuarine wetland pools, with convex hulls defining the area of ordination space occupied by points relating to each site

nMDS ordination using Bray-Curtis dissimilarities on $\log(1+x)$ transformed data; stress1 = 0.12539; symbols indicate sites, colours indicate sampling trips

One aspect not clear from the tree analysis is that in February 2005 the fauna at Twelve Mile brackish had a similar appearance to that of the group of four freshwater sites. However, there was a return to a similar composition in May 2005 (Figure 4.5). This change principally reflects a marked change in dominance of *N. erebi* (Figure 4.6) with the appearance of high densities of small individuals following flooding in late 2004 and early 2005 (Chapter 5). The marine-derived species, *Gerres filamentosus*, *Liza subviridis*, *Acanthopagrus australis* and *Herklotsichthys castlanaui*, dominated the more saline sites, while high abundances of a marine-derived species *Mugil cephalus* differentiated the

Munduran fresh sites (Figure 4.6). *N. erebi* was characteristic of the group of four freshwater sites, with increased densities of *Arius graeffei* the major factor separating the Frogmore February 2005 and Woolwash May 2005 samples from other samples at those sites. The position of Twelve Mile brackish sites towards the centre of the ordination indicates moderate levels of most species, in part a reflection of relatively high species richness at that site. It is notable that the largest vector in each direction represents a detritivore—*N. erebi*, *L. subviridis* or *M. cephalus*—a pattern seen more strongly in biomass (Chapter 5).

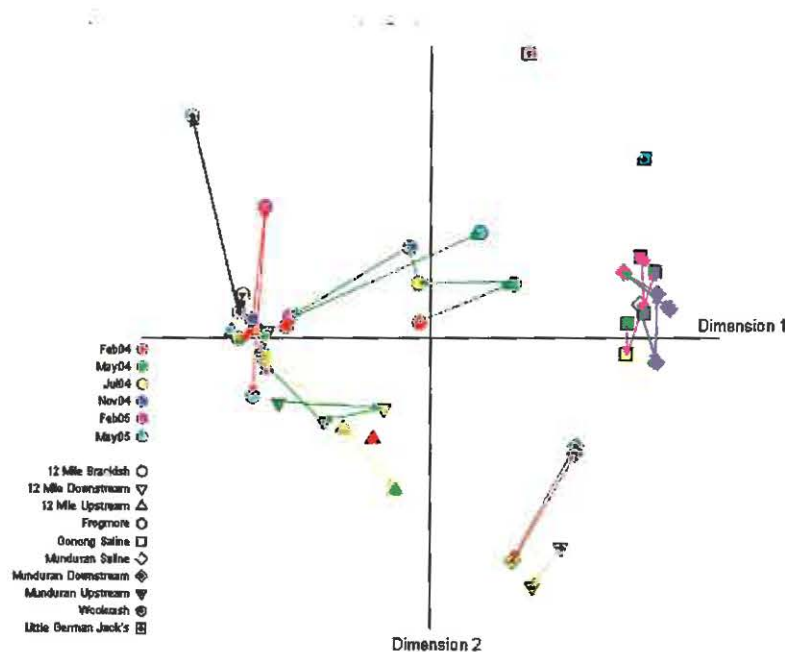


Figure 4.5. Comparison of density per net, from 12 mm mesh cast nets, for fish from Fitzroy estuarine wetland pools, with vectors indicating the pattern of temporal change at each site
nMDS ordination using Bray-Curtis dissimilarities on $\log(1+x)$ transformed data;
stress1 = 0.12539; symbols indicate sites, colours indicate sampling trips

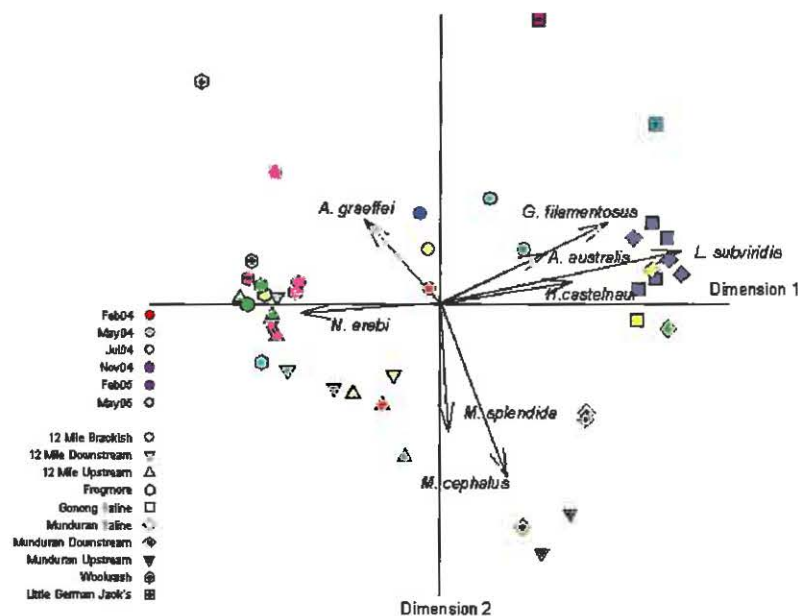


Figure 4.6. Comparison of density per net, from 12 mm mesh cast nets, for fish from Fitzroy estuarine wetland pools

nMDS ordination using Bray-Curtis dissimilarities on $\log(1+x)$ transformed data; stress1 = 0.12539; symbols indicate sites, colours indicate sampling trips; vector directions indicate the direction of greatest increase of density of the most important species; vector lengths indicate the levels of correlation with the space (highest *L. subviridis* $R^2 = 0.637$)

An nMDS ordination including only the Twelve Mile Creek sites (Figure 4.7) provides additional detail on faunal relationships at the individual system level. Communities of the two freshwater pools were usually quite similar and, except in February 2005, were distinct in structure from the community in the Brackish pool. The fauna of Twelve Mile Brackish was notable for high densities of a number of marine spawning species, particularly *L. calcarifer*, *L. subviridis*, *Elops hawaiiensis*, *G. filamentosus* and *S. multifasciata* (Figure 4.8). While the two fresh pools usually had low densities of marine spawners, they tended to have high densities of freshwater species such as *Melanotaenia splendida* and *N. erebi*.

When viewed in a temporal context, there is a tendency for the communities of all three sites to become more similar over time (Figure 4.9), converging along an axis in line with the major direction of increase of *N. erebi* (Figure 4.8). However, in May 2005 the fauna at Twelve Mile brackish rebounded (Figure 4.9) towards a more marine-dominated fauna (Figure 4.8).

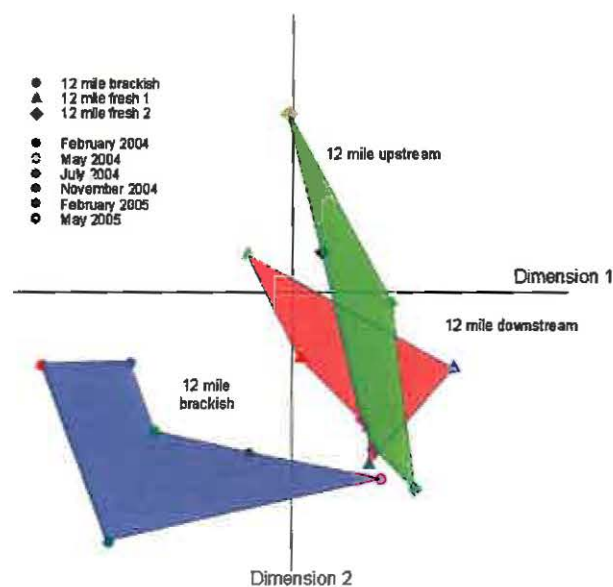


Figure 4.7. Comparison of density per net, from 12 mm mesh cast nets, for fish from Twelve Mile Creek pools, with convex hulls defining the area of ordination space occupied by points relating to each site

nMDS ordination using Bray-Curtis dissimilarities on $\log(1+x)$ transformed data;
stress1 = 0.09426; symbols indicate sites, colours indicate sampling trips

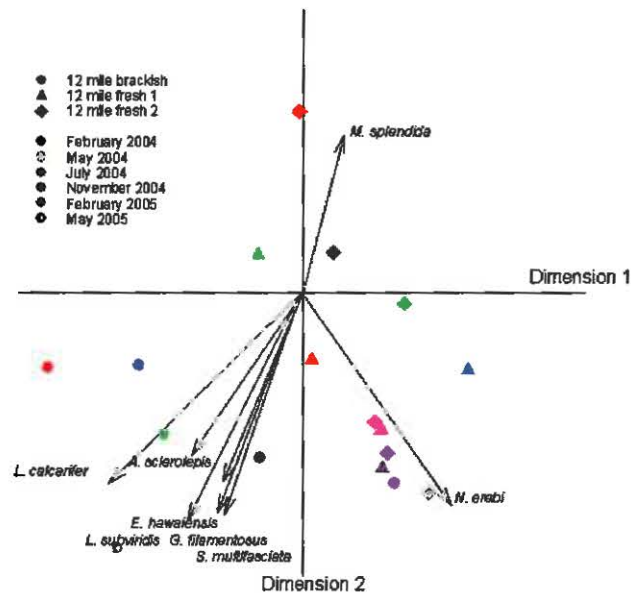


Figure 4.8. Comparison of density per net, from 12 mm mesh cast nets, for fish from Twelve Mile Creek pools, with vectors indicating the direction of greatest increase of density of the most important species

nMDS ordination using Bray-Curtis dissimilarities on $\log(1+x)$ transformed data;
stress1 = 0.09426; symbols indicate sites, colours indicate sampling trips; vector lengths indicate levels of correlation with the space (highest *L. calcarifer* $R^2 = 0.740$)

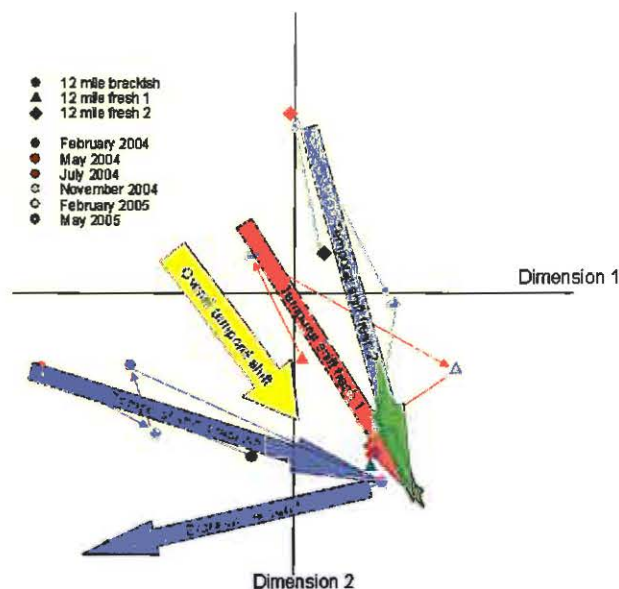


Figure 4.9. Comparison of density per net, from 12 mm mesh cast nets, for fish from Twelve Mile Creek pools, with vectors joining points indicating the pattern of temporal change at each site
 nMDS ordination using Bray-Curtis dissimilarities on $\log(1+x)$ transformed data; stress1 = 0.09426; symbols indicate sites, colours indicate sampling trips; large arrows indicate trends in temporal shift for each pool (blue, red and green) and the overall trend (yellow)

Categorisation of pools based on contributions of marine and freshwater spawners

The characters of fish faunas of the Fitzroy wetland pools are a function of their patterns of connectivity (see below), resulting in four broad faunal patterns defined by the contributions of marine versus freshwater spawning species (Figure 4.10, Table 4.3). One pool, Twelve Mile brackish (Figure 4.10a) featured a major contribution of marine spawners together with a substantial input of freshwater species. Four pools, the two Twelve Mile Freshwater pools (Figure 4.10b) and the two Munduran freshwater pools, had faunas dominated by freshwater species but with important contributions by marine species. The two large isolated lagoons, Frogmore and Woolwash (Figure 4.10c), had almost entirely freshwater faunas with only a minor contribution by marine spawners. The fauna of three pools Munduran saline (Figure 4.10d), Gonong saline and Little German Jack's, was entirely comprised of marine spawning fish.

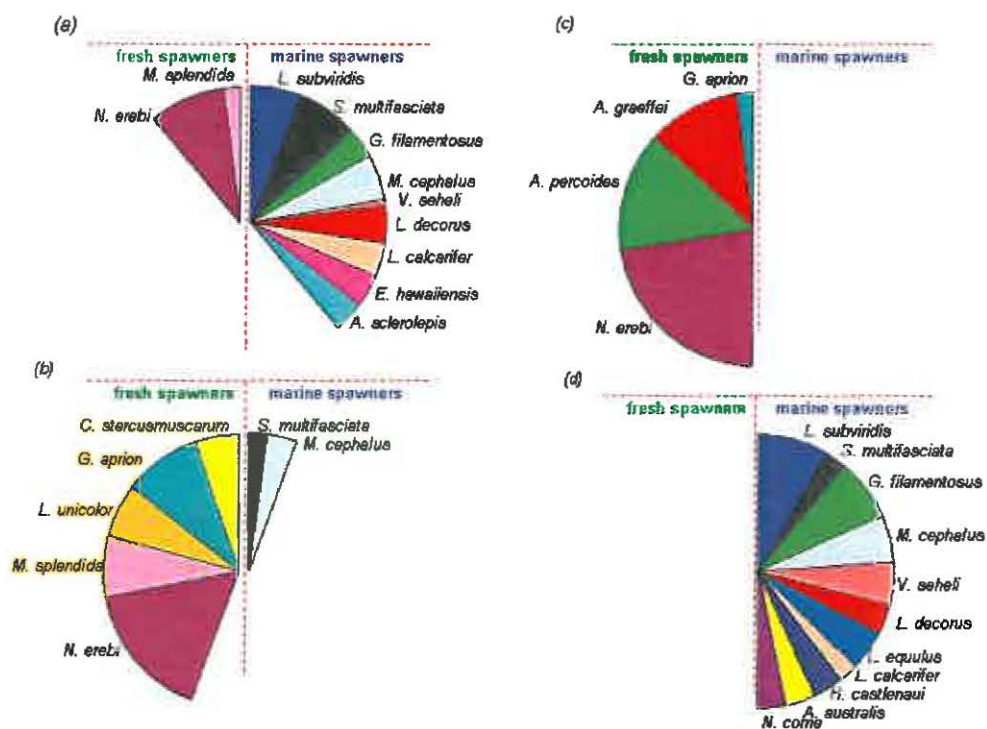


Figure 4.10. Percentage composition (log transformed density/cast net) by species for pools with different patterns of connectivity: (a) Twelve Mile brackish; (b) Twelve Mile downstream; (c) Woolwash; (d) Munduran saline

Table 4.3. Species with more than 10 individuals captured at any one site in large cast nets. Numbers in the body of the table are total numbers at a site over the study

	Marine Spawners													Freshwater Spawners									
	<i>L. subviridis</i>	<i>S. multifasciata</i>	<i>G. filamentosus</i>	<i>V. seihai</i>	<i>M. cephalus</i>	<i>L. decorus</i>	<i>L. equulus</i>	<i>E. hawaiiensis</i>	<i>L. calcarifer</i>	<i>A. sclerolepis</i>	<i>A. australis</i>	<i>H. castlanei</i>	<i>N. come</i>	<i>Ambia salis</i> spp.	<i>N. erebi</i>	<i>A. percoides</i>	<i>M. splendide</i>	<i>C. stercorarius/muscarum</i>	<i>A. graeffei</i>	<i>G. aprion</i>	<i>L. unicolor</i>	number of nets	
12 Mile brackish	18	26	1	2	3	2	3	2	17	1	1	1	1	1	1	1	1	1	1	1	1	400	
12 Mile Downstream		2			4									11	388		13	7		27	11	188	
12 Mile Upstream					5									14	305		57	30		3	12	130	
Frogmore					4				1	3				7	1630	81			28			613	
Woolwash Saline																						70	
Munduran Saline	21	11	2	1	1	1	1	1														237	
Munduran Saline	21	11	2	1	1	1	1	1														237	
Munduran Downstream	7		1		8									3			13	5				15	
Munduran Upstream					6												1	2				6	
Woolwash														6	95	71			28	2		158	
Total abundance	588	275	231	102	152	38	35	19	21	16	17	20	13	67	4040	152	88	44	57	32	24		

Both fresh and brackish sites dominated by either fresh or marine spawners. 12 mile brackish (with intermediate salinities and connectivity to both the marine environment and a substantial freshwater system) is the only brackish site to have freshwater spawners. Among the marine spawners only *M. cephalus* occurred widely in freshwater sites. The *Ambia* complex probably contained both marine and freshwater spawners.

The change in faunal composition in Twelve Mile brackish towards the compositions of the two Twelve Mile fresh pools and subsequent rebound (Figure 4.9) is clearly a reflection of temporal change in the percentage of marine spawners in Twelve Mile brackish (Figure 4.13).

Influence of pool connectivity on faunal composition and change

The three well connected pools in the Twelve Mile system (Figure 2.3) showed an upstream gradient in faunal composition (Figures 4.11 and 4.12, Table 4.3), reflecting decreasing importance of marine-spawning species and increasing importance of freshwater spawners. The fauna of Twelve Mile brackish (Figure 4.11) had a substantial marine component, emphasising its regular connection to the estuary. Marine spawners like *M. cephalus* and *S. multifasciata* were important in Twelve Mile brackish (*S. multifasciata* was probably in higher densities in February 2004 than those actually recorded, because non-quantitative cast netting among very shallow weed beds produced large catches of small individuals [>50 mm FL]).

While such species made increasingly lower contributions with distance upstream in the two freshwater pools, their presence at a low level indicates a degree of connection with the brackish pool. In contrast, the contribution of freshwater species like *M. splendida* and *L. unicolor* increased upstream. The faunas of the two Munduran Creek freshwater pools, that like the Twelve Mile freshwater pools are regularly connected to downstream marine environments, had similar faunal compositions to the Twelve Mile fresh pools. The freshwater-spawning *N. erebi* made an important contribution to the fauna of all three pools, including the brackish pool, underlining that there were high levels of connectivity in both upstream and downstream directions.

The proportional contribution of marine fish to catches in the three Twelve Mile Creek pools is shown in Figure 4.13.

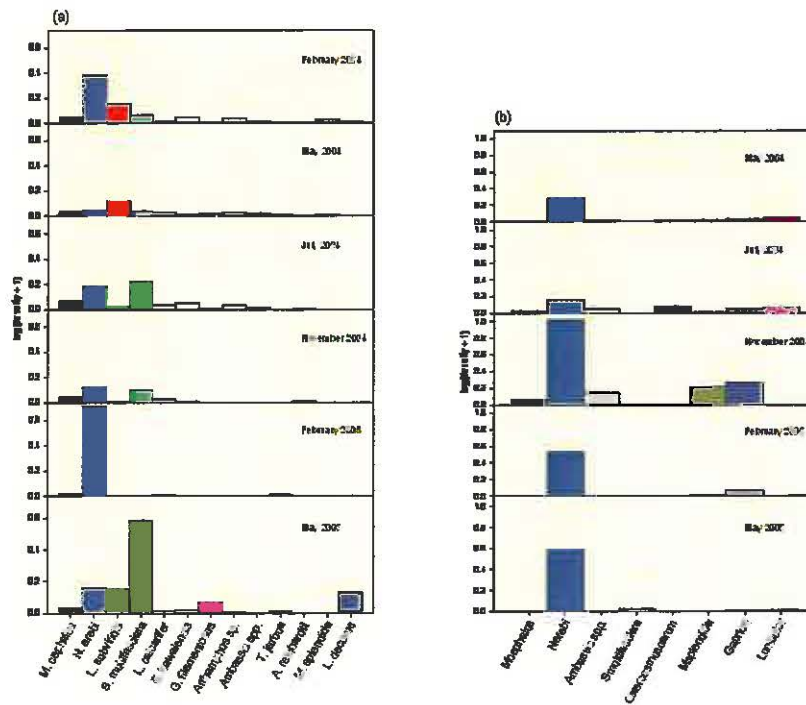


Figure 4.11. Profiles of $[\log(x+1)$ transformed] mean density of fish per net over time for 12 mm cast nets, for (a) Twelve Mile brackish and (b) Twelve Mile downstream; species occurring more than once are included

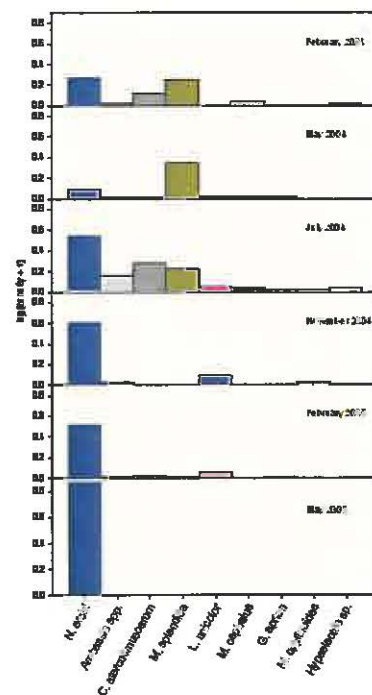


Figure 4.12. Profiles of mean density of fish per net over time for 12 mm cast nets, for Twelve Mile upstream; species occurring more than once are included

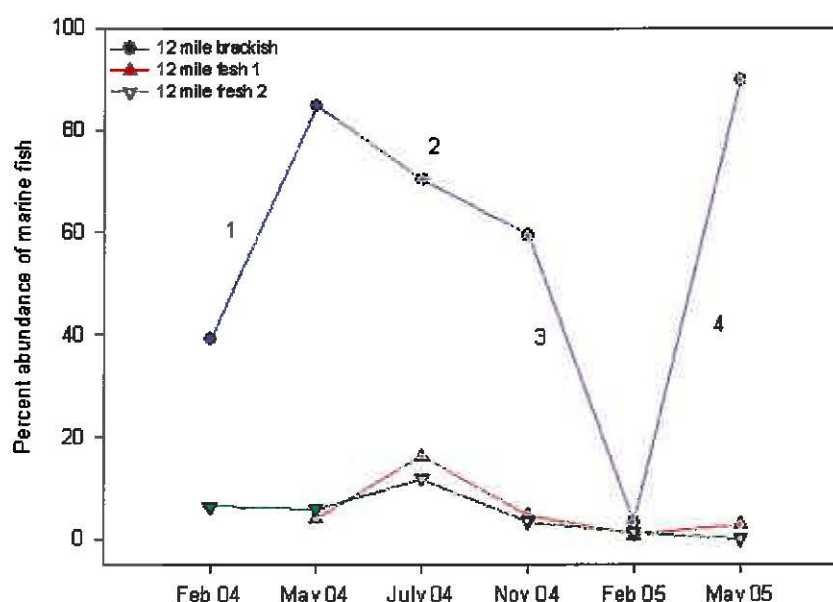


Figure 4.13. Proportional contribution of marine fish to catches in large cast nets for three Twelve Mile Creek pools

The fauna of the two isolated pools, Frogmore and Woolwash lagoons (Figure 2.2), were similar to those of the other freshwater pools, comprising mainly freshwater spawners (Figure 4.14, Table 4.3). However, unlike the other freshwater pools, the small contribution of marine spawners like *M. cephalus* was a reflection of connections a considerable time in the past, with the smallest fish present apparently entering during the last flood connection in early 2003 (Chapter 3). In contrast, Munduran (Figure 2.4) and Gonong (Figure 2.5) saline pools, which are highly connected to the marine environment, had completely marine-derived faunas (Figure 4.15).

Little German Jack's had a marine fauna (Figure 4.6) that appeared following connection but disappeared over time as the pool became inhospitable and dried out (Chapter 3). Frogmore and Woolwash lagoons demonstrated the same type of faunal change at a larger scale and over a longer time frame. Frogmore and Woolwash had similar faunal compositions until February 2005 (Figure 4.14), dominated by *N. erebi*.

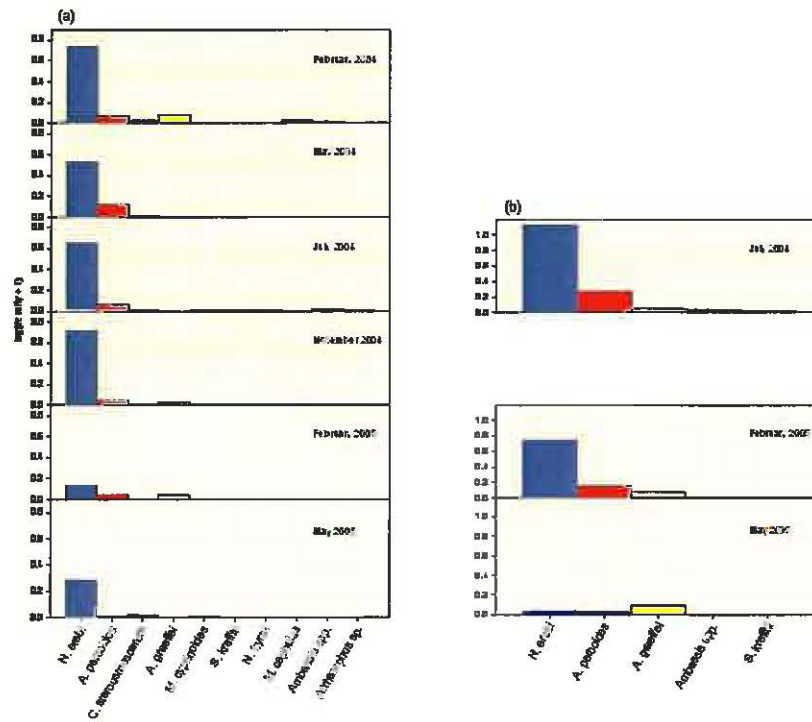


Figure 4.14. Profiles of [log(x+1) transformed] mean density of fish per net over time for 12 mm cast nets, for (a) Frogmore lagoon and (b) Woolwash lagoon; species occurring more than once are included

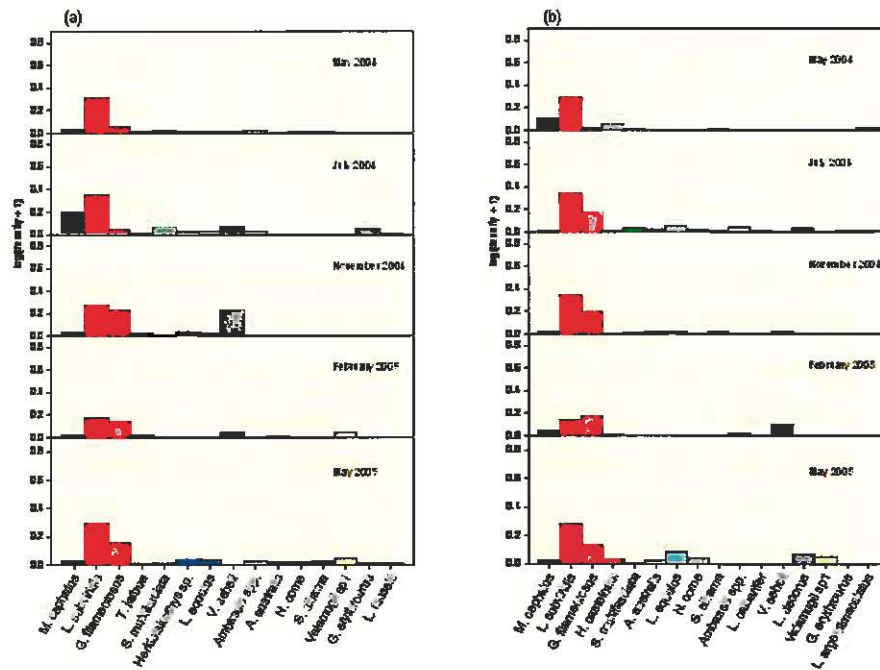


Figure 4.15. Profiles of [log(x+1) transformed] mean density of fish per net over time for 12 mm cast nets, for (a) Gonong saline and (b) Munduran saline; species occurring more than once are included

In May 2005, however, Woolwash had become very shallow (Chapter 3) and its fauna had diverged from that of Frogmore to be dominated by the ariid catfish, *A. graeffei*. By September 2005 the water level in Frogmore was below that of Woolwash in May 2005 and, despite 50 castnet samples, only 6 fish (4 *N. erebi*, 1 *A. graeffei*, 1 *Craterocephalus stercusmuscarum*) were captured. At this time Woolwash was too shallow and its banks too muddy to permit sampling, but dead *N. erebi* (1), *A. graeffei* (31) and *L. calcarifer* (11) were collected from its banks. A series of fish kills had been reported at Woolwash during August and September 2005.

Discussion

Patterns of diversity

Despite consisting of 10 pools of a variety of types including some highly connected with the estuary, the total species richness of fish from the Fitzroy floodplain wetland pools was low, with only 46 species recorded from all the pools over the entire study. This is surprising because tropical and subtropical estuarine faunas in the same biogeographic region typically have high species richnesses (91–128 species) compared to those in other parts of the world (Robertson & Blaber 1992). This low richness was also reported in a previous study of wetland pools in the Fitzroy region (Infofish 2005), and is consistent with the low species richness reported for the Fitzroy River (Johnston *et al.* in preparation).

The overall low species richness of Fitzroy floodplain wetland pools was reflected at the individual pool level, with a maximum total richness of 25 species at Munduran saline, and a maximum for any one sampling trip of 17 at Gonong saline. Species richness was apparently correlated with rank pool surface area or volume, as would be expected given our understanding of species–area relationships (McArthur & Wilson 1967, He & Legendre 1996). However, this may be misleading (Chittaro 2002) because species richness had an even stronger correlation with total number of net samples taken.

Community composition and the influence of connectivity

Different pools had distinctly different faunas. At the broadest level these differences in composition were a function of the proportion of the community comprised of marine-spawned species compared to freshwater-spawned species.

Regular connections to the marine environment allowed free access of marine fish to Gonong and Munduran saline pools, resulting in faunal composition similar to that in the main estuary. In contrast, both large and small freshwater pools, that lacked direct connection to the marine environment, had less diverse faunas, reflecting the limited diversity of Australian freshwater fish (Allen *et al.* 2002) compared to estuarine species (Robertson & Blaber 1992).

Although of relatively small size and isolated from the estuary during most of the study, direct connectivity to both the estuary and freshwater resulted in a relatively high species richness at the Twelve Mile brackish pool.

The distinctly different natures of the fish fauna of different pools was a reflection of the extent of connectivity to freshwater and marine systems. This connectivity determined both the physical nature of pools (principally the salinity regime) (Chapter 3) and the sources of faunal supply: pools with more direct connections to the marine environment had extensive marine components, while pools without direct connections to the marine environment were dominated by freshwater fish. Many of these pool faunas were stable over time, and when change did occur it again reflected patterns of connectivity.

Connectivity and patterns of faunal change

Major patterns of temporal change in fish diversity, community composition and abundance were the product of the extent and nature of connectivity. As well as influencing the supply of new fish to the pools, connectivity interacted with weather patterns to determine the trajectory of in-pool conditions over time. These two forces, the supply of fish and changes in pool conditions, combined to produce quite different faunal outcomes in different pool types: saline and freshwater pools that were components of stream systems and maintained stable fish faunas over time, whereas isolated pools showed extensive faunal change.

Free access of marine fish to Gonong and Munduran saline pools resulted in stable faunal compositions. In contrast, the four study pools that were not components of stream systems nor regularly connected to the marine

environment either dried out completely or became extremely shallow. Irregular connection to the marine environment and little freshwater inflow led the two German Jack's pools to dry out during the study. As water levels fell evaporation produced hypersaline conditions (Chapter 3) and by the time the pools dried completely all fish had died and been consumed by predators such as piscivorous birds. Frogmore and Woolwash lagoons were much larger in area and deeper than the German Jack's pools leading to a slower decrease in water levels. Moreover, as these were freshwater pools, there was no substantial increase in salinity and adverse conditions were slow to develop.

However, by May 2005 (Woolwash) and September 2005 (Frogmore) water levels had become very low, with little water over 1 m in depth (Chapter 3), and large flocks of predatory birds had moved in (Chapter 12). The decline in depth seems to have greatly advantaged these avian predators, leading to a change in dominance of the fish fauna of Woolwash by *N. erebi* through most of the study to dominance by the much larger—and apparently more difficult to catch and consume—*A. graeffei* in May 2005. Frogmore retained deeper water for longer than Woolwash did, but by September 2005 water levels had declined greatly and fish had reduced to very low densities. By this time Woolwash was almost dry and experienced a series of 'kills' of its remaining fish, which were principally larger species such as *A. graeffei* and *L. calcarifer*.

The four isolated pools moved to faunal decline at different rates. The extent to which a pool approaches its end point (i.e. ecosystem collapse), the time taken to reach the end point, and the number and size of pools reaching that point, are principally a function of climatic patterns (Figure 4.16).

This study was conducted during a drought, when a lack of major flooding prevented any substantial biological connections with other systems, and prevented pool water levels being recharged. There are a number of consequences. Firstly, the decline in water levels, and subsequent ecosystem collapses in even large pools like Frogmore and Woolwash lagoons suggests that the faunas of even the largest floodplain pools may not be immune to the effects of drought. Secondly, ecosystem services normally supplied by the pools to other ecosystems are disrupted or lost (Rosenberg & McLeod 2005).

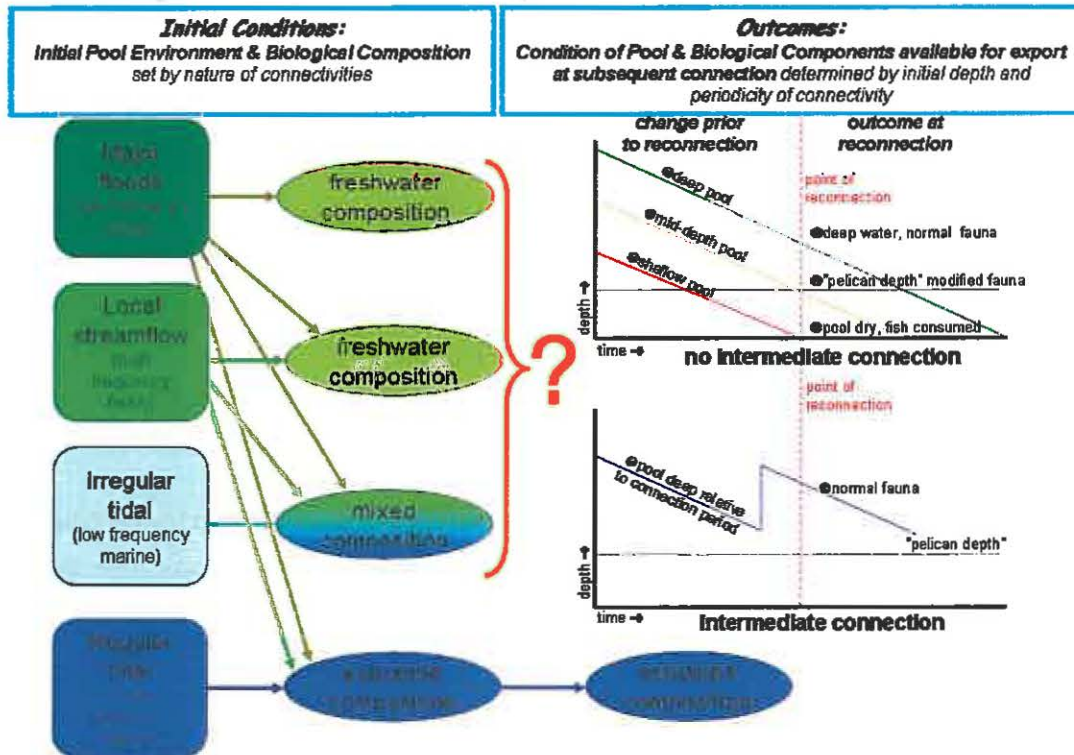


Figure 4.16. Influence of connectivity on estuarine floodplain wetland pools

After a pool's fauna is reset to initial levels during connection events, its plants and animals grow and are involved in complex ecological interactions. The outcomes of this are such things as: the growth of juveniles to adult stages, ready for export to other environments (e.g. estuary fish populations); large numbers of young individuals that can move during connections to replenish other pools; and the sequestration of nutrients and energy from the pool environs and their storage as plant and animal biomass, that can be exported to other ecosystems (e.g. estuaries or further offshore to reefs). When a pool dries out and its aquatic fauna is consumed by predators from outside the pool, all these ecosystem services are lost or, in the case of nutrients and energy, redirected to quite different ecosystems.

Thirdly, there are beneficiaries of ecosystem collapse. As pools dry, flocks of piscivorous birds move sequentially from pool to pool (Chapter 12) as shallowing water apparently makes the capture of fish easier. This both connects pools independently of aquatic connections, and supports waterbird populations (Roshier *et al.* 2002). The support of waterbird populations is likely to be extensive because the sequential shallowing of pools allows them to access a much greater proportion of the fish in each pool than would be possible if deep water was maintained. It seems likely that this results in larger waterbird populations than would otherwise be possible.

Even under drought conditions, the diverse nature of connectivities means that there are a diversity of faunal outcomes. Unlike the isolated pools the three pools at Twelve Mile Creek are part of a stream system. These pools are small but even without major floods moving down the Fitzroy River, local rainfall repeatedly replenished water levels in the Twelve Mile freshwater pools, maintaining faunal composition throughout the study. The Twelve Mile brackish pool was the only available example of a low salinity brackish pool on the Fitzroy floodplain (similar pools that were accessible had bund walls preventing ingress of marine water), but probably reflects the situation for a large number of saltpan pools prior to extensive agricultural development.

Although usually dominated by marine-spawning fish, limited connections with the marine environment meant there was considerable change over time. Both low salinities and a strong freshwater fish component were maintained throughout most of the study by downstream flow due to local rainfall. In contrast, marine connectivity was unpredictable. This was due to tidal anomalies, and the large distance the tide needed to span to reach the pool, coupled with hydraulic friction imparted by the saltpan surface (Chapter 3). However, when extensive marine connection occurred, the faunal composition quickly moved back to domination by marine species. Despite the resilience of the Twelve Mile brackish pool, its extensive faunal variability shows that there is no guarantee that connectivities will always occur frequently enough or predictably enough in this type of pool to maintain a diverse fauna. Additionally, the more extreme case of the German Jack's pools indicates that only small changes in connectivity could lead to such pools becoming inhospitable to fauna or even drying out.

Obviously, the details of these models would be different during non-drought times, and the present study can do little to make firm predictions of the structure or outcomes of such models. However, the climate of the Fitzroy region is unpredictable, and below average rainfall is common (BOM 2005). An irregular and unpredictable climate means that maintaining a diversity of pools types and sizes is crucial in supporting healthy and extensive bird populations, ensuring there are refuge areas from which the diversity of pool faunas can be re-supplied, and maintaining a continuity of delivery of ecosystem services from floodplain wetland pools to other ecosystems. The pivotal role of connectivities in the structure and functioning of floodplain wetland pools (and floodplain wetlands in general) means that it is not enough to preserve the pools themselves it is just as critical to preserve healthy connectivities between them.

Conclusion

Fitzroy estuarine floodplain wetland pools provide a diverse range of environments, harbouring diverse assemblages of fish. Patterns of connectivity between pools, between pools and other freshwater environments, and between pools and the estuary, determine both the natures of the pools and the natures of their faunas. These connectivities are determined by patterns of freshwater flow and marine connection, both of which are influenced by climatic factors: freshwater flow by local rainfall and major flooding, marine connections by the tidal patterns modified by tidal anomalies and the moisture conditions of connecting channels or saltpans.

Because these connectivities are greatly affected by small changes in rainfall and/or tidal height it is clear that they will be profoundly impacted by climate change. The impacts on connectivity of small changes in tidal level (cm) due to natural anomalies underscores that global warming–induced sea-level change will impact substantially on both connectivity and pool salinity regimes. Similarly, it is clear that more extreme weather patterns will lead to more infrequent and unpredictable connectivities, resulting in a greater number and variety of pools moving to the point of ecosystem collapse.

Chapter 5 Size structures and biomasses of fish from Fitzroy wetland pools

Marcus Sheaves and Ross Johnston

Introduction

Comparisons of compositions of fish fauna and the density of their component species provide information on diversity and overall faunal differences, and the ecological relationships between wetland pools and other ecosystems (i.e. the biological connectivity). However, much more information is available in size structures and biomasses. For instance, differences in size structure provides information on differences in patterns of reproduction between sites or recruitment to sites, while understanding patterns of biomass gives much more information on the importance of species and the functional importance of species in food chains.

This component of the study investigates patterns of size structure and biomass to add detail and depth to the understanding of similarities and differences in the fish faunas of Fitzroy floodplain wetland pools, and consequently enhances the understanding of biological connectivity.

Methods

Study sites and sampling methods have been detailed in previous chapters. Most fish captured were released unharmed, except for a small number of fish retained for laboratory studies (Table 5.1). The fish that were retained (Ethical approval number: A852_03) were euthanised in an ice-water slurry, where they were kept until they could be returned to the laboratory for dissection. To keep the number of fish retained as low as possible, the same fish were used to supply samples for stable isotope, condition and gut content studies, and to supply accurate length–weight relationships. Measuring all fish that were released would have meant fewer samples could be collected and would have prevented rapid release, thereby compromising the chances of survival of fish from large catches. Instead, released fish were categorised by eye into 10 mm size classes (fork length), using experienced observers. This categorisation was checked by taking accurate measurements whenever a small enough sample was collected to allow measurement without endangering the health of the fish.

Table 5.1. List of species and numbers of individuals retained for laboratory analyses

Species	Number retained	Species	Number retained
<i>Acanthopagrus australis</i>	7	<i>Leiognathus equulus</i>	7
<i>Ambassis interruptus</i>	7	<i>Leiopotherapon unicolor</i>	9
<i>Ambassis telkara</i>	2	<i>Liza subviridis</i>	164
<i>Amniataba percoides</i>	28	<i>Lutjanus argentimaculatus</i>	2
<i>Anguilla reinhardtii</i>	2	<i>Megalops cyprinoides</i>	11
<i>Arius graeffei</i>	37	<i>Melanotaenia splendida</i>	16
<i>Arramphus sclerolepis</i>	11	<i>Mugil cephalus</i>	118
<i>Chanos chanos</i>	9	<i>Nematalosa erebi</i>	324
<i>Craterocephalus stercusmuscarum</i>	3	<i>Neosilurus hyrtlii</i>	4
<i>Elops hawaiiensis</i>	58	<i>Pseudomugil signifer</i>	3
<i>Gerres erythrouros</i>	10	<i>Rhinomugil nasutus</i>	2
<i>Gerres filamentosus</i>	22	<i>Selenotoca multifasciata</i>	65
<i>Glossamia aprion</i>	15	<i>Siganis lineatus</i>	1
<i>Herklotsichthys castelnaui</i>	5	<i>Sillago sihama</i>	5
<i>Hypsyleotris</i> spp.	7	<i>Strongylura krefftii</i>	12
<i>Lates calcarifer</i>	47	<i>Terapon jarbua</i>	4
<i>Leiognathus decorus</i>	2	<i>Valamugil seheli</i>	6

Size

Numbers per size class were used to calculate mean fork length (\pm SE) for each pool for species with 10 or more individuals captured in that pool throughout the study. Size data for each species were grouped into 50 mm size classes to allow comparisons of changes in size structure over time at each site. Data are only presented for pools where sufficient numbers were available to provide precise estimates of size parameters.

Biomass

Length–weight relationships did not vary over space and time for any species. Consequently, data for sites and trips were pooled to produce an overall length–weight relationship for each species. These relationships were used to convert abundances per 10 mm size class to estimates of biomass per 18 mm castnet sample. The biomass estimates are biased in respect to smaller individuals that are not well represented in the 18 mm castnet samples. However, samples using the 6 mm cast net suggested that smaller fish were not in high densities at any

site so probably would not contribute greatly to biomass. Overall biomasses for trophic groups included all species. Percentage contribution to trophic groups was calculated for all species with average biomass >5 g at any site on any trip (Table 5.2). Standard error bars for biomass estimates were usually extremely small so have not been added to figures displaying percentage contribution by species.

Table 5.2. Maximum biomass per net over the study for species with a maximum biomass >5 g/net at any site at any time

Trophic group	Species	Maximum mean biomass/net(g)
Benthivore	<i>Gerres filamentosus</i>	27.6
Detritivore	<i>Mugil cephalus</i>	951.1
	<i>Nematalosa erebi</i>	463.2
	<i>Liza subviridis</i>	365.3
	<i>Valamugil seheli</i>	108.0
	<i>Carassius auratus</i>	17.1
	<i>Chanos chanos</i>	5.7
Herbivore	<i>Selenotoca multifasciata</i>	47.8
Predator	<i>Megalops cyprinoides</i>	95.7
	<i>Lates calcarifer</i>	37.8
	<i>Elops hawaiiensis</i>	29.6
	<i>Glossamia aprion</i>	14.1
	<i>Strongylura krefftii</i>	12.5
	<i>Lutjanus argentimaculatus</i>	12.5
Epibenthivore	<i>Melanotaenia splendida</i>	25.6
Omnivore	<i>Arius graeffei</i>	246.9
	<i>Acanthopagrus australis</i>	53.7
	<i>Acanthopagrus berda</i>	44.5
	<i>Neosilurus hyrtlui</i>	23.4
	<i>Bidyanus bidyanus</i>	10.4
	<i>Anguilla reinhardtii</i>	8.9
	<i>Amniataba percoides</i>	7.8
	<i>Leioptherapon unicolor</i>	5.8

Trophic groups

Trophic groups are defined as follows (see Chapter 7 for validation):

Benthivores: feed on sedentary benthic prey [mainly infaunal invertebrates]

Epibenthivores: feed on mobile prey living on or near the bottom [mainly epifaunal invertebrates]

Predators: feed on large mobile prey [fish and mobile macro-invertebrates]

Herbivores: feed principally on living plant material

Detritivores: feed principally on decomposing organic material

Omnivores: consume prey from a broad range of trophic groups

Micro-omnivores: consume small prey from a broad range of trophic groups

Planktivores: feed principally on micro-invertebrates in the water column.

Non-metric multidimensional scaling (MDS) was used to investigate relationships between pools based on both biomass by trophic group and biomass by species. Data were transformed [$\log(1+x)$] before analysis and analysed using Bray-Curtis dissimilarities. Preceding analysis, the original data matrix for species was reduced to include only species with average biomass >5g at any site on any trip, to remove any undue effects of rare species on the analysis (Gauch, 1982).

Results

Size

Twelve Mile Creek

The diverse assemblage at Twelve Mile brackish was dominated by small species (Figure 5.1a) particularly the freshwater spawning detritivore, *Nematolosa erebi*, and the marine spawning herbivore, *Selenotoca multifasciata*, but included larger marine spawners, principally the detritivore, *Mugil cephalus*, and the carnivores, *Lates calcarifer* and *Elops hawaiiensis*. In contrast, the assemblages of the two Twelve Mile freshwater pools were comprised almost entirely of small freshwater species, principally *N. erebi* (Figure 5.1b,c), with the only marine spawners being low numbers of small *S. multifasciata* and *Megalops cyprinoides* in the downstream pool and *M. cyprinoides* in the upstream pool (Table 4.2).

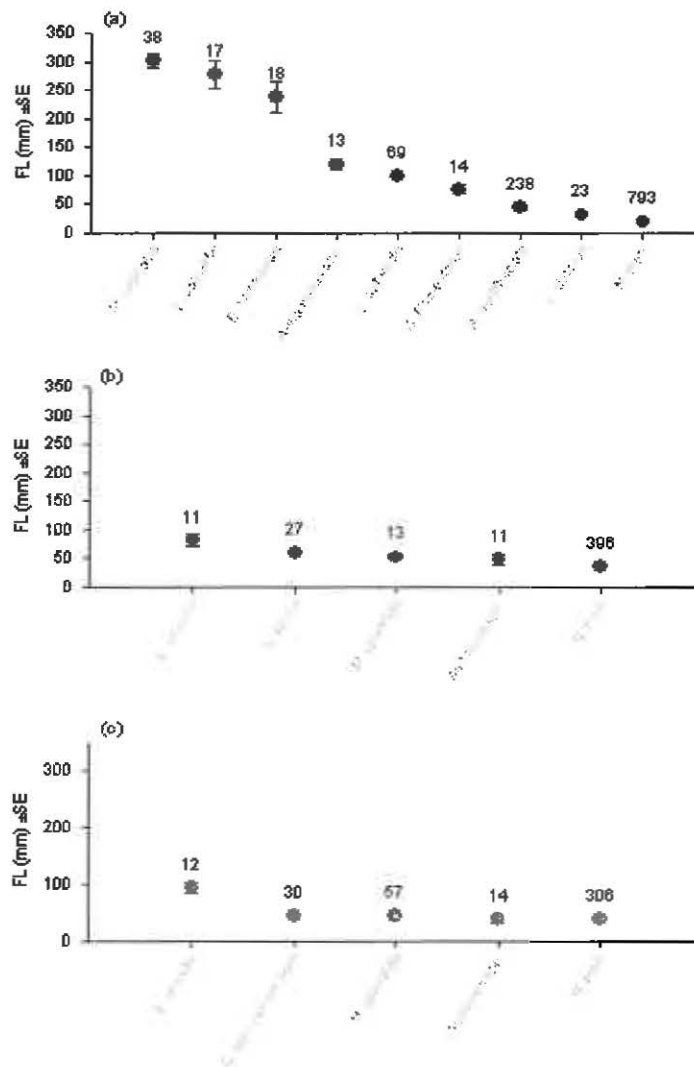


Figure 5.1. Mean fork lengths of fish with abundances of 10 or greater for (a) Twelve Mile brackish, (b) Twelve Mile downstream and (c) Twelve Mile upstream; numbers indicate sample sizes

The change in size structure of *S. multifasciata* over time in Twelve Mile brackish documents the pool's history of biological connection to the estuary (Figure 5.2), and links closely with the understanding of physical connectivity (Chapter 3). The size structure was heavily skewed towards smaller sizes, indicating connection event(s) prior to the beginning of the study; probably during flooding in early 2004 (Chapter 3). The lack of any marine connection during the majority of 2004 (Chapter 3), is reflected in a lack of small *S. multifasciata* and a progressive shift towards dominance by the larger size classes. Even though there were marine connections at the end of 2004, small *S. multifasciata* did not appear until the May 2005 sampling trip when large numbers of small individuals were again present.

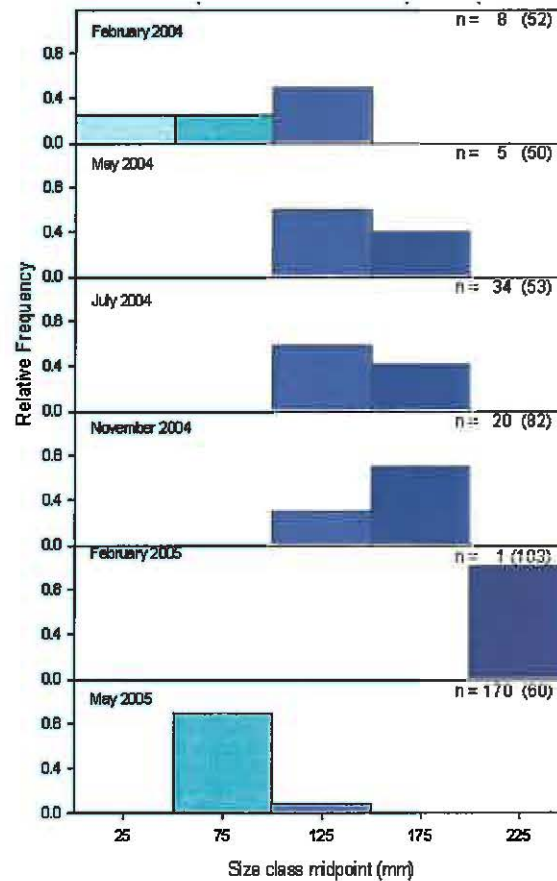


Figure 5.2. Size structure of *S. multifasciata* over time in the Twelve Mile brackish pool; numbers indicate sample sizes (number of nets)

The changes in size structure of *N. erebi* in the Twelve Mile system documents the pools' histories of interpool biological connectivity. While densities of *N. erebi* in Twelve Mile brackish fell through 2004 (Figure 4.11a), the size structure shifted progressively towards larger size classes (Figure 5.3a). In contrast, densities in Twelve Mile upstream increased through 2004 (Figure 4.12) with little change in size structure (Figure 5.3b), a pattern repeated in Twelve Mile downstream (Figures 4.11b, 5.4).

Mature females were present in all three locations in February and May 2005, indicating the potential for reproduction in all three pools. The continued presence of small *N. erebi* in the two freshwater pools indicates reproduction occurred throughout the early part of 2004 (Figure 5.4). In contrast, the lack of the smallest size classes in Twelve Mile brackish in May and July 2004 suggests that reproduction was not successful there. Small individuals (Figure 5.3a) were present in Twelve Mile brackish in high densities (Figure 4.11) in February and May 2005, suggesting that either spawning was initiated by very low salinities following flooding in late 2004 and early 2005 (Figure 3.13) or that large numbers of juveniles entered the pool from upstream during the flooding.

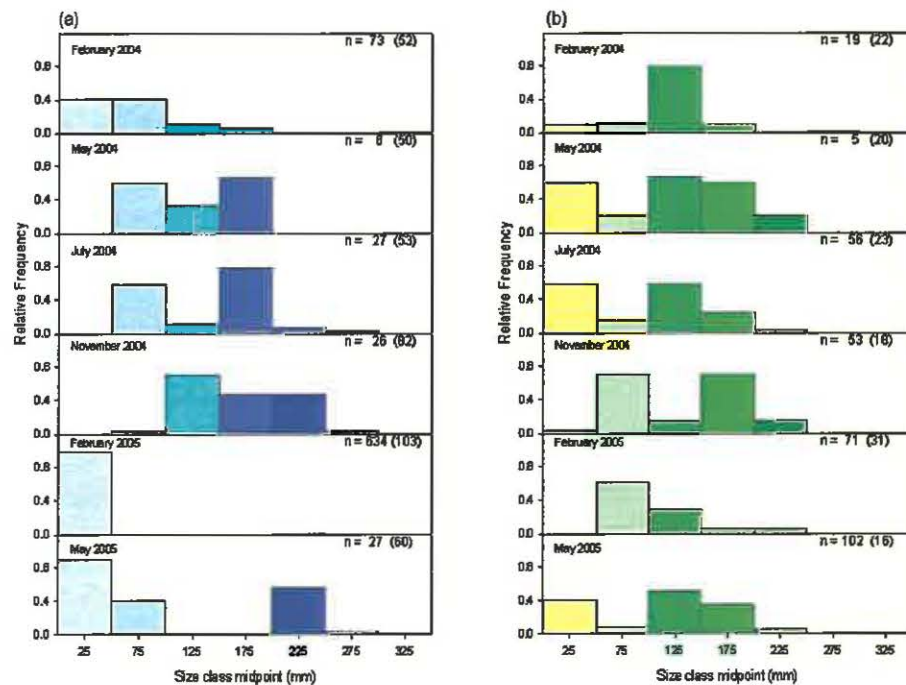


Figure 5.3. Size structures of *Nematalosa erebi* over time in (a) Twelve Mile brackish and (b) Twelve Mile upstream; numbers indicate sample sizes (number of nets)

Figure 5.4: Size structures of *N. erebi* over time in (a) 12 Mile Downstream, and (b) 12 Mile Upstream. Numbers indicate sample sizes (number of nets).

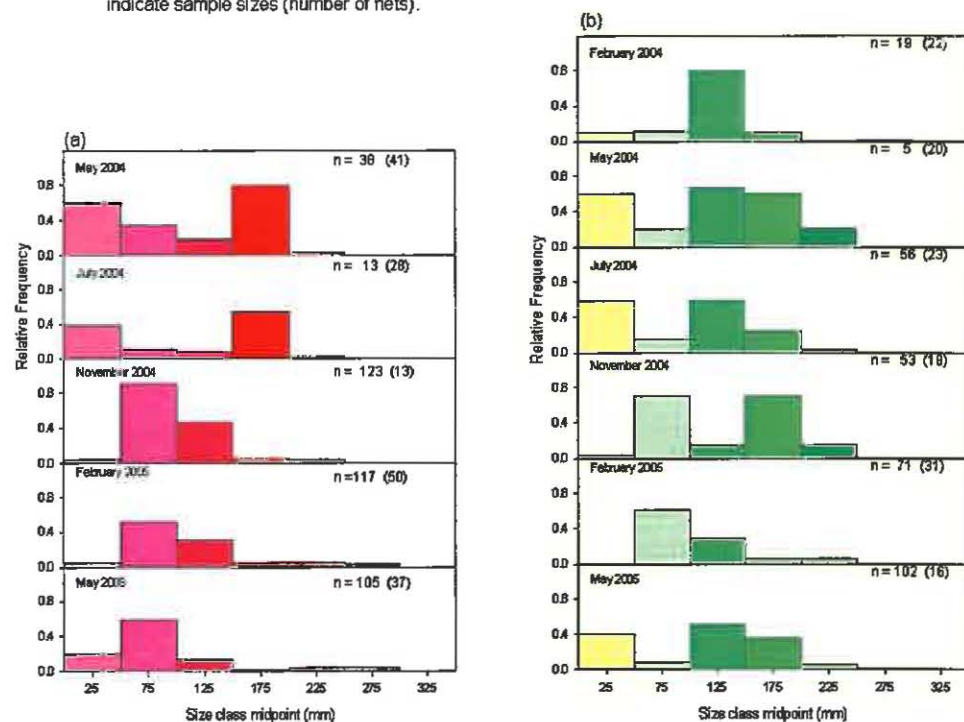


Figure 5.4. Size structures of *Nematalosa erebi* over time in (a) Twelve Mile downstream and (b) Twelve Mile upstream; numbers indicate sample sizes (number of nets)

Pools with regular estuarine connections

In contrast to the Twelve Mile brackish pool, but similar to the two Twelve Mile freshwater pools, few large fish were captured from Gonong and Munduran saline, the two pools with regular connections to the estuary (Figure 5.5). As in Twelve Mile brackish the detritivore, *M. cephalus*, was the largest species in the saline sites, but with a much smaller mean size (Munduran: 166 mm, Gonong 163 mm, Twelve Mile brackish 315 mm) (Table 5.3, Figure 5.6a). This difference probably reflects more infrequent exchange of individuals at the two saline sites compared to a lower frequency of replenishment of small marine spawned individuals at Twelve Mile brackish and growth of those already in the pool into larger size classes.

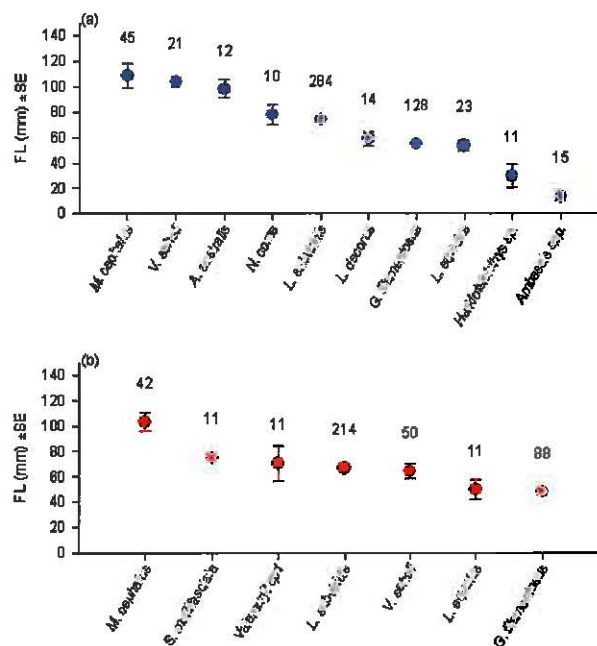
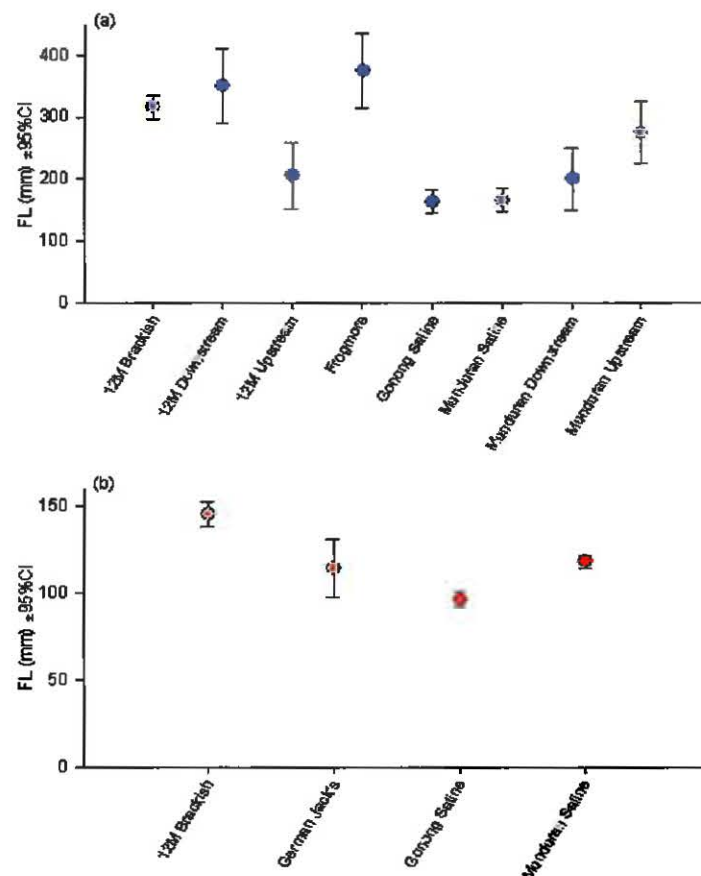


Figure 5.5. Mean fork lengths of fish with abundances of 10 or greater for (a) Munduran saline and (b) Gonong saline; numbers indicate sample sizes

The same situation exists for a second detritivore, *L. subviridis* (mean sizes: Munduran: 118 mm, Gonong 96 mm, Twelve Mile brackish 145 mm) (Table 5.3, Figure 5.6b). In fact, *M. cephalus* were smaller in Gonong and Munduran saline pools than in any of the less regularly connected pools except for Munduran downstream and Twelve Mile upstream (Table 5.3). Although the means were higher for the two saline pools, few *M. cephalus* were captured at either site (Table 4.3), leading to high variances and so little likelihood of detecting a difference if one existed. Catches at the other freshwater sites were also low but the large size of fish meant that clear differences were detected.

Table 5.3. One-way analyses of variance (ANOVA) and planned comparisons for the mean fork length of *Mugil cephalus* and *Liza subviridis* among Fitzroy wetland pools

	Comparison	F	df	p
<i>Mugil cephalus</i>	ANOVA	30.13	7/142	0
Planned comparison	Twelve Mile brackish vs. Munduran saline	121.59	1/142	0
Planned comparison	Twelve Mile brackish vs. Gonong saline	122.54	1/142	0
Planned comparison	Munduran/Gonong saline vs. Munduran downstream	1.85	1/142	0.1756
Planned comparison	Munduran/Gonong saline vs. Munduran upstream	18.02	1/142	0
Planned comparison	Munduran/Gonong saline vs. Frogmore lagoon	44.59	1/142	0
Planned comparison	Munduran/Gonong saline vs. Twelve Mile downstream	34.63	1/142	0
Planned comparison	Munduran/Gonong saline vs. Twelve Mile upstream	2.03	1/142	0.1562
<i>Liza subviridis</i>	ANOVA	48.21	3/577	0
Planned comparison	Twelve Mile brackish vs. Munduran saline	43.18	1/577	0
Planned comparison	Twelve Mile brackish vs. Gonong saline	130.59	1/577	0
Planned comparison	Munduran/Gonong saline vs. German Jack's	0.73	1/577	0.3933

**Figure 5.6. Comparison of mean fork length for (a) *Mugil cephalus* and (b) *Liza subviridis* from Fitzroy wetlands pools, for analyses in Table 5.3**

Isolated freshwater pools

Few species were captured in high densities in Frogmore or Woolwash lagoons (Table 4.2). Sizes of the abundant species were similar at the two sites with the size structure (Figure 5.7) dominated by the ariid catfish, *Arius graeffei*, a generalist omnivore.

The size structure of *N. erebi* in Frogmore lagoon over time (Figure 5.8a) was again quite different to that in Twelve Mile brackish (Figure 5.8b), with small individuals present throughout the year. This is a similar situation to that in the two Twelve Mile freshwater pools (Figure 5.4a,b), suggesting that reproduction continued for most of the year in these freshwater sites, but not in Twelve Mile brackish.

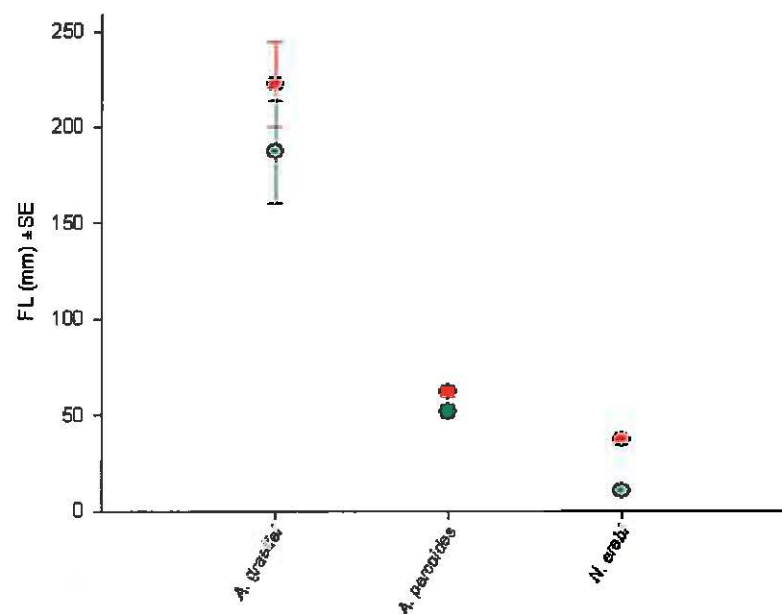


Figure 5.7. Mean fork lengths of fish with abundances >10 from Frogmore (red symbols) and Woolwash (green symbols) lagoons

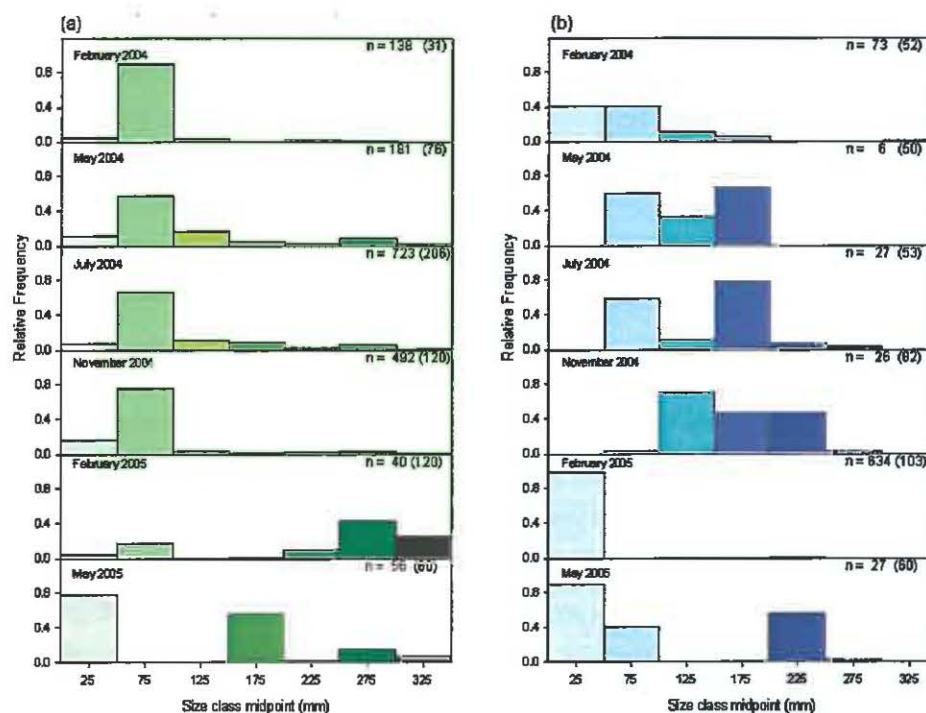


Figure 5.8. Size structures of *Nematalosa erebi* over time in (a) Frogmore lagoon and (b) Twelve Mile brackish; numbers indicate sample sizes (number of nets)

Biomass

With one major exception, biomass in all pools was always dominated by detritivores (Figures 5.9a-5.17a), and in all cases by only one or two species of detritivores (Figures 5.9b-5.17b) (the situation was the same in Munduran upstream but no figure is presented because one species, *M. cephalus*, comprised 99% of biomass). In fresh pools this was invariably *N. erebi*, in saline pools *M. cephalus* and *L. subviridis*, and in Twelve Mile brackish *N. erebi*, *M. cephalus* and *L. subviridis*. The only major exception to this pattern was at Woolwash lagoon (Figure 5.17). In July 2004, as in all the other freshwater sites, biomass was greatly dominated by *N. erebi*. In February 2005 the situation had changed, with the large omnivore, *A. graeffei*, co-dominant with *N. erebi*. By May 2005 *A. graeffei* dominated completely.

Besides the exceptional case of Woolwash lagoon, there were few cases where there was any substantial contribution to fish biomass by any species outside the three major detritivores. Only at Twelve Mile brackish (Figure 5.9) were other trophic groups well represented, with the herbivore *S. multifasciata*, and the carnivores *L. calcarifer* and *E. hawaiiensis* prominent on a number of occasions.

The initial ordination of trophic group biomass (Figure 5.18) featured a compact, centrally located group of sites, and three outliers very dissimilar to the other

sites. One of these was Woolwash in May 2005, the other two were the two Little German Jack's samples. The Woolwash sample was extreme because of the marked temporal change in trophic composition there (Figure 5.17), while the Little German Jack's samples had extremely low biomasses (Figure 5.15). By causing the majority of sites to cluster close to the centre of the ordination, the presence of these outliers made it difficult to investigate relationships at the other sites. Consequently, the ordination was run again with these three samples omitted.

The resulting ordination (Figure 5.19) shows that the points for each site form fairly compact units. There is a complex grouping of freshwater sites, differing mainly in their biomasses of detritivores, omnivores and predators. The two saline sites form a distinct group, segregated from the freshwater sites by the presence of relatively high biomasses of benthivores. The Twelve Mile brackish pool is distinct from all other sites, with a consistently high biomass of predators. The distinctness of the groups demonstrates the consistency of compositions in each pool over time, and the order of points around the polygons indicates a lack of any consistent patterns of temporal change within the pools.

When broken down to the species level the biomass data show even more distinct patterns (Figure 5.20). Even though the May 2005 Woolwash sample and the two Little German Jack's samples are still outliers, distinct, logical, compact groups of sites are evident. The saline sites group closely with high biomasses of the detritivore *L. subviridis*, and the benthivore *G. filamentosus*, as do the two Twelve Mile Creek freshwater sites which are dominated by *N. erebi*. The two adjacent freshwater lagoons, Frogmore and Woolwash, are in close proximity in the ordination, and while they also have high biomasses of *N. erebi* they have more substantial influences of *A. percoides* and *A. graeffei*. Munduran downstream is more similar in composition to the two saline sites than to the freshwater pools, emphasising the importance of *M. cephalus* and *L. subviridis* at all three sites. Twelve Mile brackish takes up an intermediate location between the fresh and saline sites, reflecting substantial biomasses of a number of species (Figure 5.9b).

One important aspect of the species biomass ordination (Figure 5.20) is that the three longest vectors (i.e. the species with the highest R^2 values) are all detritivores and this defines the major differences between groups: most freshwater sites have high biomasses of *N. erebi*; saline sites and the connected Munduran downstream freshwater pool have high biomasses of *M. cephalus* and *L. subviridis*; and Little German Jack's and Woolwash (May 2005) have very low to no biomasses of all detritivores.

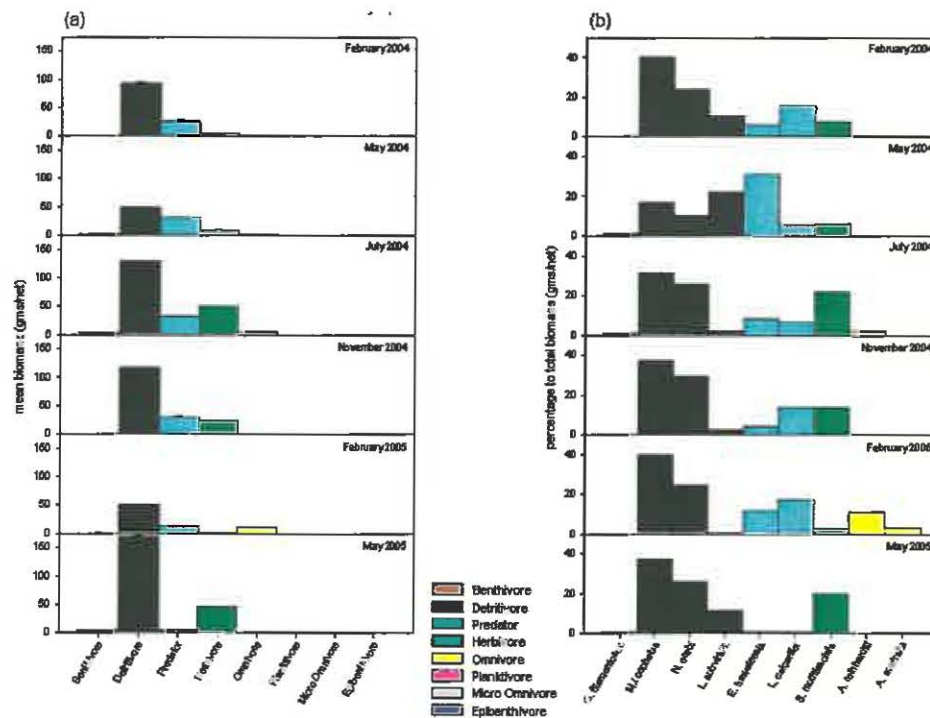


Figure 5.9. Biomass over time at Twelve Mile brackish: (a) mean biomass by trophic group (\pm SE), (b) percentage contribution to total biomass by species

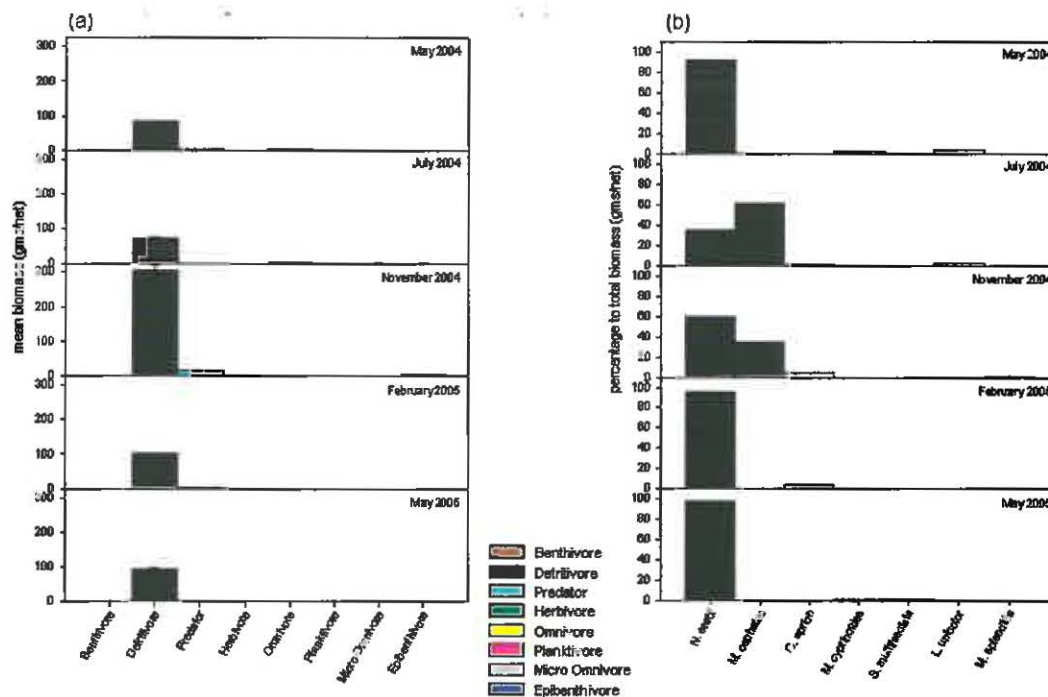


Figure 5.10. Biomass over time at Twelve Mile downstream: (a) mean biomass by trophic group (\pm SE), (b) percentage contribution to total biomass by species

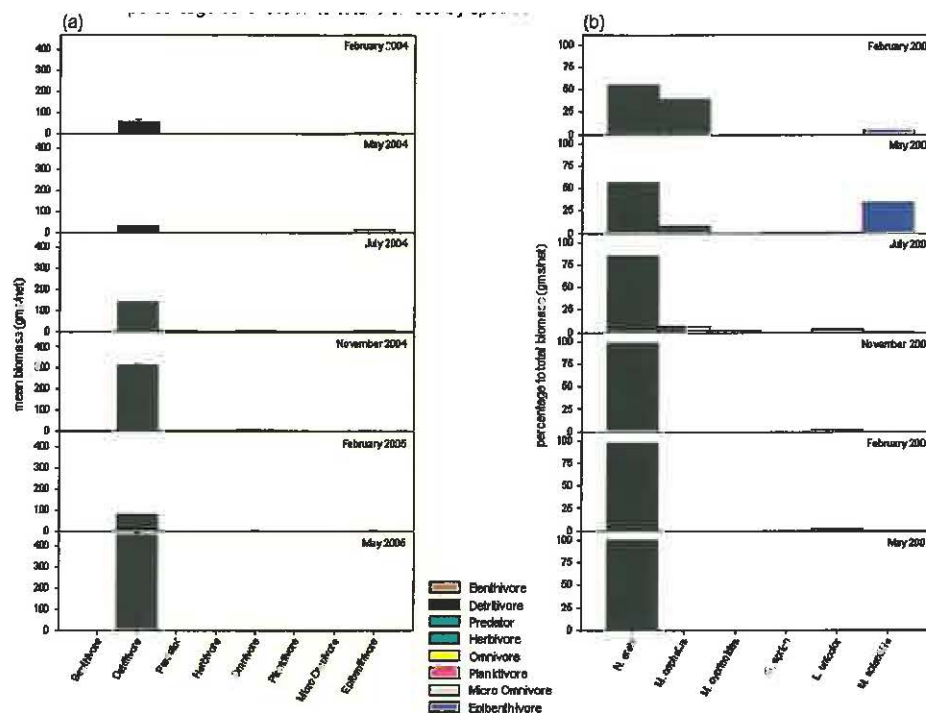


Figure 5.11. Biomass over time at Twelve Mile upstream: (a) mean biomass by trophic group (\pm SE), (b) percentage contribution to total biomass by species

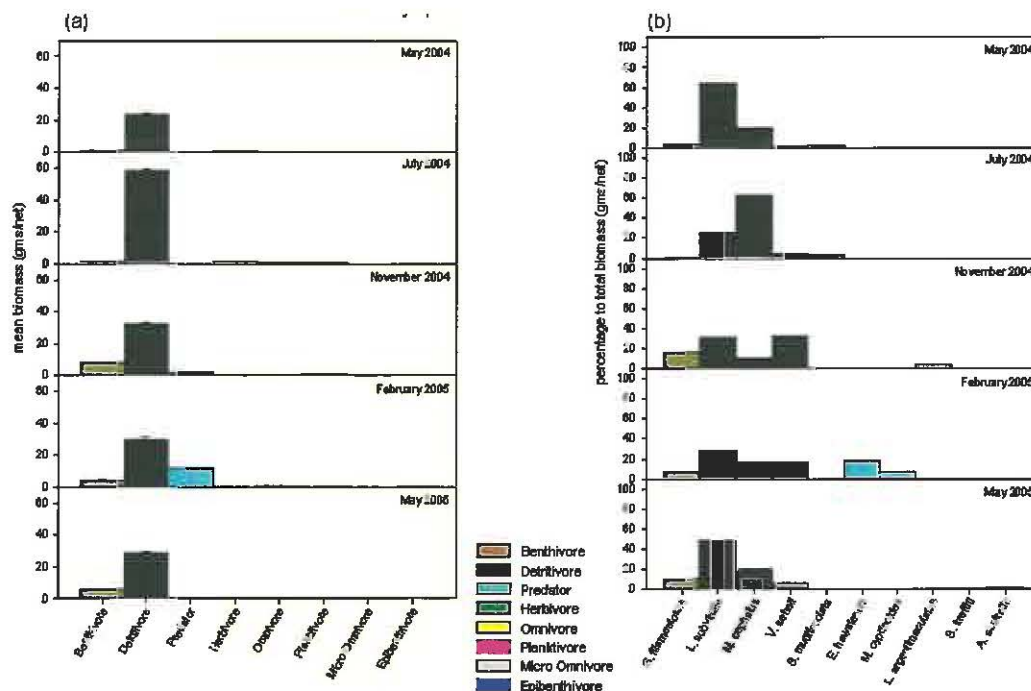


Figure 5.12. Biomass over time at Gonong saline: (a) mean biomass by trophic group (\pm SE), (b) percentage contribution to total biomass by species

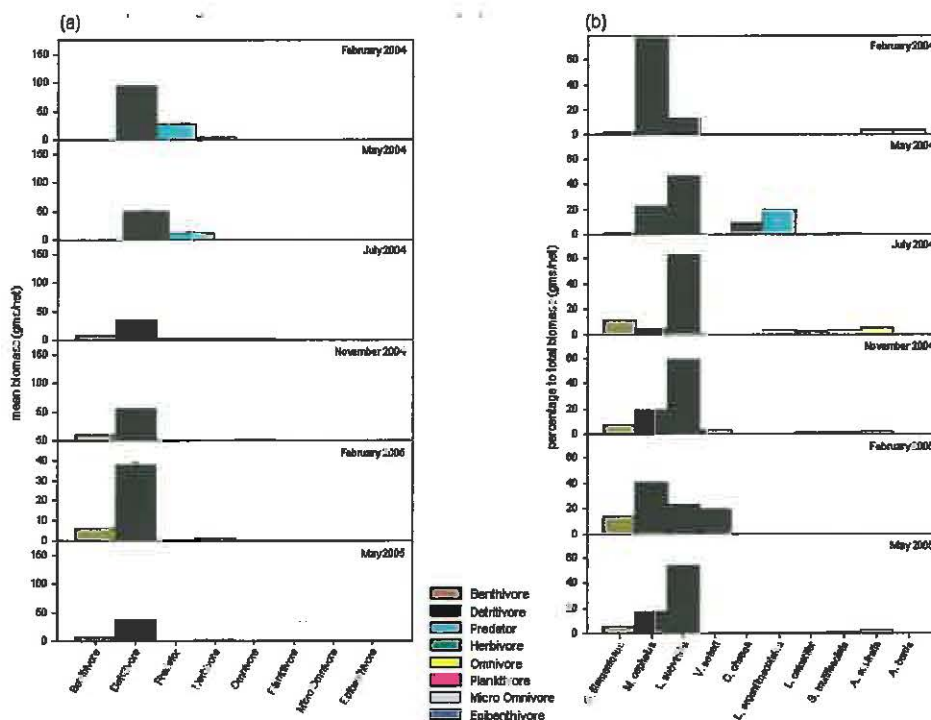


Figure 5.13. Biomass over time at Munduran saline: (a) mean biomass by trophic group (\pm SE), (b) percentage contribution to total biomass by species

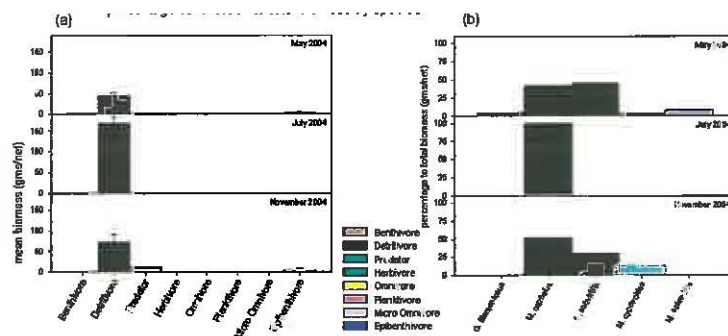


Figure 5.14. Biomass over time at Munduran downstream: (a) mean biomass by trophic group (\pm SE), (b) percentage contribution to total biomass by species

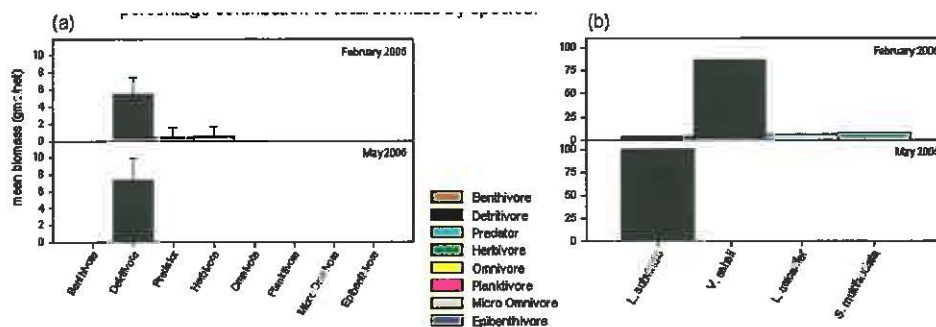


Figure 5.15. Biomass over time at Little German Jack's: (a) mean biomass by trophic group (\pm SE), (b) percentage contribution to total biomass by species

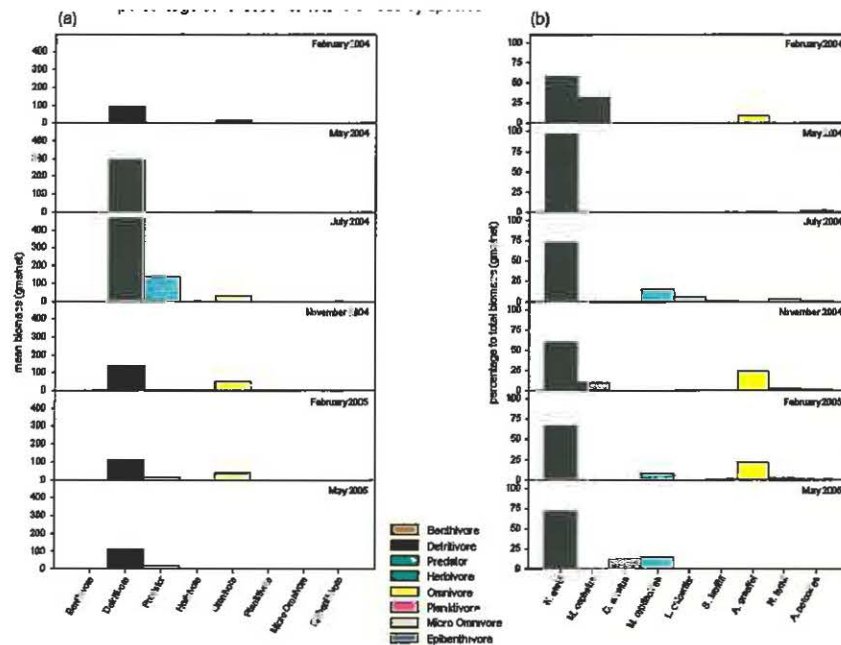


Figure 5.16. Biomass over time at Frogmore lagoon: (a) mean biomass by trophic group (\pm SE), (b) percentage contribution to total biomass by species

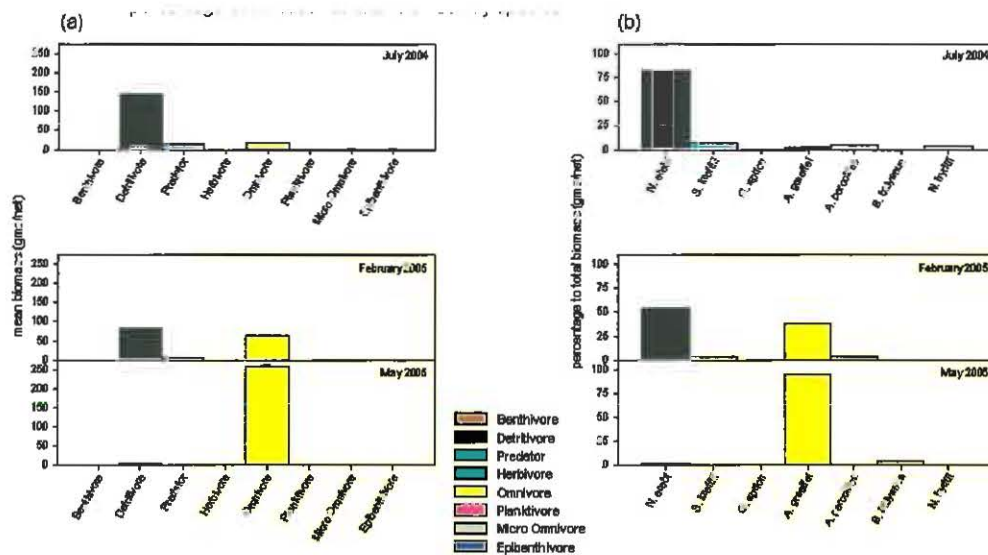


Figure 5.17. Biomass over time at Woolwash lagoon: (a) mean biomass by trophic group (\pm SE), (b) percentage contribution to total biomass by species

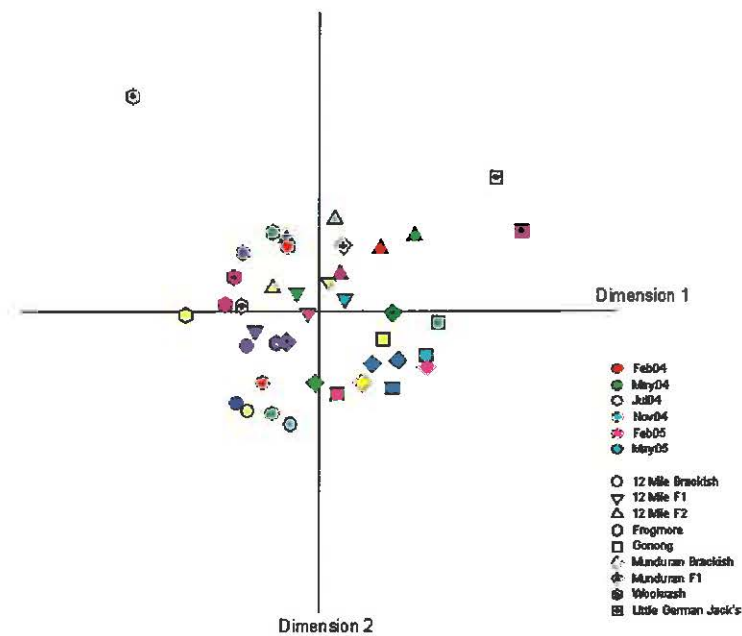


Figure 5.18. Two-dimensional MDS solution (Stress1=0.16498) using Bray-Curtis dissimilarities on $\log(x+1)$ transformed data, for trophic groups from Fitzroy wetland pools

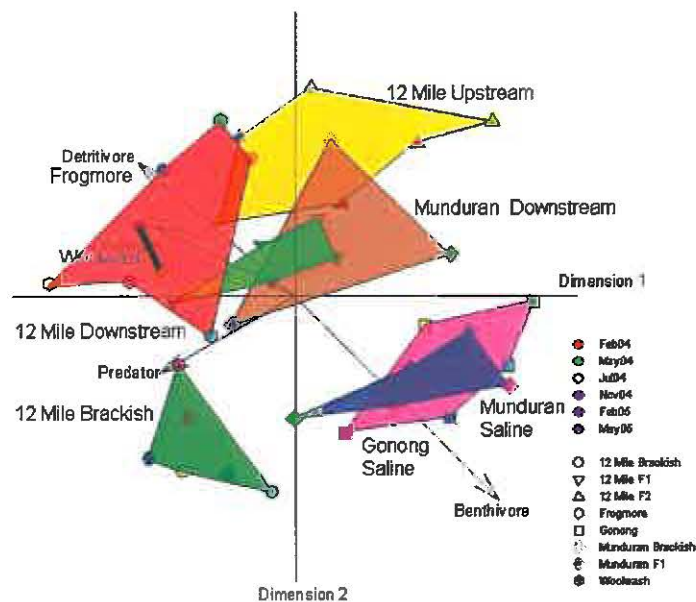


Figure 5.19. Two-dimensional MDS solution (Stress1=0.167892) using Bray-Curtis dissimilarities on $\log(x+1)$ transformed data, for trophic groups from Fitzroy wetland pools. Data for Little German Jack's and one Woolwash sample have been omitted; coloured polygons link the outer boundaries of points for each site; vectors represent the correlation of trophic groups with the MDS space, and point in the direction of their greatest increase; vector lengths are proportional to the R^2 value of a regression between the trophic groups and the configuration of points in the MDS space.

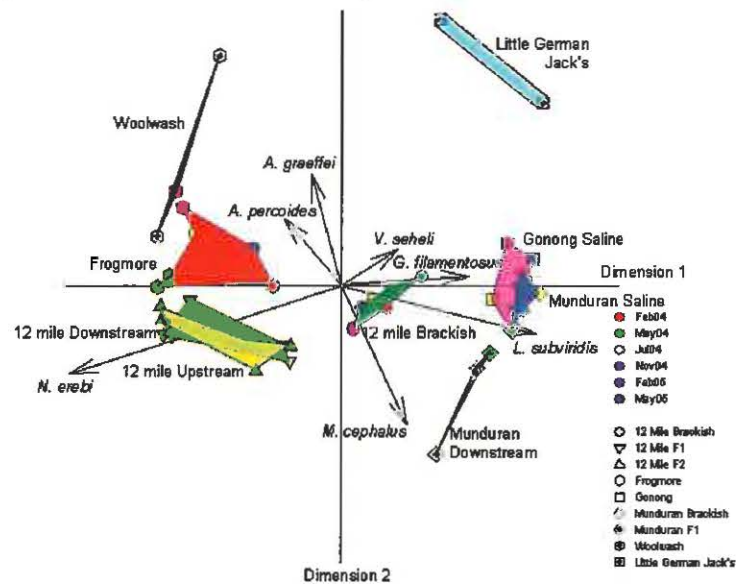


Figure 5.20. Two-dimensional MDS solution (Stress1=0.11468) using Bray-Curtis dissimilarities on $\log(x+1)$ transformed data, for trophic groups from Fitzroy wetland pools
Coloured polygons link the outer boundaries of points for each site; vectors represent the correlation of species with the MDS space, and point in the direction of their greatest increase; vector lengths are proportional to the R^2 value of a regression between the species and the configuration of points in the MDS space.

Discussion

Trophic dominance

The fauna of Fitzroy wetland pools were dominated by detritivores. Except in one instance, this dominance prevailed regardless of pool type, size, season or connectedness. The pervasive impact of detritivores provides a clear indication of the basic similarity of the pools' ecosystems and ecosystem processes. The identity of the detritivores varied between pool types—*N. erebi* in freshwater pools and *M. cephalus* and *L. subviridis* in marine pools—but all were relatively large species, despite their low trophic position. While by no means unique, this situation is unusual. In many marine systems, basal food resources (plants or detritus) are fed on primarily by small individuals (Robertson *et al.* 1992), often invertebrates (Robertson 1991), which are in turn the food of larger prey.

The trophic domination by large detritivores has far reaching consequences. The large biomass of detritivorous fish and the low abundance of other primary consumers (herbivorous fish, detritivorous or herbivorous invertebrates), suggest that most of the biological production in the pools is based on detritus rather than terrestrial plants. This reliance on detritus, despite type of pool or pool setting (forest, saltpan, pasture etc., Chapter 2), suggests strongly that the ecosystems are not critically reliant on one type of primary producer but utilise whatever sources of carbon are available to maximise productivity.

The direct use of a basal food resource by relatively large animals, that are then fed on directly by top predators (birds and fish) (Chapter 7), means that food webs leading to predators are short and simple. Consequently, energy is transferred efficiently to organisms at the top of the food web with a minimum of thermodynamic loss. The conversion of detritus to a large biomass of fish provides the opportunity for large amounts of productivity to be exported from the pools, either through migration of the detritivores themselves or the movement of the predators that consume them. This situation is quite different to our understanding of many other marine wetland systems in northern Australia, where tight recycling retains organic carbon in mangrove forests (Robertson 1986; Robertson *et al.* 1992). The apparent high predatory impact on these detritivore populations by birds (Chapter 12) means that carbon isn't only exported to marine or upstream systems during stream flow or marine connection events, but is transported to physically unconnected pools and terrestrial systems through the movements of birds.

Beyond overall dominance

Despite the overall domination of detritivores the pools could be organised into groups based on their trophic compositions. In freshwater pools, domination by detritivores was strong. In contrast, the more diverse saline pools had a small but significant component of benthic feeding fish, while the Twelve Mile brackish pool was distinguished by relatively high biomasses of predators. When biomasses are viewed at a species level it is clear that connectivity and salinity are major forces determining the details of the patterns of biomass. Fresh and saline pools had quite different species biomass profiles, while pools with strong connections to each other had similar patterns of species-specific biomass; and adjacent sites had similar detritivore species.

Of the wetland pools studied, only at Woolwash lagoon was there a major departure from the domination by detritivores. Although in July 2004 the trophic structure in Woolwash was indistinguishable from that in the nearby Frogmore lagoon or other freshwater pools, by February 2005 omnivores had become unusually important and by May 2005 completely dominant. This corresponded to a fall in water level in Woolwash to a point where large flocks of predatory waterbirds moved in and apparently consumed large numbers of the dominant detritivore *N. erebi*, but had less impact on the much larger bottom-dwelling *A. graeffei*. This shift from domination by detritivores to domination by omnivores represents a major shift in trophic structure, inevitably leading to a complete change in ecosystem function; essentially ecosystem collapse. Even if rainfall had partially refilled Woolwash, averting complete faunal loss as the pool finally dried out, the extreme reduction in detritivores means that the functionally different ecosystem in Woolwash would remain until reproduction reinstated the dominance of *N. erebi* or Woolwash was reconnection to other systems.

Connectivity

Details of changes in size structure of fish in Fitzroy wetland pools provide a basis for a deeper understanding of biological connectivity. They provide information on the processes that link physical and biological connectivity, and that modify the potential links provided by physical connectivity to produce outcomes of biological connectivity.

Most pools either remained isolated (e.g. Frogmore, Woolwash) or were regularly connected (e.g. Munduran and Gonong saline) so only provide information on the extreme scenarios. In contrast, because of its complex physical connection

patterns during the study period, the Twelve Mile Creek system provides details of intermediate states. The fish assemblage there comprised a mix of marine and freshwater species, apparently maintained in the pool by connections to both the estuary and freshwater pools in the Twelve Mile system. However, the faunal mix, and its changes over time did not simply mirror the patterns of physical connectivity but reflected the modifying effects of biological processes.

Except on one occasion, the marine spawner *S. multifasciata* was found only in saline or brackish pools (Table 4.3). Small individuals were present in the Twelve Mile brackish pool in February 2004 (Figure 5.2), following connection to the estuary during flooding earlier in the year. Small individuals were then absent for the rest of 2004, and there was a progressive shift towards larger size classes. These changes were presumably the result of growth, and perhaps predation of small individuals. Small individuals were not captured again until May 2005, when they were captured at high densities (Figure 4.11a). This influx of small individuals coincides with, and is presumably the result of, connections to the estuary in early 2005 (Chapter 3).

The lack of small *S. multifasciata* in early 2005, despite connection at the end of 2004, emphasises that physical connection only leads to biological connection if it occurs at appropriate times. Although details of the spawning season of *S. multifasciata* are lacking (Froese & Pauly 2005), it is probable that like a majority of marine species (Longhurst & Pauly 1987) it spawns over the warmer months of the year. Consequently, there were probably no juveniles available to recruit into Twelve Mile brackish during the marine connections that occurred late in 2004.

The one occasion that *S. multifasciata* was captured in a freshwater pool was in the Twelve Mile downstream pool, the pool directly upstream of Twelve Mile brackish, in May 2005, indicating that marine species were capable of passing upstream beyond the tidal influence if physical connections were suitable.

Some details of downstream connectivity are exemplified by the abundant *N. erebi*. Although small *N. erebi* were captured at all freshwater sites throughout most of the year, small individuals were absent from Twelve Mile brackish during mid 2004, suggesting they did not spawn, or spawning was unsuccessful there, possibly as a result of elevated salinities. The presence of large numbers of small individuals in early 2005 suggests that either spawning was initiated when salinities fell to very low levels following flooding, or that juveniles from upstream were washed into the brackish pool during flood connection.

Chapter 6 Densities and trophic roles of invertebrate fauna of Fitzroy wetland pools

Marcus Sheaves, Ross Johnston, Katya Abrantes and Janine Sheaves

Introduction

Although fish and birds are the most conspicuous components, wetland pools typically contain a diversity of smaller, less obvious organisms. These occupy a range of habitats, from infauna buried in the sediment, through epifauna occupying sediment or plant surfaces, to mobile fauna and plankton in the water column. Moreover, these animals are important contributors to ecosystem function, performing key roles in food webs, recycling organic material, mediating nutrient flows, contributing to overall productivity and so on.

Typically, pool faunas reflect their salinity regimes (Blinn *et al.* 2004, Hart & Lovvorn 2005): freshwater pools have a rich fauna of insects, and specialist freshwater crustaceans and molluscs, while marine pools have a diversity of marine crustaceans, molluscs and polychaete worms. While there is an expectation that invertebrate faunas of Fitzroy wetland pools will reflect their salinity regimes, no detailed understanding of the invertebrate components of such pools exists for Australia's dry tropical or subtropical areas. Gaining a more region-specific understanding is particularly important as the study is dealing with pools of mixed and variable salinity as well as pools that are strongly marine- or freshwater-influenced. The extent to which the invertebrate fauna of these mixed salinity pools are of freshwater or marine origin is unknown.

This chapter investigates the invertebrate fauna of Fitzroy wetlands pools.

Methods

Invertebrate samples were collected in February, May, July and November 2004. Sampling focussed on a selection of pools (Table 6.1) to represent the range of pool types present: Twelve Mile brackish (mixed salinity pool), Twelve Mile upstream (in-stream freshwater pool), Frogmore (isolated freshwater pool), Gonong saline (highly connected marine pool) and Munduran saline (highly connected marine pool, possibly having a greater freshwater influence than Gonong saline).

Table 6.1. Summary of organisms captured during invertebrate sampling in Fitzroy wetland pools; grab data are mean density/litre; scoopnet data are mean number/scoop

Group	Common Name	Family	12 Mile brackish		12 Mile upstream	Frogmore		Gonong		Munduran
			Grab	Scoop	Scoop	Grab	Scoop	Grab	Scoop	Grab
Arachnida	Wolf spider	Lycosidae		18.0	1.0		2.2			
Crustacea	Amphipod	Corophiidae		27.0						
	Amphipod	Gammarida	15.0					7.2		15.3
	False spider crab	Hymenosomatidae						0.8		2.4
	Isopod	Flabellifera								1.1
	Prawn	Penaeidae						0.9	2.0	
	Seed shrimp	Ostracoda					19.5	0.8		
	Shrimp	Palaemonidae			1.0		1.0		2.0	4.0
	Shrimp	Atyidae		37.8	134.9		250.8			
Insecta	Alderfly	Sialidae	1.1							
	Backswimmer	Notonectidae		3.0	1.0		5.5			
	Beetle	Ptilodactylid larvae					1.0			
	Water scavenger beetle	Hydrochidae					1.0			
	Biting midge	Ceratopogonid larvae	2.4							
	Caddisfly	Plectrotarsidae				3.7	1.0			
	Creeping water bug	Naucoridae		1.0			1.0			
	Damselfly	Synlestid larvae	1.3							0.9
	Damselfly	Zygoptera larvae		3.5	3.0		24.4			
	Diving beetle	Dysticidae			9.0	1.5	2.7			
	Dragonfly larva	Aeshnidae		1.0	1.8	2.0	7.7			
	Dragonfly larva	Odonata larvae								1.3
	Giant water bug	Belostomatidae			2.0					
	non-biting midge	Chironomid larvae	8.4		15.0	4.0	12.7	1.1		1.8
	Small water strider	Veliidae					13.0			
	Giant water bug	Belostomatid larvae		3.0						
	Water boatman	Corixidae	2.1	1.0	1.0	2.0	12.4			
	Water measurer	Hydrometridae					1.0			
	Water measurer	Hydrometrid larvae					1.0			
	Water scavenger beetle	Hydrophilidae					2.0			
	Water scavenger beetle	Hydrophilid larvae			1.5		1.5			
	Water strider	Gerridae					6.6			
Mollusca	Freshwater snail	Hydrobiidae	8.8	10.3	2.6	1.0	18.0			
	Freshwater snail	Planorbidae			2.3		8.9			
	Pond snail	Lymnaeidae			1.0	1.5	12.6			
	Sand cockle	Tellinidae	0.8							
	Sculptured snail	Thiaridae								1.3
	Shore snail	Neritidae						0.8		
	Sunset clam	Psammobiidae								1.5
Polychaeta	Marine worm	Capitellidae	8.1					4.0		6.5
	Marine worm	Nereidae						68.5		84.6
	Marine worm	Paraonidae						3.8		
Teleostei	Goby	Gobiidae	1.0		1.0		11.3			

Two sampling approaches were used. A van Veen grab (2 l capacity) was used to collect animals living in or on the substratum. At least 10 samples were taken at each site on each occasion. For Frogmore, 20 samples were collected to provide adequate representation of its larger area. No grab samples were collected from Twelve Mile upstream because its substrate was too hard for penetration by the grab. Grab samples were collected from Twelve Mile brackish and Munduran

saline in February, May and July 2004, Gonong saline in May and July 2004, and Frogmore in May 2004.

Scoop nets were used to collect small fauna associated with submerged vegetation. At least 10 scoop net sweeps were made through submerged bank-side vegetation whenever it was available. Scoop samples could be collected from Twelve Mile upstream on all trips in 2004, from Frogmore in February, May and July 2004, from Twelve Mile brackish in February and November 2004 and Gonong saline in July 2004.

Although many animals could be identified to species, a large number of others were larval or juvenile forms preventing confident allocation to a particular species. Consequently, for consistency, all taxa are reported at the level of family or subfamily. Taxonomic compositions were compared between sites for both grab and scoop net samples using non-metric multidimensional (MDS) scaling of Bray-Curtis dissimilarities, after data were first $\log(1+x)$ transformed.

Multiple regression of invertebrates on the MDS dimensions was used to determine the relationships between the invertebrates and the configuration of points in the MDS ordination space. The directions of greatest increase were defined by the regression coefficients for the dimensions and the lengths of vectors were set proportional to the R^2 values, to indicate the strength of the relationships (Sheaves & Molony 2000). Where grouping was suggested by the position of points, the coherence of the groups was investigated using hierarchical cluster analysis, on Bray-Curtis dissimilarities with Ward's linkage method.

Invertebrates were classified into trophic groups using all available literature. If there was conflict between sources, Gooderham & Tsyrlin (2002) was used as the standard. MDS using Bray-Curtis dissimilarities on row standardised data was used to investigate patterns of invertebrate trophic composition among wetland pools. Standardising by row totals converted the data into proportional contribution of trophic groups at each site. Under this standardisation two sites would be similar if they had similar proportional contributions by the various trophic groups. Where grouping was suggested by the position of points, the coherence of the groups was investigated using hierarchical cluster analysis, on Bray-Curtis dissimilarities with Ward's linkage method.

Trophic groups and levels

Trophic groups are defined as follows (NOTE: This varies from the groups defined for fish but is in line with literature descriptions).

Predators: feed by capturing other animals

Herbivores: feed principally on living plant material

Omnivores: consume prey from a broad range of trophic groups (plant and animal)

Omnivorous detritivores: feed on plant and animal prey as well as detritus

Phyto-detritivores: consume both plants and detritus

Scavengers: feed on dead animals.

Trophic levels are:

Plants and detritus

Herbivores and phyto-detritivores

Omnivores, scavengers and omnivorous detritivores

Predators.

Results**Taxonomic composition**

Forty-one invertebrate taxa and one fish were recorded from grab and scoop net sampling (Table 6.1). Although sampling quite different habitats in quite different ways, both grab (Figure 6.1a,d,f,h) and scoop (Figure 6.1b,c,e,g) samples showed a dominance of insects at freshwater sites. Insects were particularly diverse at Frogmore (Figure 6.1e), contributing substantially to the high taxonomic richness there. Insects, crustaceans and molluscs occurred at all sites, although taxonomic details differed between sites (Table 6.1). The other major group, polychaete worms, were confined to sites with some marine influence. Although Twelve Mile brackish had both marine and freshwater components its overall diversity was only comparable with the marine sites and, at least in terms of scoop net samples, lower than the freshwater sites (Figure 6.1b,c,e,g).

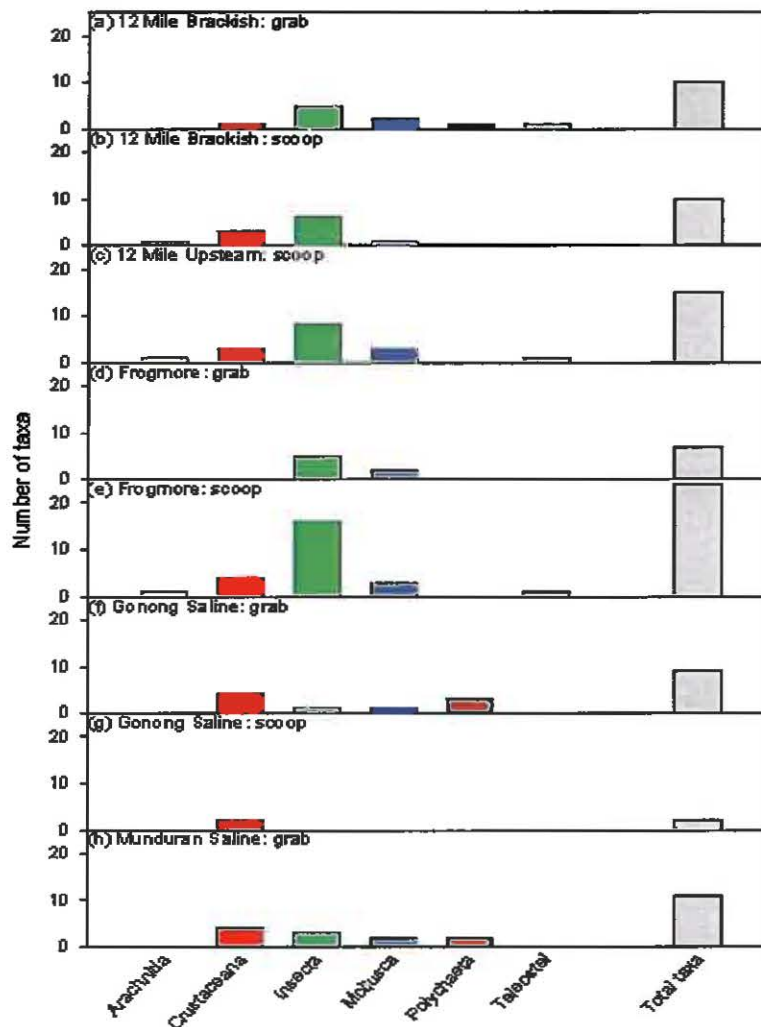


Figure 6.1. Compositions of invertebrate fauna from Fitzroy wetland pools: (a) Twelve Mile brackish grab samples; (b) Twelve Mile brackish scoop samples; (c) Twelve Mile upstream scoop samples; (d) Frogmore grab samples; (e) Frogmore scoop samples; (f) Gondong saline grab samples; (g) Gondong saline scoop samples; (h) Munduran saline grab samples

Scoop net samples were dominated by insects and shrimps (Table 6.1), and showed considerable change over time (Figure 6.2) that can be largely explained by changes in submerged vegetation (Table 6.2). High densities of insect larvae, planorbid snails and atyid shrimps were recorded from Frogmore in February and May 2004, when there were areas of submerged grass along the water's edge. These taxa were also high in Twelve Mile upstream in May and July 2004, when pool levels were low enough to sample around water lilies (*Nymphaea* spp.) and cabomba (*Cabomba caroliniana*). Even though the grass edges of the pool could be sampled in February and November, catches of these species were low, suggesting that they remained among the submerged vegetation. In July 2004 Gondong saline and in November 2004 Frogmore had relatively high densities of palaemonid shrimps. No suitable habitat was available for scoop netting in Munduran saline or in Gondong saline except in November 2004.

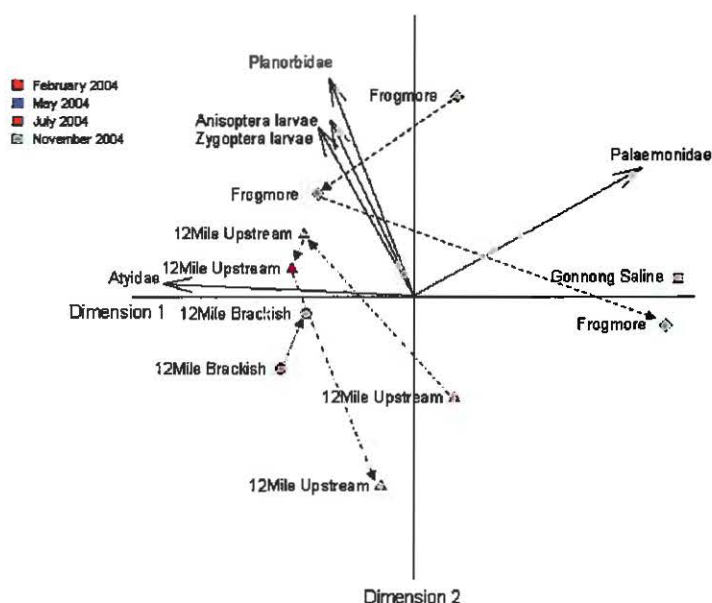


Figure 6.2. Two-dimensional MDS of invertebrate composition from scoopnet samples from Fitzroy wetland pools using Bray-Curtis dissimilarities on $\log(x+1)$ transformed data (Stress1=0.07933)

Dashed vectors indicate trajectories of change over time; solid vectors indicate the direction of greatest increase in densities of taxa, with vector lengths proportional to R^2 (largest $R^2 = 0.7405$)

Table 6.2. Availability of submerged vegetation over time along the edges of Fitzroy wetland pools

Sampling date	Twelve Mile brackish	Twelve Mile upstream	Frogmore lagoon	Gonong saline	Munduran saline
February 2004	Grass, reeds at edge of pool submerged to 0.25 m	Grass, reeds at edge of pool submerged to 0.15 m. Extensive beds of <i>Cabomba</i> and <i>Nymphaea</i>	Grass at edge of pool submerged to 0.5 m.	No submerged vegetation	No submerged vegetation
May 2004	No submerged vegetation	Extensive beds of <i>Cabomba</i> and <i>Nymphaea</i>	Small amount of submerged grass along banks	No submerged vegetation	No submerged vegetation
July 2004	No submerged vegetation	Extensive beds of <i>Cabomba</i> and <i>Nymphaea</i>	Little submerged vegetation	Small area of grass submerged to 0.1 m	No submerged vegetation
November 2004	Grass, reeds at edge of pool submerged to 0.25 m	Grass, reeds at edge of pool submerged to 0.15 m. Extensive beds of <i>Cabomba</i> and <i>Nymphaea</i>	Small amounts of submerged algae	No submerged vegetation	No submerged vegetation

In contrast to the scoopnet data, grab samples showed relatively low levels of change over time and clear differentiation of saline sites from brackish and freshwater sites (Figure 6.3). The brackish site was distinguished by consistently high densities of sialids (alderflies), hydrotbiids (freshwater snails) and gammarids (amphipods), while saline sites were distinguished by high densities of nereids (polychaete worms). The one truly freshwater site, Frogmore, had very high densities of chironomids (non-biting midges) compared to the other sites.

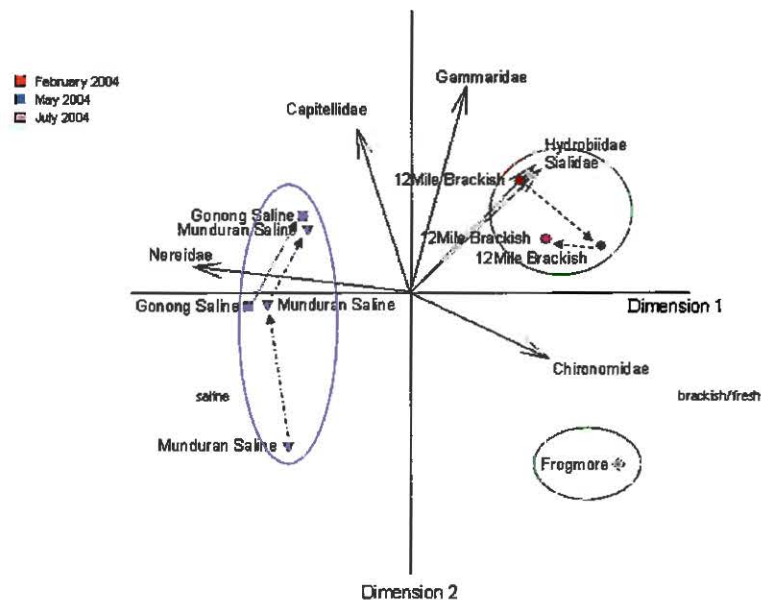


Figure 6.3. Two-dimensional MDS of invertebrate composition from benthic grab samples from Fitzroy wetland pools using Bray-Curtis dissimilarities on $\log(x+1)$ transformed data (Stress1=0.03365)

Dashed vectors indicate trajectories of change over time; solid vectors indicate the direction of greatest increase in densities of taxa, with vector lengths proportional to R^2 (largest $R^2 = 0.8181$); ellipses represent groups identified by cluster analysis at a linkage distance of 45% of maximum distance, using Ward's linkage method

Trophic composition

Table 6.3 shows the trophic categorisation of invertebrates sampled at all Fitzroy wetland pool sites.

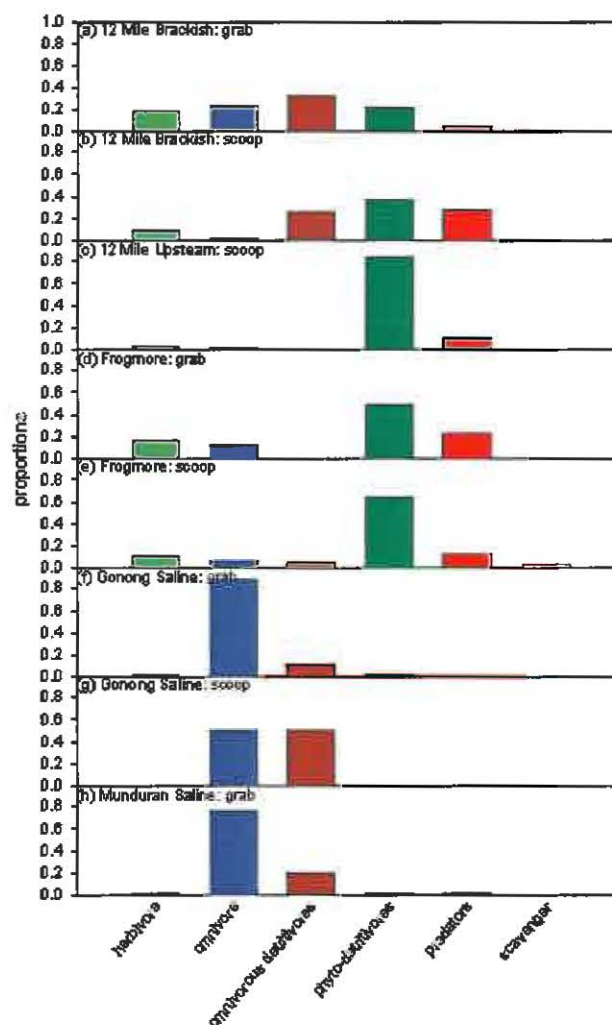
Table 6.3. Trophic categorisation of invertebrates from Fitzroy wetland pools

	Trophic category					
	Predators	Omnivore	Omnivorous detritivores	Phyto-detritivores	Herbivore	Scavenger
Arachnida	Lycosidae					
Crustacea	Hymenosomatidae	Penaeidae	Corophiidae	Atyidae		
	Flabellifera		Gammarida			
			Ostracoda			
			Palaemonidae			
Insecta	Sialidae	Corixidae		Ptilodactylid larvae	Hydrochidae	Velidae
	Notonectidae			Ceratopogonid larvae	Hydrophilidae	Hydrometridae
	Naucoridae			Plectrotarsidae		Hydrometrid larvae
	Synlestid larvae			Chironomid larvae		
	Zygoptera larvae					
	Dysticidae					
	Aeshnidae					
	Odonata larvae					
	Belostomatidae					
	Belostomatid larvae					
	Hydrophilid larvae					
	Gerridae					
Mollusca			Tellinidae		Hydrobiidae	
			Psammobiidae		Planorbidae	
					Lymnaeidae	
					Thiaridae	
					Neritidae	
Polychaeta		Capitellidae				
		Nereidae				
		Paraonidae				

In general, both grab and scoop sampling techniques produced similar trophic composition at each site. Twelve Mile brackish had reasonably similar densities of most trophic groups apart from scavengers (Table 6.4). In contrast, freshwater sites tended to have greater densities of phyto-detritivores, and saline sites higher densities of omnivores and omnivorous detritivores than other trophic groups. The differences are clearer when the data are viewed as proportional contributions (Figure 6.4), emphasising the clear dominance of phyto-detritivores in fresh sites and omnivores in saline site. Ordination and cluster analysis (Figure 6.5) clearly differentiated the pools into three groups on the basis of their trophic compositions.

Table 6.4. Densities of invertebrates from Fitzroy wetland pools per trophic group; grab data are mean density/litre; scoopnet data are mean number/scoop

Invertebrate	12Mile brackish		12Mile upstream	Frogmore		Gonong		Munduran
	Grab	Scoop	Scoop	Grab	Scoop	Grab	Scoop	Grab
Herbivore	8.8	10.3	5.9	2.5	42.5	0.8		1.3
Omnivore	11.2	1	2	2	23.7	77.2	2	91.1
Omnivorous detritivore	15.8	27	1		20.5	8.8	2	24.3
Phyto-detritivore	10.8	37.8	149.9	7.7	265.5	1.1		1.8
Predator	2.4	29.5	19.3	3.5	51.6			2.2
Scavenger					15			
Total density	49	105.6	178.1	15.7	418.8	87.9	4	120.7

**Figure 6.4. Comparison of proportions of invertebrates by trophic group from Fitzroy wetland pools: (a) Twelve Mile brackish grab samples; (b) Twelve Mile brackish scoop samples; (c) Twelve Mile upstream scoop samples; (d) Frogmore grab samples; (e) Frogmore scoop samples; (f) Gondong saline grab samples; (g) Gondong saline scoop samples; (h) Munduran saline grab samples**

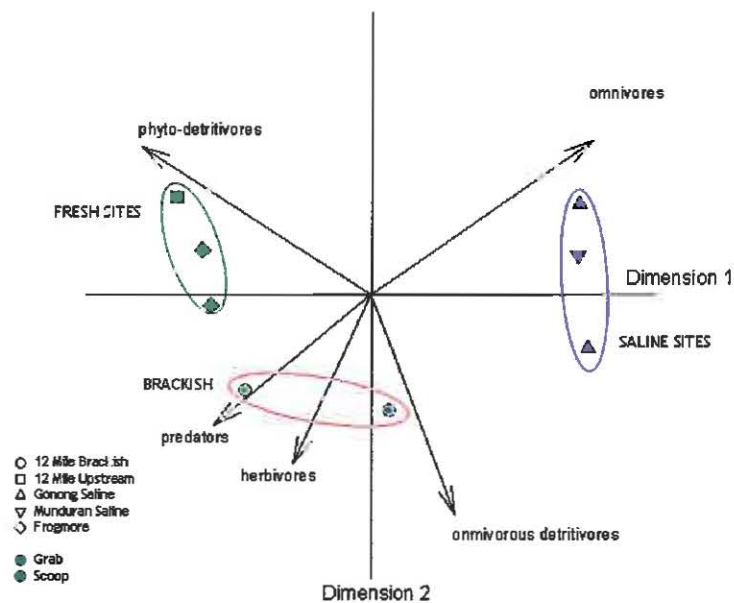


Figure 6.5. MDS comparing trophic compositions of invertebrate fauna from Fitzroy wetland pools using Bray-Curtis dissimilarities on row standardised data

Vectors indicate the direction of greatest increase in density of trophic groups, with vector lengths proportional to their correlation with the ordination space (highest $R^2 = 0.9468$); ellipses represent groups identified by cluster analysis at a linkage distance of 50% of maximum distance, using Ward's linkage method

The nature of the trophic data (densities of different mixes of taxa, sizes etc. between sites) makes formal statistical comparison of dubious validity; overall scoop net densities per trophic group tended to be higher in brackish and freshwater sites than at the one saline site where scoop netting was possible (Table 6.4). In contrast, grab densities per trophic group tended to be higher at the saline sites.

Even though information from the two gear types was not directly comparable, both methods showed similar proportional contributions by trophic group at sites where both could be used successfully (Figure 6.4). Consequently, densities per trophic group were averaged across gear types and sites to estimate approximate proportional contributions per trophic group to construct invertebrate sub-food web models for freshwater (Figure 6.6) and saline (Figure 6.7) pools, and for Twelve Mile brackish (Figure 6.8). Scavengers made up only a minor component at one site, so were excluded from food web models.

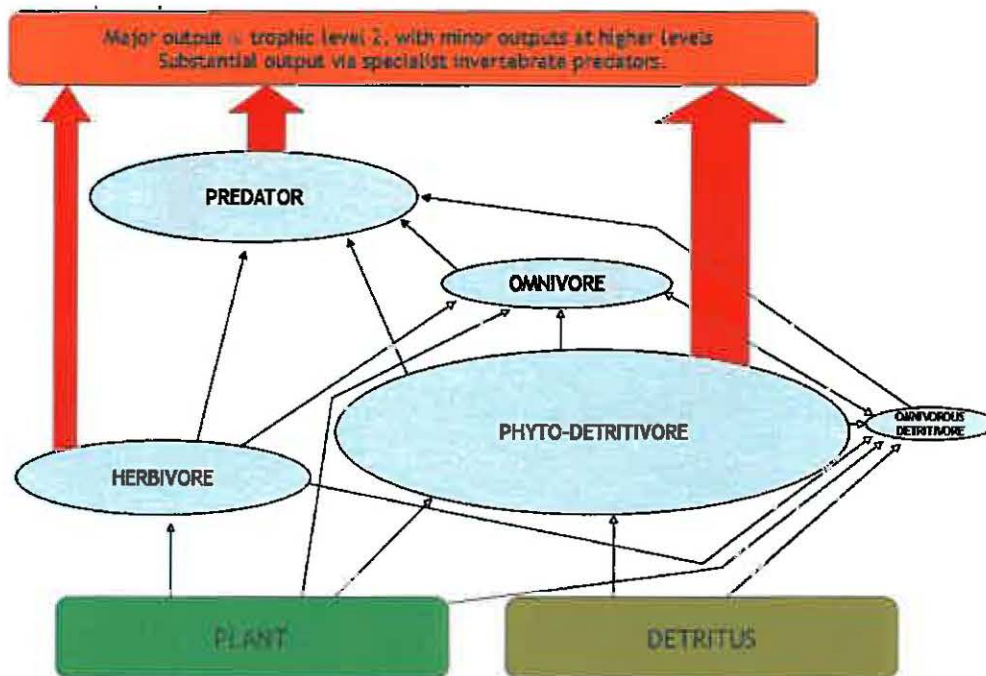


Figure 6.6. Invertebrate sub-food web model for freshwater pools

Areas of ellipses for invertebrate trophic groups are proportional to percentage contribution; small black arrows indicate implied trophic linkages; red arrows indicate potential outputs to other components of the overall pool food web, with their thickness indicating implied importance

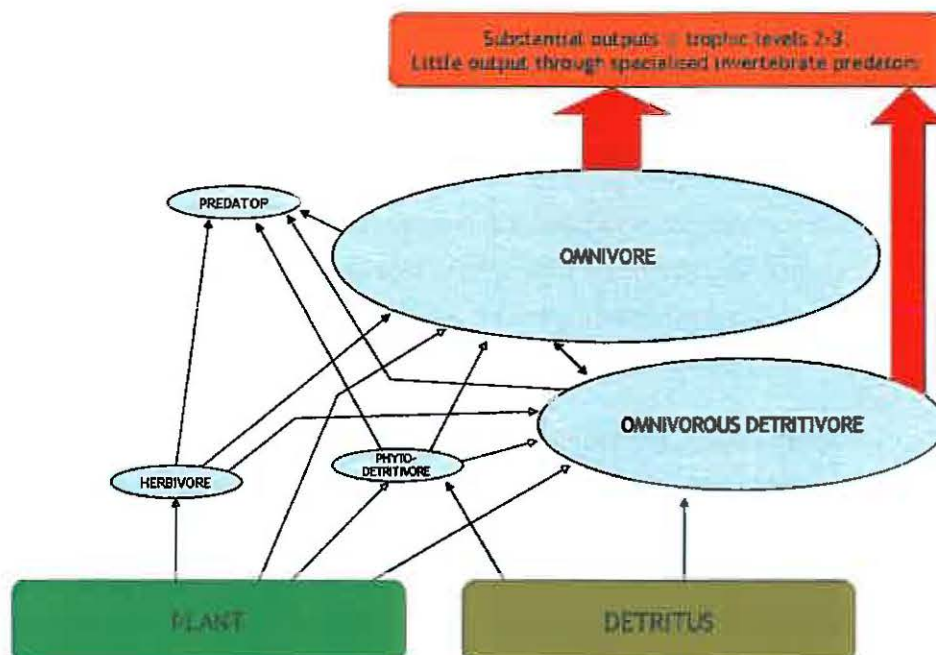


Figure 6.7. Invertebrate sub-food web model for saline pools

Areas of ellipses for invertebrate trophic groups are proportional to percentage contribution; small black arrows indicate implied trophic linkages; red arrows indicate potential outputs to other components of the overall pool food web, with their thickness indicating implied importance

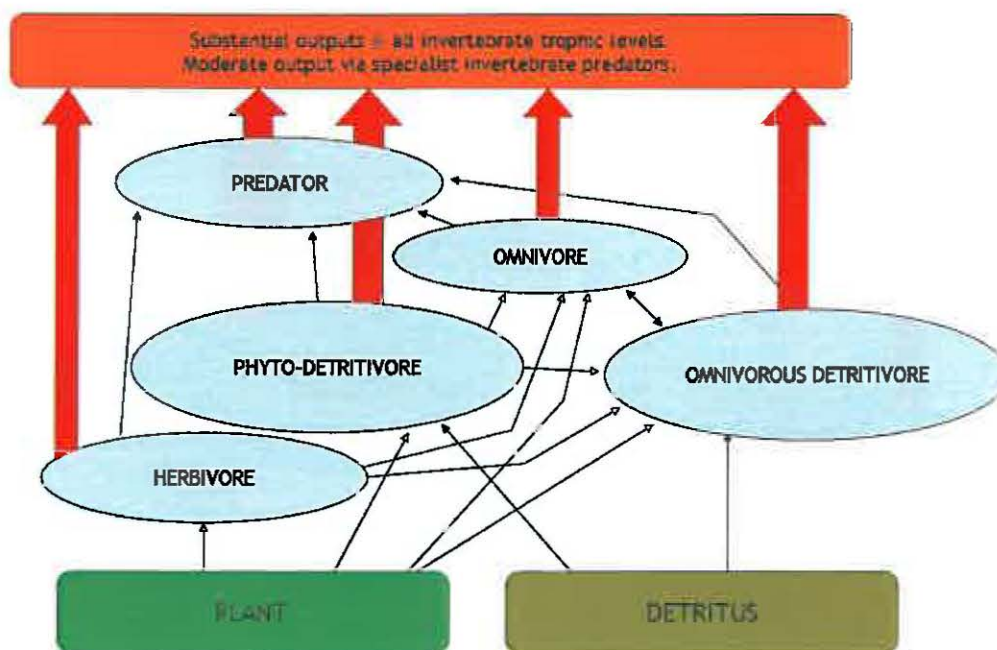


Figure 6.8. Invertebrate sub-food web model for the Twelve Mile brackish pool
 Areas of ellipses for invertebrate trophic groups are proportional to percentage contribution; small black arrows indicate implied trophic linkages; red arrows indicate potential outputs to other components of the overall pool food web, with their thickness indicating implied importance

Discussion

Taxonomic composition

Fitzroy wetland pools have rich invertebrate faunas, largely in line with expectations based on their salinity regimes, their habitat settings and their levels of connectivity to other systems. As in other tropical and subtropical freshwater environments (Williams

1998), insects, crustaceans and freshwater molluscs were abundant in both isolated and in-stream freshwater pools faunas. Saline pools had typical estuarine faunas (Bolduc & Afton 2003) of polychaete worms and marine molluscs and crustaceans, but small numbers of insect larvae were also present. The Twelve Mile brackish pool had a varied fauna with both marine and freshwater components, but despite its varied nature it was no more diverse than the faunas of the saline or freshwater pools.

Benthic grab samples showed strong and consistent faunal differences among the three types of pool. In contrast, there was considerable variation in the composition of scoopnet catches over time. However, this variation is probably an

artefact. Unlike the constant availability of the soft sediments needed for benthic grab samples, the availability of aquatic vegetation varied with water level and season, making inconsistent representation of the associated fauna unavoidable.

With a few exceptions (e.g. lycosid spiders and predatory nereid worms) the invertebrates captured fulfil trophic roles low in food webs, feeding directly on plants or detritus, or on the bacterial films associated with decaying matter.

Trophic roles

The division of invertebrate taxonomic compositions into distinct fresh, brackish and saline faunas was unsurprising. It does, however, have considerable consequences for the trophic composition of these faunas. This can be seen most clearly in the extreme cases, with invertebrate fauna of saline pools mainly comprised of omnivores and omnivorous detritivores, while those of freshwater pools were dominated by phyto-detritivores. These trophic consequences lead to quite different models of the invertebrate sub-food webs for the different types of pools, and consequently different implications for the relationship between invertebrate sub-food webs and the complete food webs of the pools.

Invertebrate sub-food webs of freshwater pools feature a substantial phyto-detritivore component as the major pathway for nutrition to pass into and through the web (Figure 6.6), and a smaller, but significant, herbivore component. There is also a substantial density of predators. This predator component serves to complicate the sub-web, redirecting energy to a greater diversity of invertebrates and increasing the number of trophic transfers within the sub-web. Thus more energy is lost within the sub-web in producing the suite of invertebrates present than would be the case if there was no invertebrate predator component and energy simply passed to herbivores and detritivores that were then fed on by predators from outside the sub-web (e.g. fish).

The sub-food web of saline pools (Figure 6.7) is quite different. Neither plant feeding group (i.e. herbivores and phyto-detritivores) is prominent. Rather, most of the energy passes through the two omnivore groups (omnivores and omnivorous detritivores), suggesting a much greater importance of detritus relative to living plants in the saline than in the freshwater pools. The invertebrate predator component was very small. This means that pathways of energy flow within the sub-web are less complex than in freshwater pools, and probably that less energy is lost in trophic transfers within the sub-web. Additionally, the lack of invertebrate predators suggests that this role is taken over by predators from outside the invertebrate sub-web.

In contrast to the other two sub-webs, the Twelve Mile brackish invertebrate sub-web (Figure 6.8) is much more complex. All five trophic groups are well represented, indicating a much more complex sub-web than for the other two pool categories, probably with more substantial energy loss due to greater numbers of trophic transfers. Both plants and detritus seem to be important nutritional bases, with a diversity of organisms using a diversity of feeding modes. As with freshwater pools, invertebrate predators were important, contributing a similar proportion of invertebrate density. The sub-web of Twelve Mile brackish could be viewed as combination of the fresh and saline webs, or perhaps as an intermediate state. This intermediate status is interesting; it may confer opportunistic resilience on the brackish pool. The invertebrate sub-web may be able to swap between the saline and fresh sub-web structures when pool salinities swing towards particular extremes, thereby switching functionality.

These webs are based on the standing crop of invertebrates; essentially a snapshot in time, with no consideration of the real dynamics of the sub-webs over time. For instance, knowledge of the longevities of the various components would be necessary to determine the true relative densities of the different trophic groups; despite a small biomass, a group with a short life-cycle and therefore rapid turnover, can make a contribution to trophic exchange disproportionate to its instantaneous density. Consequently, such things as the extent to which phyto-detritivore biomass passes to invertebrate predators cannot be fully understood without an extensive understanding of the ecology and biology of all the major components.

Chapter 7 Diets of fish from Fitzroy wetland pools

Marcus Sheaves and Ross Johnston

Introduction

Fish occupy Fitzroy wetland pools at high densities (Chapter 4) and biomasses (Chapter 5), and thus are likely to be important contributors to ecosystem function. Beyond this, wetlands around the world (Laffaille *et al.* 2000, Manson *et al.* 2005) and in the Fitzroy itself (Infotish 2005) are important nursery habitats for many species of fish. The most direct way in which fish interact with other ecosystem components is through feeding relationships.

The types of food eaten, and changes in food supply over time, directly impact on the nutrition of the fish, their rates of growth and patterns of mortality, and therefore impact on nursery-ground value. Furthermore, the availability of particular food types affects the structure of fish communities (Grenouillet *et al.* 2002, Wildhaber & Lamberson 2004). Looking at it from the other direction, fish predation can be a significant source of mortality on both invertebrates (Wilson & Sheaves 2001) and other species of fish (Baker & Sheaves 2005). In this way, fish feeding influences community structure and community change (Skov *et al.* 2002). Through both their effects on other community members and on the fish themselves, food type and food availability are critical to ecosystem productivity and the export of energy in the form of the biomass of emigrating animals.

This component of the study investigates the diets of fish from wetland pools in detail.

Methods

All fish used for detailed biological analyses [diet (this chapter), stable isotope, (Chapter 8) and biochemical condition (Chapter 10)], were chilled on ice immediately following capture, and dissected on return to the laboratory. Ice chilling was used instead of more usual formalin fixation because applying formalin to samples in the field is a time-consuming process. To use it in this study would have compromised the ability to release fish surplus to laboratory requirements quickly enough to ensure a high likelihood of survival (see Chapter 4). For dietary analysis the gut (stomach plus intestine) was removed and, if dietary analysis was not immediately possible, stored frozen until detailed analysis could be conducted.

Both stomachs and intestines were cut open and their contents identified to as low a taxonomic level as possible. As intestines provided no additional useful information only data from the more identifiable stomach content were used for further analysis. In addition to recording the presence of all taxonomic groups, relative proportions of different prey categories were determined by the following method (Hislop 1980). The stomach content was spread thinly over a petri dish inscribed with a series of 50 mm transect lines marked at 1 mm intervals.

The proportion of intervals intersecting particular prey types was used as an estimate of proportional dietary contribution. These data were not used in final analyses because the great variety of food types (detritus and plant cells to whole fish) and differences in decomposition (undigested invertebrates and fish to pairs of fish otoliths) meant that it was impossible to use the data comparatively. As a result the presence of prey types was used in the analysis, with the basic data being the number of fish of a species with each prey category collected on each sampling trip from each wetland pool. Because numbers for many prey species were very low they were aggregated into broad groups to facilitate analysis (Table 7.1).

Four common species, *Nematalosa erebi*, *Mugil cephalus*, *Liza subviridis* and *Selenotoca multifasciata*, fed extensively on phyto-detritus, a combination of living plant cells and dead organic particles. These species comprised the greatest biomass of fish in the pools (Chapter 5), so understanding their diets in detail was a clear priority. However, the literature is not explicit on the important issue; the extent to which each species consumes detritus as opposed to living plant material. To address this important issue a new, simple method of separating detritus from living plant material by centrifuging, was developed. The steps in this process were as follows:

Centrifuge separation method:

1. Remove foregut contents (oesophagus and gizzard, or muscular oesophagus/stomach in fish without gizzard [e.g. *S. multifasciata*]).
2. Place gut content in a test tube and dilute and mix thoroughly with a 1:6 Ludox:water solution.
3. Centrifuge for 5 min @ 4000 rpm. This produces sediment and detrital layers at the bottom of the tube, and leaves fresh/live plant cells as well as any residual gut lining at the surface of the liquid.
4. Measure thickness of the sediment and detrital layers.

5. Decant (with pipette) fresh vegetation from solution, residual gut lining material can be removed at this point.
6. Place fresh vegetation in a clean tube, bringing across as little Ludox solution as possible. Add approximately 8 mls water, mix then spin at 4000 rpm for 5 min. This should produce a layer of compressed vegetative matter at the base of the tube (now 'packed' equivalently to sediment and detritus). If vegetation has not compressed into a discrete layer (this may happen if too much Ludox is carried over to the second tube), decant as much liquid as possible, add another 8 ml of water and spin again. If the vegetation contains rigid structure (e.g. stems), it may need to be broken up with a sharp instrument and spun a third time to gain equivalent 'packing' to the sediment and detrital layers.
7. Measure thickness of the vegetative layer. This produces layers of plant cells, detritus and sediment that are discrete and equivalently packed. Although the equivalence of packing is subjective, microscopic examination shows it is similar between fractions (i.e. plant, detritus and sediment) and repeatable for a sample. Thus, although direct comparison of the exact amount of each component is not possible, comparison of relative contributions of detritus and plant material between individuals, species, sites and/or times is reasonable.

Statistical analysis

Diet data were analysed using multivariate and univariate classification and regression trees (De'ath & Fabricius 2000; De'ath 2002), fitted using 10-fold cross-validation (Breiman *et al.* 1984). Multivariate results were displayed graphically using principal coordinates analysis, based on Bray-Curtis extended dissimilarities. Before analyses data were $(x+1)$ transformed to prevent undue influence of highly abundant dietary items in the analysis (Gauch, 1982, Jongman *et al.* 1995).

Results

Of the common fish of Fitzroy wetlands pools (Chapter 4), the guts of enough of the individuals (five or more) of 14 species contained prey for some level of meaningful dietary analysis (Table 7.1).

Table 7.1. Percentage of fish (empty fish excluded) from Fitzroy wetland pools that had consumed various dietary components; only species for which four or more individuals examined contained prey are presented; numbers next to fish species names indicate the number of guts examined that contained food

Species		Phytodetritus	Sand	Seeds	Micro-crustaceans	Shrimps	Insects	Insect larvae	Bivalves	gastropods	fish	tortoise
<i>Amniataba percooides</i>	28	96	4	4	50		25	75			7	
<i>Arius graeffei</i>	7	94	41	21	76	18	74	74	3	18	26	3
<i>Arramphus sclerolepis</i>	6	100						17				
<i>Chanos chanos</i>	5	75	75									
<i>Elops hawaiiensis</i>	58	2					35	15			62	
<i>Gerres filamentosis</i>	5	100	40				40			40		
<i>Lates calcarifer</i>	47	5				27	19	15			58	
<i>Liza subviridis</i>	51	100	67									
<i>Megalops cyprinoides</i>	11	2					75	50			25	
<i>Melanotaenia splendida</i>	16	100	13				44	31				
<i>Mugil cephalus</i>	47	98	93	2	11			2		2		
<i>Nematalosa erebi</i>	117	95	79	14	19		1			1		
<i>Selenotoca multifasciata</i>	24	100	21	8	4	4						
<i>Strongylura krefftii</i>	12					13					100	

General diet

Overall, diets could be differentiated into two broad groupings on the basis of the percentage of fish that consumed animal prey (Figure 7.1). A group of six species (*Arramphus sclerolepis*, *Chanos chanos*, *Liza subviridis*, *Mugil cephalus*, *Nematalosa erebi* and *Selenotoca multifasciata*) had consumed less than 20% animal prey. Substantial proportions of all these species had consumed phyto-detritus (Table 7.1). On the basis of low presence of animal prey and high levels of phyto-detritus this group of species was designated as phyto-detritivores.

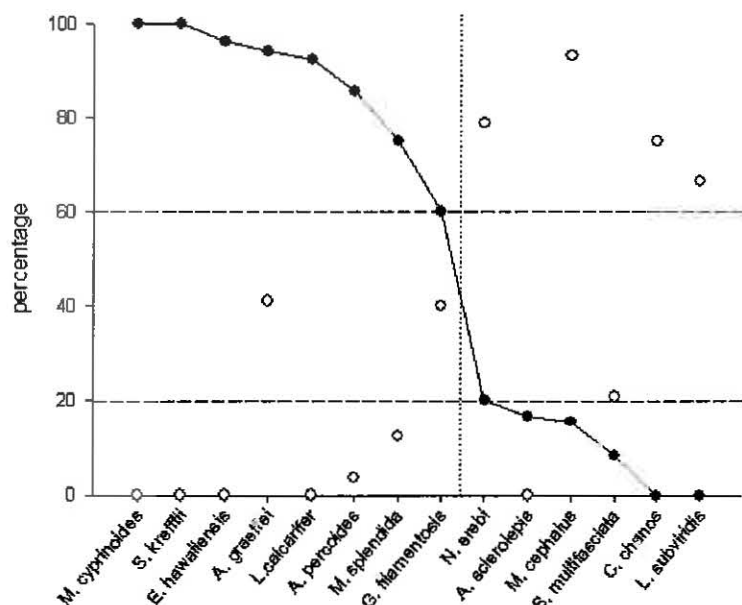


Figure 7.1. Percentage of individual fish (species with four or more individuals examined) that consumed animal prey (filled circles and solid line) and inorganic sediment (open circles). Horizontal dashed lines indicate the 20% and 60% levels; vertical dotted line indicates the split between phyto-detritivores and animal feeders.

While most of the phyto-detritivores ingested large amounts of inorganic matter (Figure 7.1) both *S. multifasciata* and particularly *A. sclerolepis* had ingested very little. The pelagic nature of *A. sclerolepis* and the absence of inorganic material suggests that it is a herbivore [probably a herbivorous omnivore as a reasonable proportion of individuals had consumed insects (Table 7.1)], rather than a detritivore. The low level of sediment ingested by *S. multifasciata* and centrifuge analysis (below) suggests it is also a herbivore. Except for four obvious predators [*Elops hawaiiensis*, *Lates calcarifer*, *Megalops cyprinoids*, *Strongylura krefftii*] most individuals of all other species had also consumed phyto-detritus (Table 7.1), but in all these cases 60% or more individuals had consumed animal prey (Figure 7.1), indicating they were higher-level consumers. As is always the case when phyto-detritus is consumed together with other prey, it is difficult to determine the extent to which the presence of phyto-detritus reflects use as a food source or is simply the result of accidental ingestion.

Dietary details from stomach content analysis

Regression tree analysis (Figure 7.2) indicated four dietary groups:

- (1) the six phyto-detritivores defined above, which consumed little but phyto-detritus (Figures 7.2, 7.3ab,);
- (2) medium to large omnivores (*Arius graeffei*, *Amniataba percoids*) regularly selecting a broad range of prey types, particularly insects, insect larvae and micro-crustaceans (Figures 7.2, 7.3a,b);
- (3) The four predators defined above (Figures 7.2, 7.3a,b); and
- (4) a pair of small carnivores (*Gerres filamentosis*, *Melanotaenia splendida*) which fed on a variety of prey (Figures 7.2, 7.3a,b).

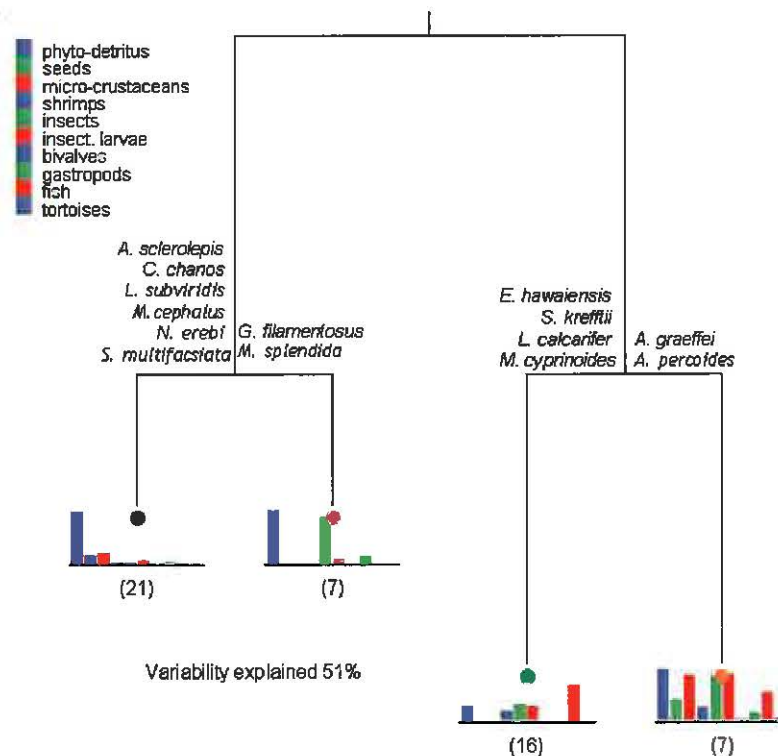


Figure 7.2. 1 SE regression tree for comparisons of diet for 14 species of fish from Fitzroy wetland pools
Data have been transformed $[\log(x+1)]$; numbers in brackets indicate sample sizes

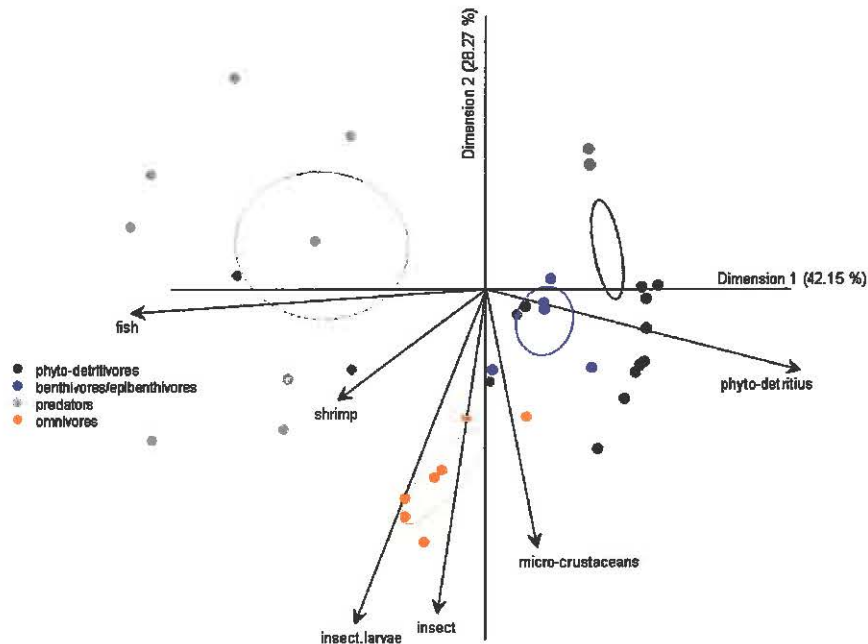


Figure 7.3a. Principal coordinates analysis of diet of 14 species of fish from Fitzroy wetland pools, using Bray-Curtis extended dissimilarities on $\log(x+1)$ data
Point colours indicate trophic groups; vectors indicate the direction of greatest increase of proportional contribution of particular prey types; ellipses are 90% confidence regions for group centroids

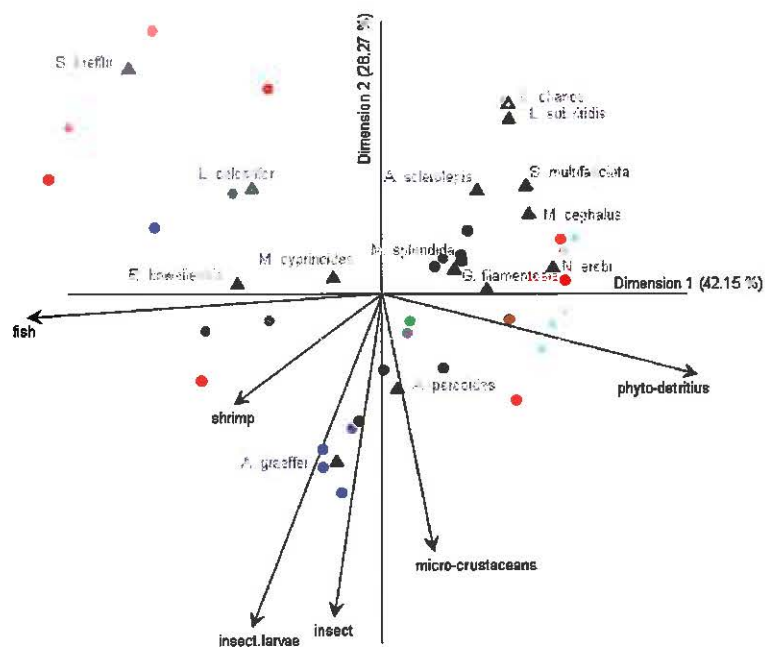


Figure 7.3b. Principal coordinates analysis of diet of 14 species of fish from Fitzroy wetland pools, using Bray-Curtis extended dissimilarities on $\log(x+1)$ data
Grey triangles indicate centres of density of species (grey labels); points indicate groups as in Figure 7.3a; vectors indicate the direction of greatest increase of proportional contribution of particular prey types; ellipses are 90% confidence regions for group centroids

Although these latter two species formed a single group they occurred in different environments (*G. filamentosis*: marine; *M. splendida*: fresh), and their grouping together seems to relate simply to the occurrence of insects in both diets (Table 7.1, Figure 7.2). Previous detailed studies suggest that *G. filamentosis* feeds mainly on benthic prey within the substrate (Wilson & Sheaves 2001), which is supported by relative high occurrences of inorganic sediment particles in fish in the present study (Figure 7.1). In contrast, low levels of sediment particles (Figure 7.1) and a diet of insects and insect larvae (Table 7.1, Figure 7.2) (Froese, & Pauly 2005) suggest *M. splendida* is more accurately classified as an epibenthic feeder.

Although location and trip were included in the regression tree analysis, neither was indicated as important in the 1-SE, four-leaf regression tree [generally considered the most appropriate tree under 10-fold cross-validation (Breiman *et al.* 1984), usually providing a similar result to that of an ANOVA ($\alpha=0.05$), in cases where ANOVA is appropriate]. No split was made on location until the six-leaf tree and none on trip until an eight-leaf tree, indicating a lack of substantial dietary differences between pools or trips.

Details of the diets on phyto-detritivores from centrifuge separation

There were sufficient guts from *L. subviridis* (39), *M. cephalus* (49), *N. erebi* (56) and *S. multifasciata* (27) available to allow meaningful centrifuge analysis.

A univariate regression tree clearly separated the phyto-detritivores into three groups based on the ratios of plant material/detritus in their diets (Figure 7.4).

S. multifasciata, the most herbivorous with 60% of individuals consuming only live plant material (Figures 7.4, 7.5c), was at one dietary extreme. The herbivorous, rather than detritivorous, nature of the diet of *S. multifasciata* is supported by the low occurrence of inorganic sediment ingested (Table. 7.1). All other phyto-detritivores, except the pelagic *A. sclerolepis*, ingested large amounts of inorganic matter. The opposite extreme was represented by *L. subviridis*, *N. erebi* and small *M. cephalus* (Figures 7.4, 7.5 a,b,d) where few individuals consumed high ratios of living plant material and most individuals consuming moderate to high proportions of detritus. Between the extremes was large *M. cephalus* with a highly variable plant/detritus ratios and a moderate percentage (35%) consuming only plant material (Figures 7.4, 7.5e). Again there were no detectable influences of pool or trip.

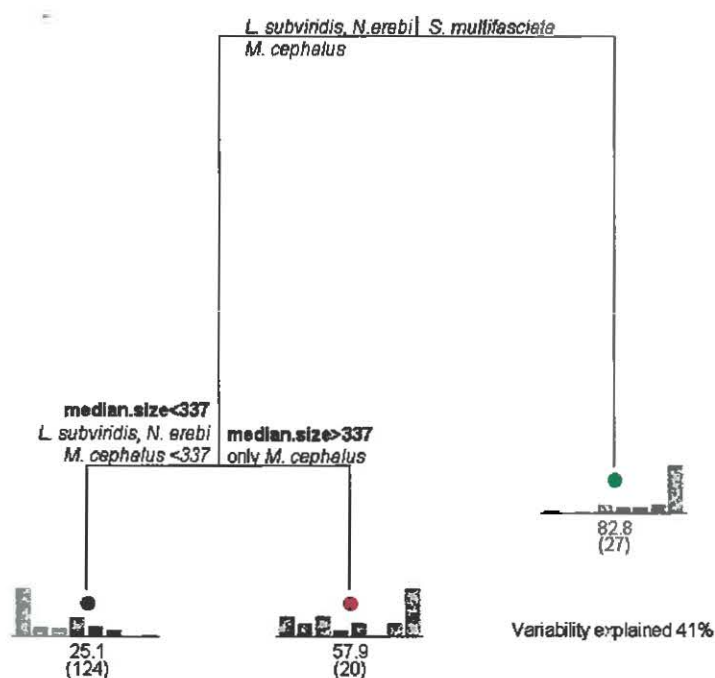


Figure 7.4. Univariate regression tree [1 SE tree, log(x+1) transformed data] differentiating the diets of four phyto-detritivores from Fitzroy wetland pools
Data are the proportional contribution of plant material to gut content

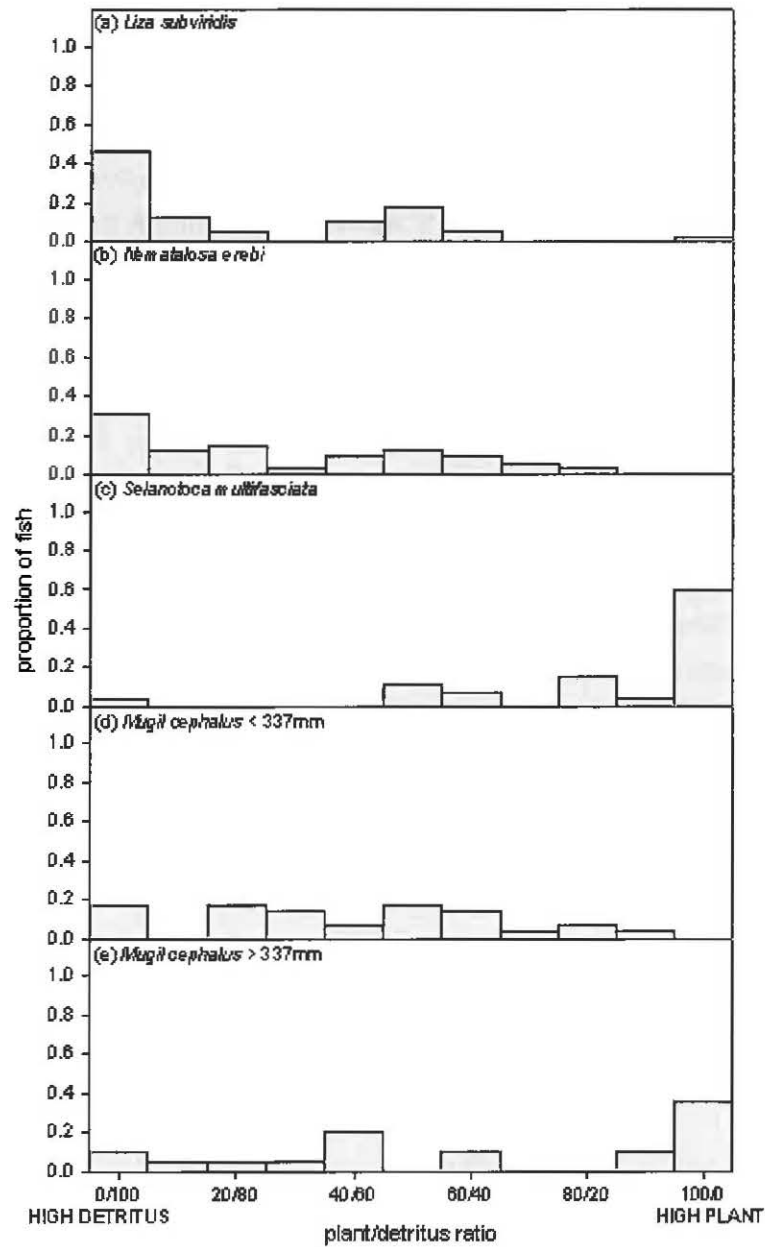


Figure 7.5. Proportion of fish with different ratios of living plant material (black bars) to detritus (grey bars) to total organic matter component of foregut contents

(a) *Liza subviridis*; (b) *Nematalosa erebi*; (c) *Selenotoca multifasciata*;
(d) *Mugil cephalus* < 337 mm; (e) *Mugil cephalus* > 337 mm

Discussion

Overall, the diets of major fish species of the Fitzroy wetland pools (Table 7.2) were similar to those reported for the same species from other environments (Blaber 1976, de Silva & Wijeyaratne 1977, Whitfield & Blaber 1978). Despite many species being present in pools with a variety of salinities and a range of levels of connection to other marine or freshwater environments, there was no evidence of spatial variation in diet of any species. Similarly, despite sampling throughout the year there was no indication of marked temporal change in diet.

Table 7.2. Trophic categorisations of fish from Fitzroy wetland pools

Species	Trophic category
<i>Amniataba percooides</i>	Omnivore
<i>Arius graeffei</i>	Omnivore
<i>Arramphus sclerolepis</i>	Herbivorous omnivore
<i>Chanos chanos</i>	Detritivore
<i>Elops hawaiiensis</i>	Predator
<i>Gerres filamentosis</i>	Benthivore
<i>Lates calcarifer</i>	Predator
<i>Liza subviridis</i>	Detritivore
<i>Megalops cyprinoides</i>	Predator
<i>Melanotaenia splendida</i>	Micro-omnivore
<i>Mugil cephalus</i>	Detritivore
<i>Nematalosa erebi</i>	Detritivore
<i>Selenotoca multifasciata</i>	Herbivore
<i>Strongylura krefftii</i>	Predator

Across all the pools, biomass was dominated by the six phyto-detritivores *A. sclerolepis*, *C. chanos*, *L. subviridis*, *M. cephalus*, *N. erebi* and *S. multifasciata* (Chapter 5). Such species generally consume a mixture of small, living plant cells and decaying organic material (along with its associated microbial film) (Michaelis 1993). Typical gut content consists of thousands of these fine particles, usually well mixed together. The large number and high degree of mixing makes their separation into component fractions difficult; not only must individual cellular components be identified but each particle needs to be separated from other particles. Consequently, determining the extent to which such species consume living plant material as opposed to detritus is a vexed problem.

However, in the present study, by the use of a simple centrifuging protocol, it was possible to clearly differentiate detritivores from herbivores based on the percentage of plant versus detritus cells they consumed. Four of the species, *C. chanos*, *L. subviridis*, *M. cephalus* and *N. erebi*, were detritivores (Table 7.2), while only one, *S. multifasciata*, was almost completely herbivorous. The final species, *A. sclerolepis*, was designated a herbivorous omnivore because it included a reasonable proportion of animal prey in its diet and previous studies (Robertson & Klumpp 1983) have shown related species to switch from herbivorous feeding during the day to feeding on micro-invertebrates at night.

Chapter 8 Trophic support of Fitzroy wetland pool ecosystems

Marcus Sheaves, Andrew Reville, Katya Abrantes and Ross Johnston

Introduction

While gut content analysis gives direct information on prey consumed by animals, it does not give information on what is actually assimilated. In many cases (e.g. predators) gut content information may be sufficient, but in the case of phyto-detritus feeders gut content analysis gives relatively diffuse information, essentially limited to the relative extent to which they consume detritus, living plant material and animal matter (Chapter 7). The dominance of fish biomass by phyto-detritivores in the Fitzroy wetland pools (Chapter 5) means that understanding their diet is a key to understanding the nutritional basis of food webs in the pools.

Stable isotope analysis is one technique that can be used to specifically investigate the identity of carbon actually assimilated, and thereby determine the primary producers most important in underpinning food webs (Peterson & Howarth 1987, Hesslein *et al.* 1991). The two isotopes are most commonly used are carbon (ratio of $^{13}\text{C}/^{12}\text{C}$: denoted as $\delta^{13}\text{C}$) and nitrogen (ratio of $^{15}\text{N}/^{14}\text{N}$: denoted as $\delta^{15}\text{N}$). Carbon isotopic ratios provide information on the identities of primary producers because they are set during photosynthesis and are specific to the primary producer. Nitrogen isotopic ratios depend on the source of nitrogen utilised and change in specific steps at each trophic transfer, providing information on the number of trophic steps an animal is above the primary producers; its trophic level.

The primary aims of this section of the study are (1) to determine the extent to which the sources of primary production supporting phyto-detritivores change between pools, and (2) to gain an understanding of the length of food chains in the wetland pools.

Methods

Stable isotope signatures

Samples of fish, invertebrates and primary producers for carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope analyses were collected from the pools throughout the study period. Small animals were analysed whole, but for larger animals (principally fish and large crustaceans) white abdominal muscle tissue was used for stable isotope analysis, and was separated from exoskeletal and intestinal material under a dissecting microscope using fine forceps.

All available plants and sources of detritus were collected. Estimates of the relative abundance of all macroscopic plants in and around the pools were made. Higher plants and green filamentous algae were collected by hand at each site. Two size fractions of seston, which included living plankton and suspended particulate organic matter, were collected by pumping the water with a bilge pump through 250 μm and 53 μm plankton nets. Where a conspicuous layer of microphytobenthos (MPB) was present, samples were collected by carefully removing the layer from the substrate, then washing it through a 5 μm filter with distilled water and removing all residual sediment particles under a dissecting microscope. Where no obvious layer of MPB was present, MPB was collected by scraping the surface sediments with a spatula and filtering the material through a 53 μm sieve into a glass bottle.

Colloidal silica (LUDOXTM) was added to a density of 1.2 and about two hours later the surface material was collected and washed into a 5 μm GF/F Whatman filter. Inspection under a microscope revealed that this fraction was composed mainly of diatoms and other microalgae together with a small amount of detritus. A coarse fraction of benthic particulate organic matter (cPOM) (250–1000 μm) was obtained by carefully disturbing the water just above the sediment with a spatula and collecting the suspended material by pumping it with a bilge pump through a 1000 μm and then a 250 μm sieve. A finer fraction (fPOM) was collected by passing the filtrate through a 125 μm sieve. The collected material was placed in glass vials with colloidal silica (LUDOXTM, density = 1.2) for two hours, after which the layer of floating material was pipetted off and washed through a 53 μm sieve.

All samples were processed within a day or two of collection. Basal carbon sources (primary producers and detritus) and animal tissues were dried to a constant weight at 60°C, then homogenised with a mortar and pestle. Samples were analysed by CSIRO Tasmania and Griffith University, Queensland, where

the isotopic signatures were determined using a mass spectrometer coupled with an element analyser. Results are expressed as per mil deviations from the standards, as defined by the equation: $\delta^{13}\text{C}$, $\delta^{15}\text{N} = [(R_{\text{sample}}/R_{\text{reference}}) - 1] \times 10^3$, where $R = {}^{13}\text{C}/{}^{12}\text{C}$ for carbon and ${}^{15}\text{N}/{}^{14}\text{N}$ for nitrogen. PDB limestone and atmospheric dinitrogen served as reference standards for ${}^{13}\text{C}$ and ${}^{15}\text{N}$, respectively. Duplicates were run every 12th sample and two standards were also run after every 12 samples. Results had a precision of 0.3 ‰ (1 SD) for $\delta^{13}\text{C}$ and 0.1 ‰ (1 SD) for $\delta^{15}\text{N}$, which was maintained with reference samples of calibrated Australian National University (ANU) cane sucrose for $\delta^{13}\text{C}$ and atmospheric dinitrogen for $\delta^{15}\text{N}$. The nitrogen and carbon content of each sample were also measured.

Statistical analysis

The IsoSource mixing model of Phillips and Gregg (2003) was used to determine the relative importance of different producers to the nutrition of penaeids at each site. This model uses mass balance assumptions and calculates the possible combinations of the different autotrophs that can explain the isotopic signatures of consumers, by analysing small increments (2% in this case) of each of the autotrophs' possible contributions, from 0 to 100%. The combinations that correspond to a result within a small distance of that of the consumer are considered feasible solutions, with the results being a distribution of feasible solutions for each of the autotrophs (Phillips & Gregg 2003). Based on the estimates of relative abundance, producers present in low abundance at a pool were omitted from analyses. Producers possessing similar signatures were grouped to minimise the number of sources and hence narrow the range of possible solutions (Phillips *et al.* 2005). Fractionation values of phyto-detritivores were set equivalent to one trophic level. This was obviously suitable for the plants consumed directly but not necessarily for plants consumed after decomposition into detritus. However, preliminary studies suggested it was best to assume no additional fraction during decomposition to detritus (see below).

Trophic fractionation values of 1.3 $\delta^{13}\text{C}$ and 2.9 $\delta^{15}\text{N}$ [mean values for muscle tissue (McCutchan *et al.* 2003)] were assumed for all fish and crustaceans where isotopic signatures were estimated from muscle tissue. Ratios of stable isotopes can change between diet and consumer due to differential digestion or fractionation during assimilation and metabolic processes (McCutchan *et al.* 2003), and the exact degree of fractionation assumed has a substantial bearing on the interpretation of the contribution of specific dietary components.

Consequently, it was important to validate the fractionation values assumed for phyto-detritivorous fish. When it has been attempted, fractionation values are usually validated experimentally. However, this was not a realistic option with phyto-detritivores because if detritus was provided in an experimental situation there was no way of determining what components of the detritus were actually assimilated, and consequently what the correct dietary stable isotope values were. Consequently, an indirect approach was used, in which the stable isotope signature of the large predatory fish, *Lates calcarifer*, was related to its possible dietary sources in an IsoSource model, using the assumed fraction values, and the results compared to its diet as detailed in Chapter 7.

Fractionation values of $0.3 \delta^{13}\text{C}$ and $2.1 \delta^{15}\text{N}$ [mean values for whole animals (McCutchan *et al.* 2003)] were used for all invertebrates analysed whole. In contrast to fish, where trophic fractionation values have been determined experimentally (McCutchan & Lewis 2002) and been applied successfully in many experimental studies, specific fractionation values for most invertebrate groups are poorly understood. Consequently, there is no certainty that the average fraction adjustments used (McCutchan & Lewis 2002) were appropriate for particular invertebrate groups, and no data were available for independent evaluation.

Assumptions

Isotope signatures of decomposed plant material

Evaluation of the contribution of different sources of primary production in systems dominated by detritus feeders is complicated for three reasons: (a) it is difficult to unambiguously identify the original source of much of the decomposed material; (b) the extent to which detritivores derive nutrition from the decomposing material itself, rather than the microbial community using the material as a substrate, is unclear; and (c) the extent (and even the direction) of changes in producer isotopic signatures due to secondary processing by decomposers such as microbes and fungi is unknown. These problems make it difficult to determine appropriate source values to assign to potential primary producers and difficult to determine the correct number of trophic steps and levels of fractionation at each step, to assume between detritivores and the original producer isotopic signatures.

The first problem was addressed by investigating the change in stable isotope profiles from fresh to decomposed leaves of the mangrove, *Aegiceras corniculatum*, a species for which decomposed leaves could be unambiguously identified from a number of pools.

The second and third problems (use of decomposing material versus attached microbial component, and effect of secondary processing) are generally unresolved for any system necessitating the pragmatic assumptions that the source material is the major contributor to nutrition and that any bacterial component assimilated by the detritivore has the same signature as the substrate on which it is growing (i.e. fractionation is assumed to be zero).

Detailed isotope signatures

The high cost of analyses meant that extensive temporal and spatial replication was not possible at all sites. Consequently, more extensive sampling was concentrated at one site, the Twelve Mile Creek brackish site, which had physical conditions intermediate between other sites and had a mixture of marine- and freshwater-derived fauna. More detailed studies concentrated on this pool. The results of these studies were assumed to apply to the other pools.

Results

Producer stable isotope profiles

The suites of potentially important primary producers varied among sites; however, six producer groups [the saltbush, *Atriplex muelleri*, the salt couch, *Sporobolus virginicus*, MPBs (micro-phytobenthos), seston (suspended organic particles including organic detritus, inorganic particles and phytoplankton), green filamentous algae and fPOM (fine particulate organic matter)] occurred at three or more sites (Figure 8.1), allowing investigations of changes in producer isotope profiles.

The clearly identifiable plant species, *A. muelleri* and *S. virginicus*, showed little variation in $\delta^{13}\text{C}$ as did MPBs (Fig 8.1a), while the other three groups showed considerable variability in $\delta^{13}\text{C}$. This variation probably reflected contributions of different decaying plants to the seston and fPOM at different sites, and a mixture of different species in the case of green filamentous algae. In contrast, $\delta^{15}\text{N}$ values varied greatly for *A. muelleri* and to a lesser extent for other producer groups. The variation in nitrogen sources among sites, and the indication of different composition of the complex producer groups (seston, fPOM, green filamentous algae) between sites meant that IsoSources modelling of stable isotope ratios could only sensibly be investigated on a site-by-site basis.

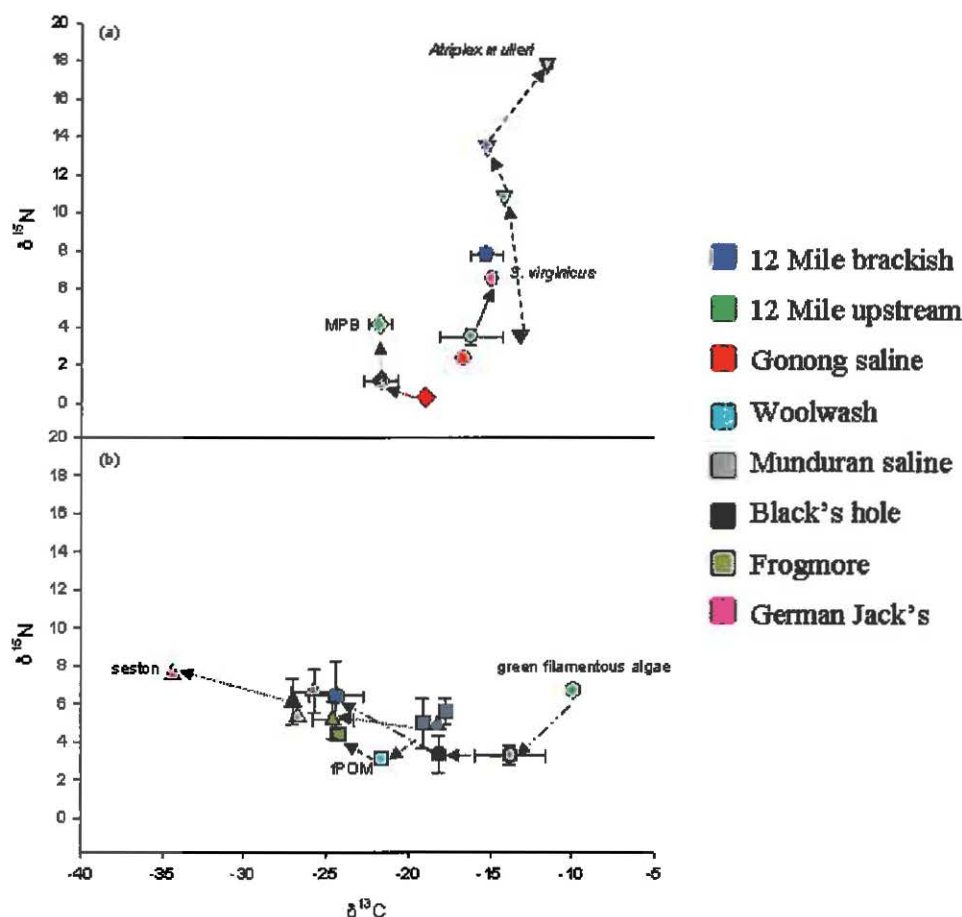


Figure 8.1. Comparison of stable isotope ratios for producer groups common to three or more sites. Data are means ± 1 SE; (a) groups with little variation in $\delta^{13}\text{C}$; (b) groups with little variation in $\delta^{15}\text{N}$

Isotope signatures of decomposed plant material

There was no indication that decomposed *A. corniculatum* leaves differed substantially from fresh leaves in either $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ (Table 8.1, Figure 8.2), a result consistent with other work on decomposing mangrove leaves (Schwamborn *et al.* 2002). Because it was not possible to clearly identify the source of most other decomposing material, this result was assumed to hold for other plants and a single trophic step was assumed between sources of detritus and detritivores.

Table 8.1. Comparison of stable isotope values for fresh and decomposed *Aegiceras corniculatum* leaves

Effect	Mean Square	df	F	p
$\delta^{13}\text{C}$	1.989	1/9	1.617	0.2354
$\delta^{15}\text{N}$	0.2282	1/9	0.1542	0.7037

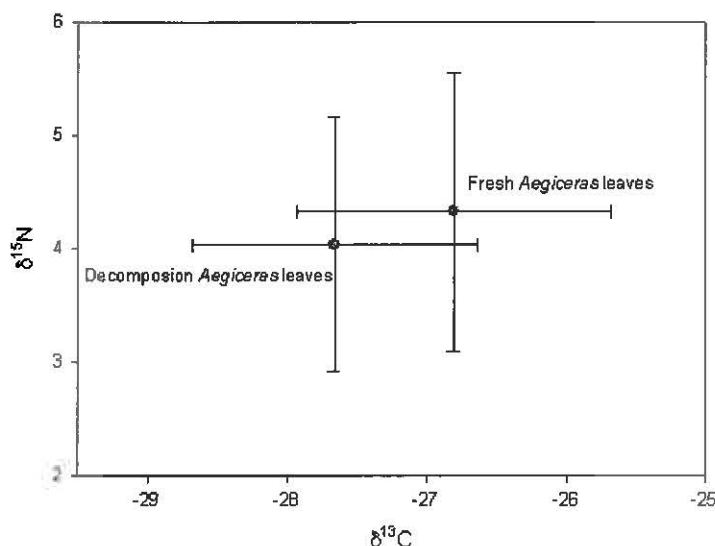


Figure 8.2. Comparison of stable isotope profiles of fresh and decomposed *Aegiceras corniculatum* leaves

Temporal variation in isotope signatures

In the Twelve Mile brackish pool, where temporal variation in isotopic signatures was investigated, eight consumers (the crustaceans: *Cardinia nilotica* and *Corophium* sp.; and the fish: *Elops hawaiiensis*, *Lates calcarifer*, *Liza subviridis*, *Mugil cephalus*, *Nematalosa erebi* and *Selenotoca multifasciata*) were captured on more than three sampling occasions, providing useful data for temporal comparisons.

Most comparisons showed little indication of temporal variation, but there were some exceptions. For both $\delta^{13}\text{C}$ (Table 8.2) and $\delta^{15}\text{N}$ (Table 8.3) two species showed substantial temporal variations and one species showed weak evidence of temporal change. Both $\delta^{13}\text{C}$ (Figure 8.3a) and $\delta^{15}\text{N}$ (Figure 8.3b) varied substantially over time for the shrimp *Cardinia nilotica*, with both values differing for each month when the shrimp was captured. In contrast, *Corophium* sp. showed substantial differences in $\delta^{15}\text{N}$ only between May 2004, and November 2004 and February 2005 (Figure 8.4), and only a weak indication of variation in $\delta^{13}\text{C}$. There was a substantial difference in $\delta^{13}\text{C}$ for *Liza subviridis* only between July 2004 and September 2005 (Figure 8.5) but no difference in $\delta^{15}\text{N}$. The only other indication of difference was a weak indication of change in the $\delta^{15}\text{N}$ value of *Lates calcarifer*.

Table 8.2. Comparison of $\delta^{13}\text{C}$ stable isotope values over time for eight species from the Twelve Mile brackish pool; Species showing clear effects are highlighted in bold

Species	Mean Square	df	F	p
<i>Caridina nilotica</i>	6.641	2/5	87.44	0.0001
<i>Corophium</i> sp.	4.049	3/3	8.42	0.0567
<i>Elops hawaiiensis</i>	0.255	2/2	0.39	0.7184
<i>Lates calcarfier</i>	0.845	4/4	0.85	0.9004
<i>Liza subviridis</i>	5.382	4/3	14.19	0.0273
<i>Mugil cephalus</i>	5.781	3/6	1.1	0.4200
<i>Nematalosa erebi</i>	2.623	3/10	0.3	0.8256
<i>Selenotoca multifasciata</i>	5.952	4/4	1.58	0.3353

Table 8.3. Comparison of $\delta^{15}\text{N}$ stable isotope values over time for eight species from the Twelve Mile brackish pool; Species showing clear effects are highlighted in bold

Species	Mean Square	df	F	p
<i>Caridina nilotica</i>	2.053	2/5	81.05	0.0001
<i>Corophium</i> sp.	0.609	3/3	19.56	0.0179
<i>Elops hawaiiensis</i>	0.527	2/2	3.02	0.2487
<i>Lates calcarfier</i>	0.665	4/4	5.82	0.0582
<i>Liza subviridis</i>	0.548	4/3	2.03	0.2932
<i>Mugil cephalus</i>	3.39	3/6	2.87	0.1259
<i>Nematalosa erebi</i>	0.744	3/10	1.23	0.3510
<i>Selenotoca multifasciata</i>	0.522	4/4	0.74	0.6081

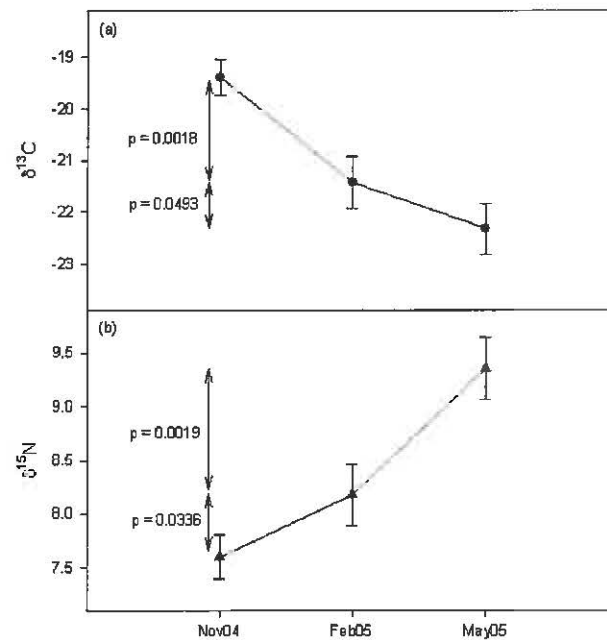


Figure 8.3. Comparison of (a) $\delta^{13}\text{C}$ and (b) $\delta^{15}\text{N}$ values for *Caridina nilotica* over time at the Twelve Mile Creek brackish pool
Two-headed arrows and associated p values indicate probability of two means differing estimated using a *post hoc* HSD test for unequal sample sizes

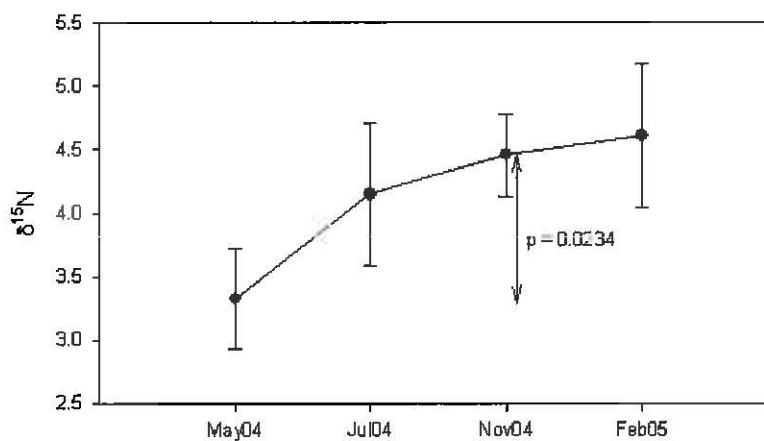


Figure 8.4. Comparison of $\delta^{15}\text{N}$ values for *Corophium sp.* over time at the Twelve Mile Creek brackish pool
Two-headed arrows and associated p values indicate probability of two means differing estimated using a *post hoc* HSD test for unequal sample sizes

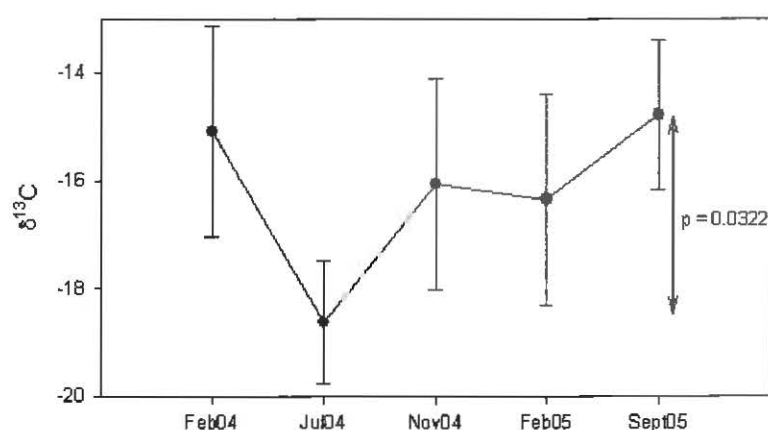


Figure 8.5. Comparison of $\delta^{13}\text{C}$ values for *Liza subviridis* over time at the Twelve Mile Creek brackish pool
Two-headed arrows and associated p values indicate probability of two means differing estimated using a *post hoc* HSD test for unequal sample sizes

General patterns in isotope signatures

As is usually the case, consumers tended to be more enriched in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ than most producers for brackish (e.g. Twelve Mile brackish Figure 8.6), freshwater (e.g. Twelve Mile upstream Figure 8.7) and saline (e.g. Gonong saline Figure 8.8) sites. However, while consumer and producer signatures were well separated in saline sites, there was considerable overlap in freshwater and brackish sites, particularly in the case of gastropods and insects.

Across all types of pools, fish tended to be more enriched in $\delta^{15}\text{N}$ than were other consumer groups. This should not be taken as an unambiguous indication that fish occupy higher trophic positions, as is often the interpretation, because the degree of fractionation depends on the type of consumer and the type of tissue analysed, as well as the number of trophic steps between producer and consumer. However, when species details are considered (e.g. Twelve Mile brackish, Figure 8.9), it is clear that food chains in the pools were short. Predatory fish, like *E. hawaiiensis* and *L. calcarifer*, were only one trophic step above phyto-detritivores (assuming fraction of 2.9 $\delta^{15}\text{N}$ per trophic step) making a two-step food chain (Figure 8.9).

The omnivorous benthic invertebrate feeders *A. australis*, *G. filamentosus* and *A. reinhardtii* had values about half a step above polychaete worms, about one trophic step above crustaceans like *Macrobrachium adscitum*, and about two steps above a variety of insect larvae, all of which are typical prey. These prey

are a mixture of primary and secondary consumers indicating that food chains leading to these species were no more than three steps long. Other benthic feeders, like *A. telkara*, had lower $\delta^{15}\text{N}$ signatures, an indication of preferential targeting of different parts of the resource.

There was little clear pattern in $\delta^{15}\text{N}$ values (Figure 8.10). However, particularly for fish (Figure 8.10a) and crustaceans (Figure 8.10b), freshwater in-stream pools tended to have more depleted $\delta^{13}\text{C}$ values than large freshwater lagoons did, while saline pools had intermediate levels, suggesting differences in the types of producers at the bases of food chains in the different types of pools. At a more detailed level, there were clear differences in sources of primary production among pools over and above taxonomic differences.

While there were clear differences in the sources of nutrition for different species of phyto-detritivorous fish within any pool, the sources of nutrition of each species varied more greatly between pools (Figure 8.11), and signatures of different species from each pool formed distinct clusters. At Gonong saline *M. cephalus* and *L. subviridis* differed substantially from the other phyto-detritivores but their signatures were highly enriched in $\delta^{15}\text{N}$ compared to producers at Gonong brackish, suggesting these two species may have only recently entered the pool (see below). When these two points are ignored, the data indicate clear differences in nitrogen sources between major pool types: freshwater pools (Munduran fresh, Twelve Mile upstream and downstream, Frogmore and Woolwash) had intermediate ^{15}N values, while the two saline pools had relatively depleted values and Twelve Mile brackish relatively enriched values.

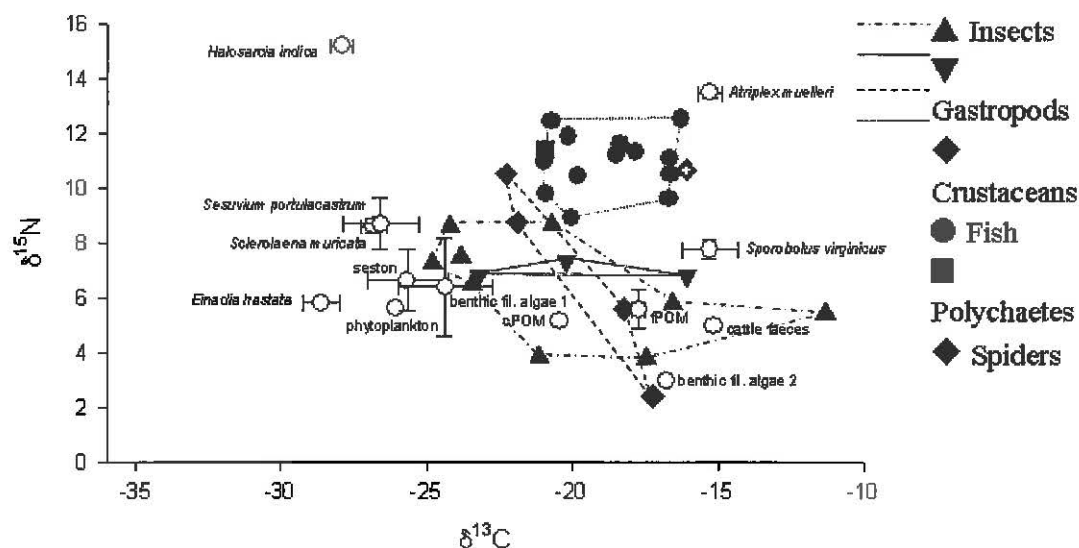


Figure 8.6. Mean stable isotope values for producers (unfilled symbols) and consumers (filled symbols) at Twelve Mile brackish; error bars for producers are standard errors

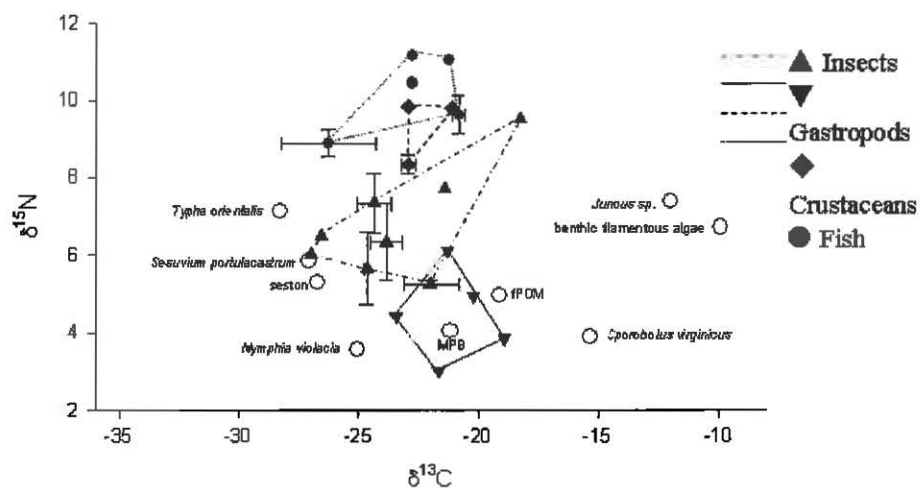


Figure 8.7. Mean stable isotope values for producers (unfilled symbols) and consumers (filled symbols) at Twelve Mile upstream; error bars for producers are standard errors

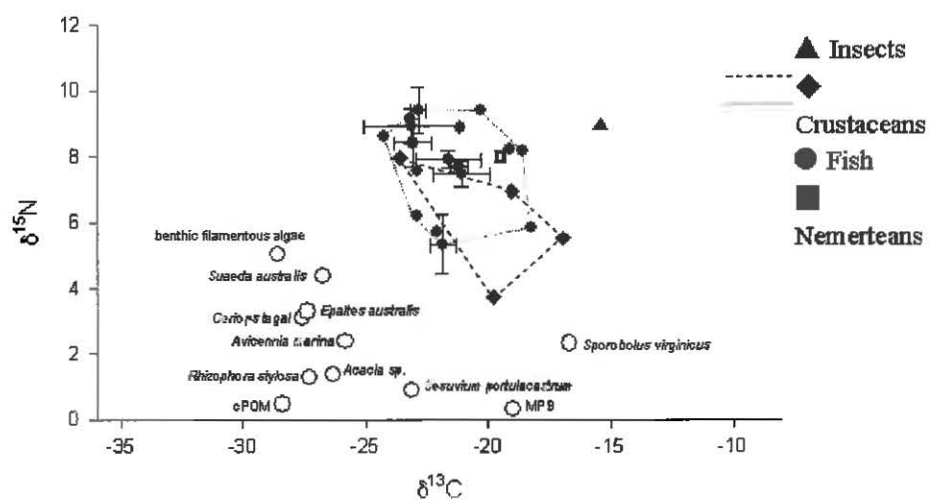


Figure 8.8. Mean stable isotope values for producers (unfilled symbols) and consumers (filled symbols) at Gonong saline; error bars for producers are standard errors

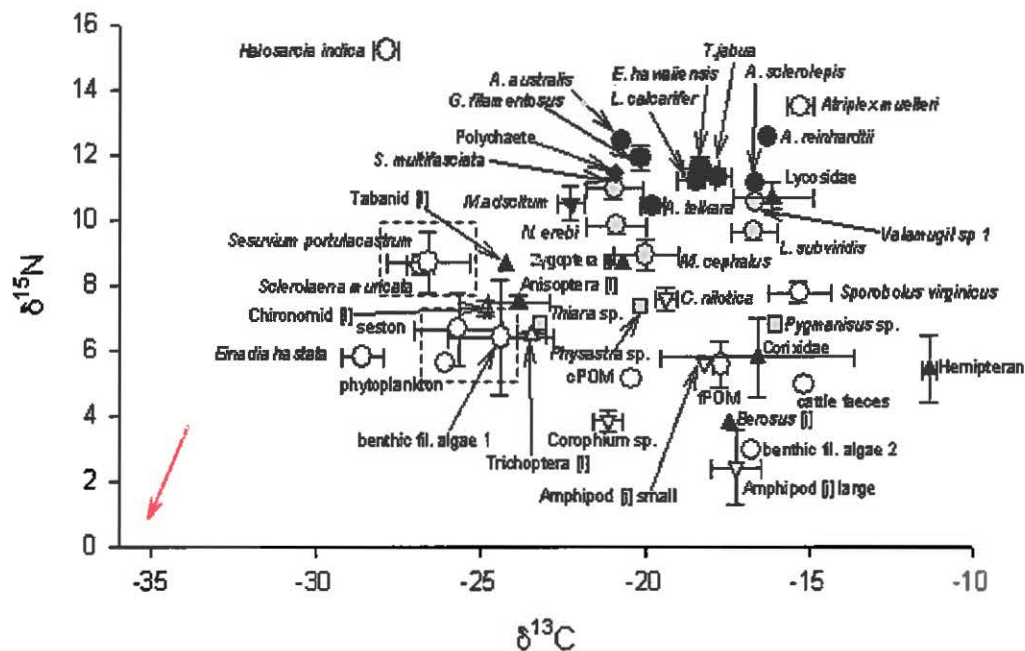


Figure 8.9. Mean stable isotope values for producers (unfilled symbols) and fish (filled symbols—grey: primary consumers; black: higher-order consumers) at Twelve Mile brackish; error bars are 1 standard error. Dashed boxes indicate primary producers grouped for IsoSource analyses; red arrow in bottom left indicates the approximate change in signature for one trophic step assuming changes in $\delta^{13}\text{C}$ of 1.3 and $\delta^{15}\text{N}$ of 2.9.

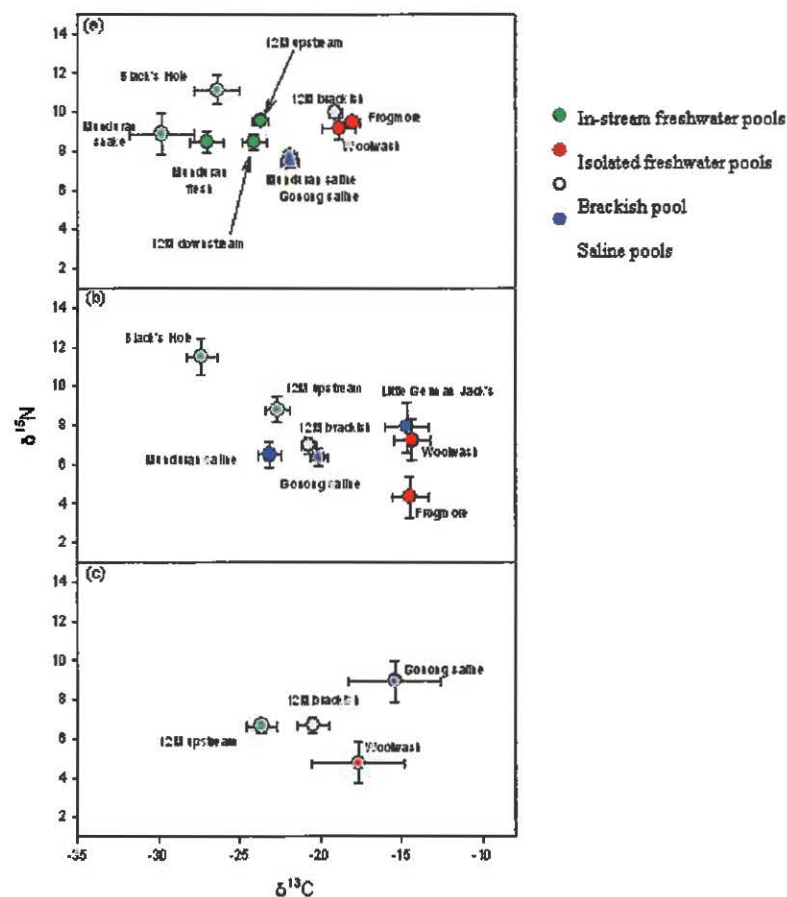


Figure 8.10. Comparison of mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for (a) fish, (b) crustaceans and (c) insects among Fitzroy wetland pools; error bars are 1 SE.

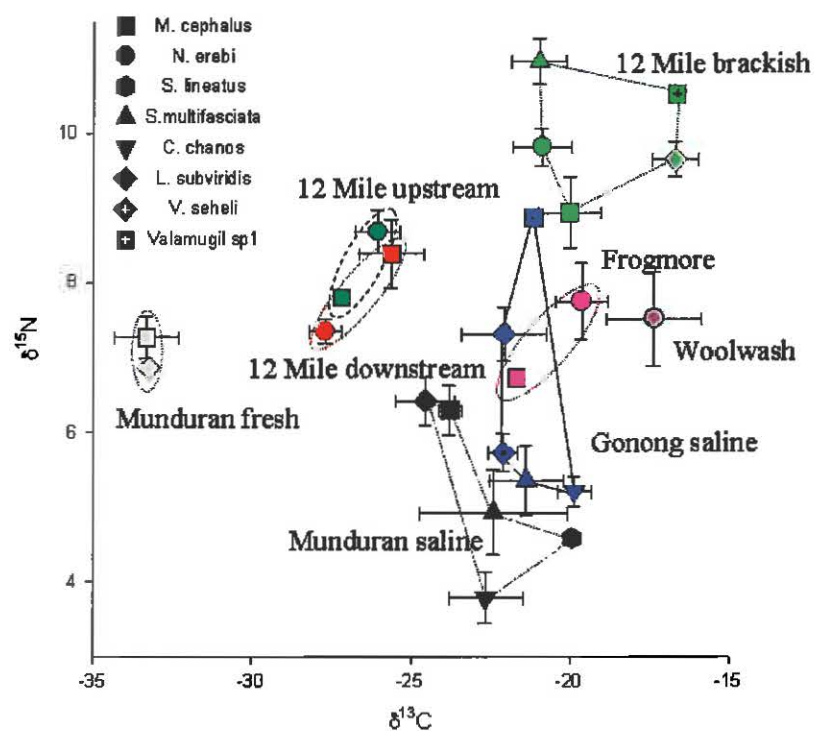


Figure 8.11. Comparison stable isotope profiles of detritivorous fish among Fitzroy wetland pools; error bars are 1 SE; sites are colour-coded

IsoSource models

Box 8.1 summarises the appropriate approach to interpreting IsoSource output.

Box 8.1. Interpreting IsoSource analyses

The IsoSource modelling of Phillips and Gregg 2003 addresses the problem of determining the proportional contribution of several sources of nutrition to a consumer when there are many more sources ($>n+1$) than isotopic signatures. It employs a linear model approach based on mass balance equations. All possible combinations of each source's contribution (0–100%) are examined in small increments (2% in this case), and all combinations that sum to the observed consumer isotopic signature are considered feasible solutions.

The outputs of IsoSource analyses presented here take a graphical form with a number of features:

1. A series of points representing the source isotopic signatures, connected by a polygon joining the peripheral points. Any consumer signature that falls within this polygon, after correction for fractionation, has definable 'feasible solutions'. If the corrected signature falls outside the polygon, an important source has been overlooked or the consumer has migrated from elsewhere.
2. The original consumer isotopic signature (a yellow point), and its signature corrected for fractionation (a red point connected to the original signature with an arrow). The usefulness of the model depends on the accuracy of the fractionation estimates.
3. A graphical representation (relative frequency of contributions for each 2% increment) of the distribution of feasible solutions for each nutritional source. These are termed 'feasible solutions' and should be viewed as a distribution of possible solutions rather than considering some average contribution.

The *Lates calcarifer* example below shows the distribution of feasible solutions for one source of nutrition. It has a range of solutions from zero (no input) to a maximum of about 40%, indicating that under a number of scenarios the source made a substantial feasible contribution. The median of around 20% is interesting but, given the level of uncertainty associated with fractionation estimates and potential errors in the estimation of isotopic signatures, it should not be the primary focus of interpretation. However, where the range is small and the median is about zero, it seems reasonable to assume that the source is unlikely to be of importance. In the *Lates calcarifer* example, most of the distribution is above zero, indicating that the producer made a feasible contribution to most models. Given this, and the 40% maximum contribution, it seems safe to conclude that this source is likely to make a small-to-medium contribution to the nutrition of the consumer.

Lates calcarifer from Twelve Mile brackish

While predators were in low abundances in most sites, there was sufficient dietary data for *Lates calcarifer* from Twelve Mile brackish for informative IsoSource analysis that could be compared to dietary analysis (Chapter 7) as a means of investigating the usefulness of the assumed fraction values. Eight animal taxa were possible contributors to the diet of *L. calcarifer* (Figure 8.12). Fractionation estimated for a single trophic step moved the isotopic signature to the centre of the polygon of the possible contributors (Figure 8.12), which were principally primary consumers, suggesting two trophic steps from phyto-detritus to the top of

the food chain. IsoSource modelling (Figure 8.12) indicated reasonable 'feasible contributions' from most sources, with corixids and insect larvae contributing to most models and, despite a broad range of possible contributions, *C. nilotica* and *M. cephalus* having substantial inputs (over 60%) to a number of models. This outcome aligns closely with dietary analysis (Chapter 7) supporting the assumption that the fractionation values assumed for fish (1.3 $\delta^{13}\text{C}$ and 2.9 $\delta^{15}\text{N}$) are appropriate in this study.

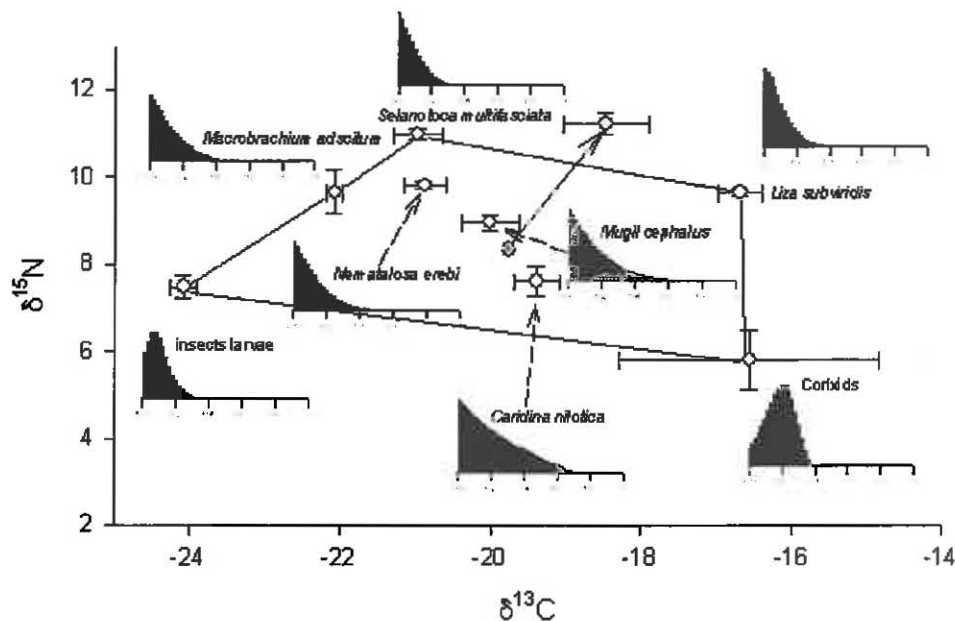


Figure 8.12. IsoSource results for *Lates calcarifer* from Twelve Mile brackish; error bars are standard errors

IsoSource models of producer importance to primary consumers

Twelve Mile brackish

Samples were collected from thirteen potential primary producer groups at the Twelve Mile brackish pool (Figure 8.9). Two species, *Halosarcia indica* and *Atriplex muelleri*, had stable isotope signatures very different from all other producer groups. However, these species were only present in low abundances at the site, so were not included in IsoSource models. *Sesuvium portulacastrum* and *Sclerolaena muricata* had almost identical signatures, so were combined as a single group. Similarly, seston, phytoplankton and benthic filamentous algae sp.1, had very similar signatures so were combined into a single group represented by the group means. Thus eight producers or producer groups were included in IsoSource models for Twelve Mile brackish (Figures 8.13-8.17, 8.19-8.22).

With its mixture of fresh and marine species, the Twelve Mile Creek brackish pool had a richer fauna of phyto-detritus-feeding fish (i.e. primary consumers) than did any other pool. The four species that primarily fed on detritus—the mullet *Liza subviridis*, *Mugil cephalus*, juveniles of an unidentifiable *Valamugil* species and the bony bream *Nematalosa erebi*—demonstrated two different dietary compositions. *Liza subviridis* (Figure 8.13) and *Valamugil* sp. (Figure 8.14) had relatively enriched $\delta^{13}\text{C}$ signatures, leading to IsoSource models with a broad range of feasible contributions by the salt couch, *Sporobolus virginicus* and the reed *Juncus* sp. The phytoplankton/benthic filamentous algae/seston group, fine and coarse POM, cattle faeces, and benthic filamentous algae type 2, had relatively small ranges of feasible contributions with median contributions at or close to zero, indicating they were unlikely to be major contributors to nutrition.

In contrast, although the *Sclerolaena muricata*/*Sesuvium portulacastrum* group had relatively low feasible contributions, for both species the median was well above zero, indicating that a small contribution by one or both of these species was likely. This was especially the case for *Valamugil* sp., where the range of feasible contributions did not include zero, indicating that all feasible IsoSource compositions included this group. Again, in contrast, *M. cephalus* (Figure 8.15) and *N. erebi* (Figure 8.16) had relatively depleted $\delta^{13}\text{C}$ signatures, with the most likely feasible contributions from the *S. muricata*/*S. portulacastrum* group and the phytoplankton/benthic filamentous algae/seston group, with all models for *N. erebi* containing the *S. muricata*/*S. portulacastrum* group.

Selenotoca multifasciata (Figure 8.17) had a $\delta^{13}\text{C}$ signature close to those of *M. cephalus* and *N. erebi* but a more enriched $\delta^{15}\text{N}$ signature (Figure 8.9). Like *L. subviridis* and *Valamugil* sp., only *S. virginicus*, *Juncus* sp. and the *S. muricata*/*S. portulacastrum* group had substantial feasible contributions to the nutrition of *S. multifasciata* (Figure 8.17), but in contrast to *L. subviridis* and *Valamugil* sp., all feasible models had a substantial contribution from the *S. muricata*/*S. portulacastrum* group.

Gut content analysis (Chapter 7) showed *S. multifasciata* consumed substantial amounts of green plant material, apparently filamentous algae. Although most IsoSource models suggested only low contributions of filamentous algae, the different $\delta^{15}\text{N}$ level of *S. multifasciata* from the other primary consumer fish supports the idea of dietary difference. On these grounds the value for the filamentous algae/seston/phytoplankton group (the algal group with the largest feasible contributions) was set at its 99th percentile value (10% contribution) and other sources re-evaluated. Under this scenario only *Sclerolaena*/*Sesuvium* (54%) and *S. virginicus* (38%) made additional feasible contributions.

The $\delta^{15}\text{N}$ signatures of many invertebrate primary consumer groups from Twelve Mile brackish were too depleted, compared to any of the primary producer set, to allow IsoSource models to be developed. In fact many were too depleted even without any fractionation adjustment applied (Figure 8.9).

After adjustment for fractionation, invertebrate primary consumers showed a range of $\delta^{13}\text{C}$ values somewhat greater than (but including) those of phyto-detritivorous fish (Figure 8.18). In contrast, $\delta^{15}\text{N}$ signatures of the invertebrates were lower than those of fish.

These relatively depleted $\delta^{15}\text{N}$ signatures mean that in contrast to fish, where models suggested nutrition based largely on higher plant detritus, IsoSource models for invertebrates indicated that algae and similar sources were usually the principal contributors to nutrition (Figures 8.19–8.22). However, models for some taxa did indicate a substantial input by cattle faeces or higher plants (e.g. the gastropod *Pymanisus* sp., Figure 8.21).

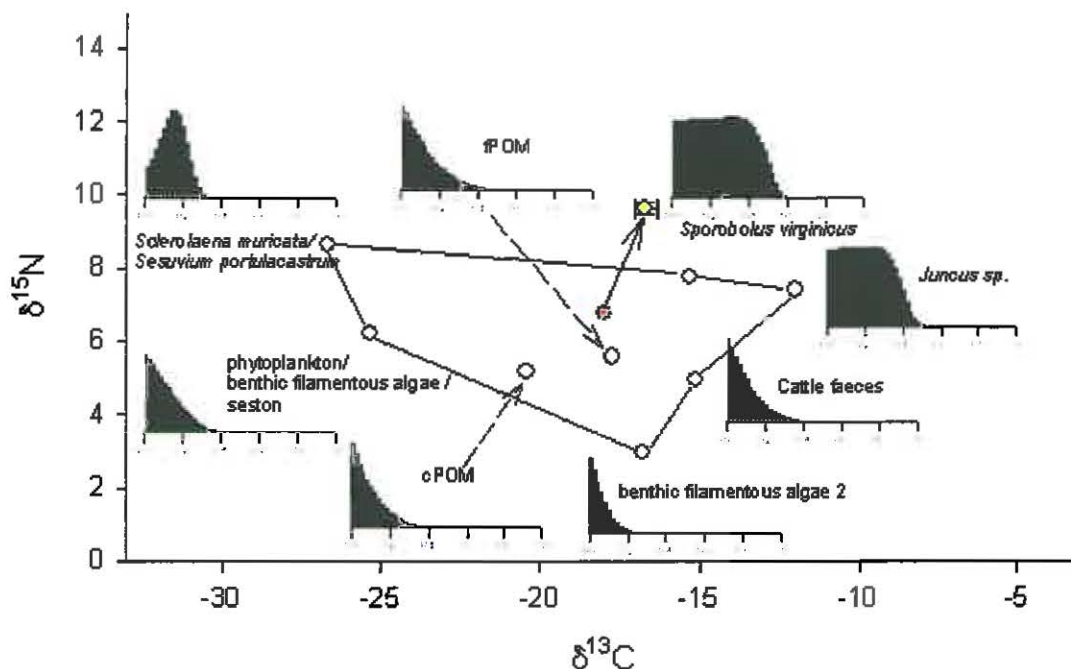


Figure 8.13. IsoSource results for *Liza subviridis* from Twelve Mile brackish; error bars are standard errors

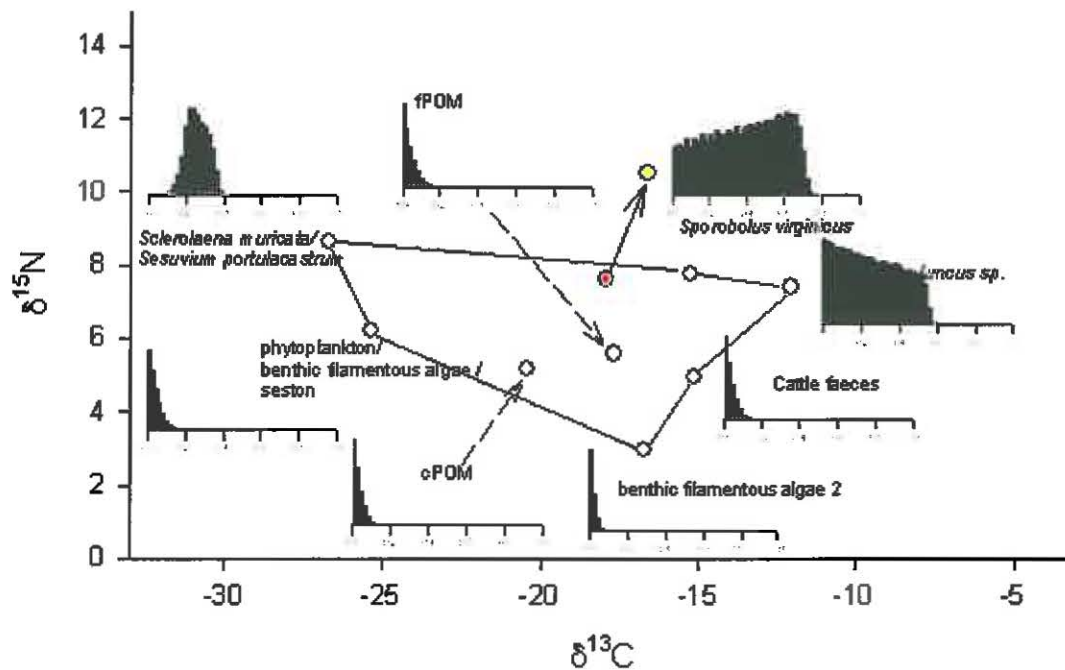


Figure 8.14. IsoSource results for *Valamugil sp.1* from Twelve Mile brackish; error bars are standard errors

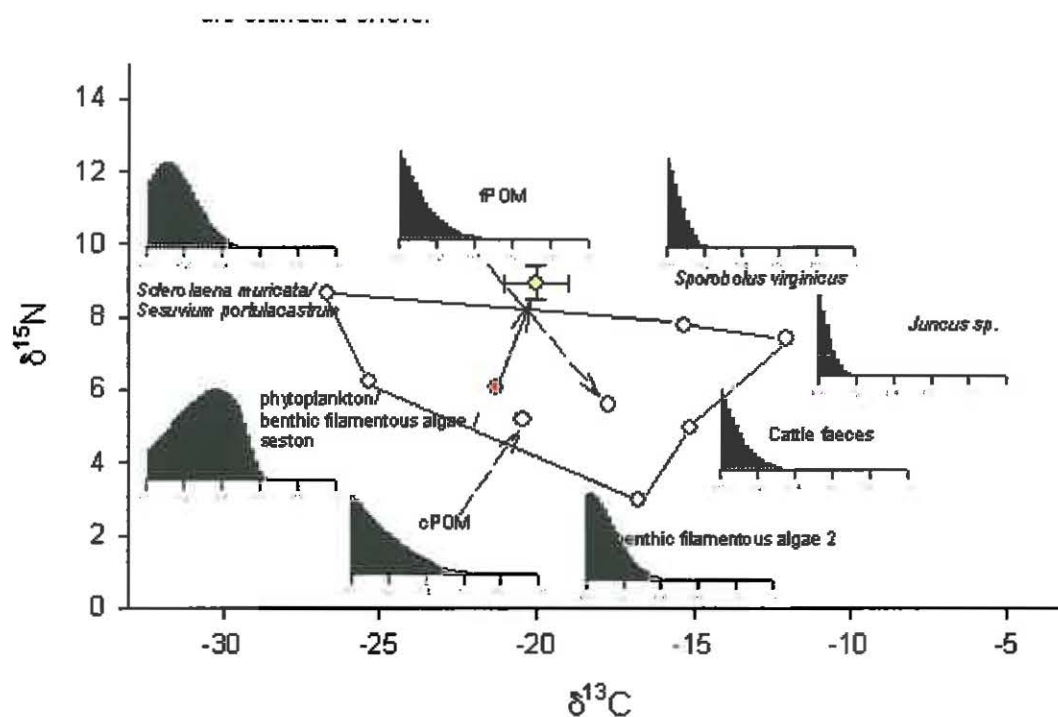


Figure 8.15. IsoSource results for *Mugil cephalus* from Twelve Mile brackish; error bars are standard errors

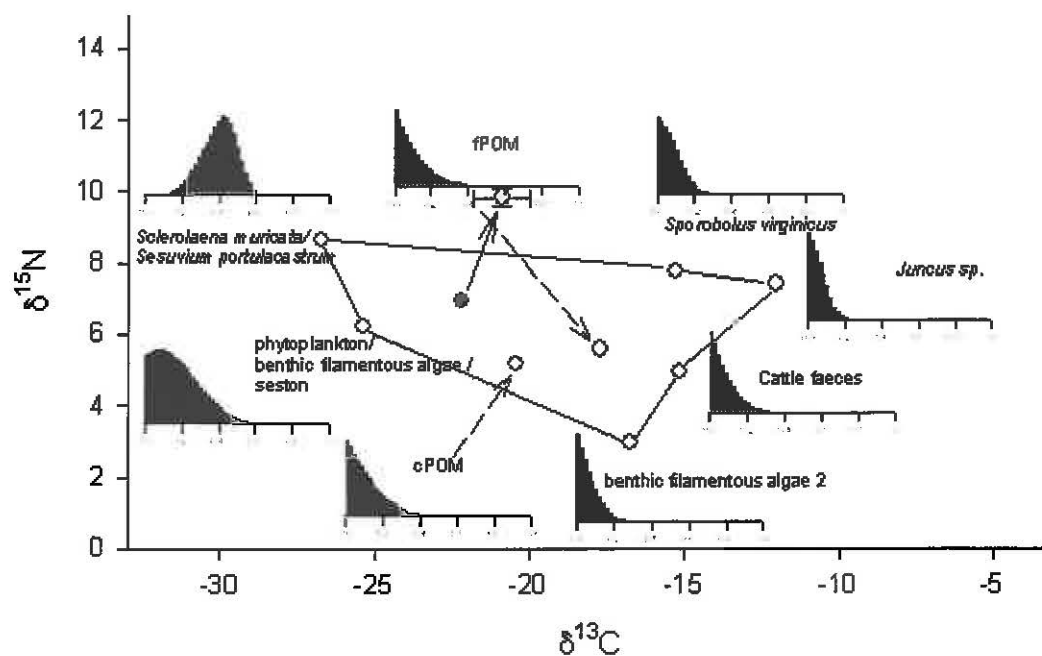


Figure 8.16. IsoSource results for *Nematalosa erebi* from Twelve Mile brackish; error bars are standard errors

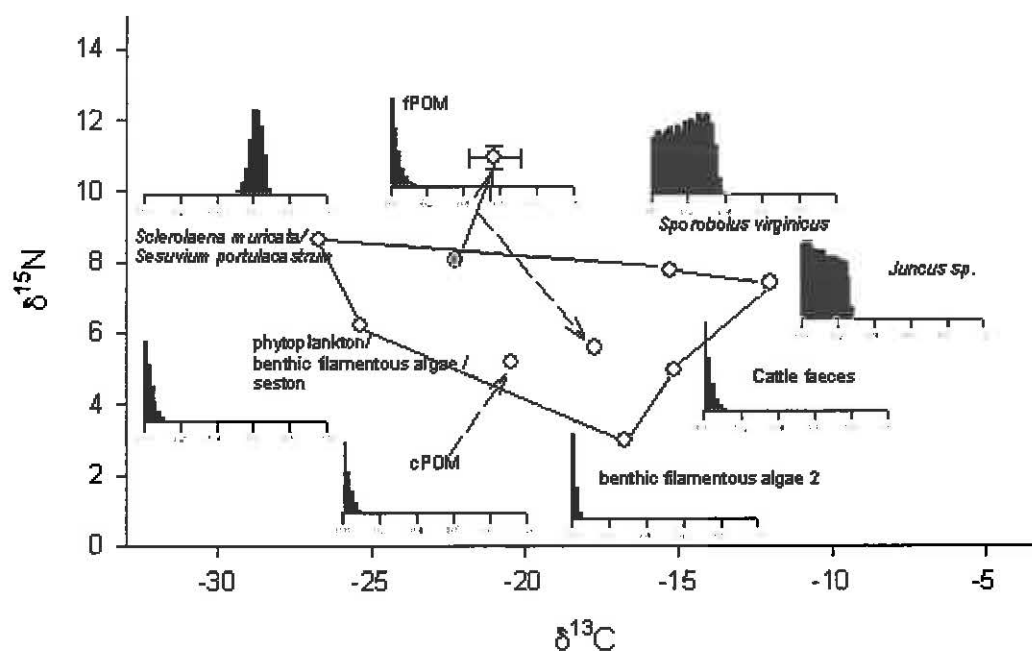


Figure 8.17. IsoSource results for *Selenotoca multifasciata* from Twelve Mile brackish; error bars are standard errors

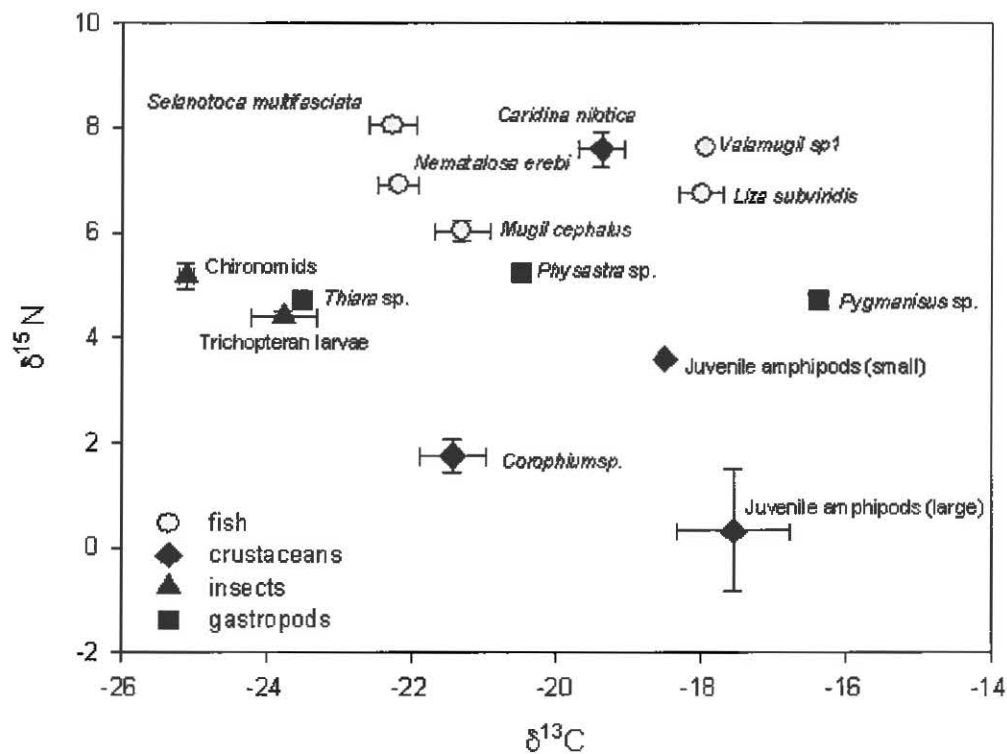


Figure 8.18. Stable isotope profiles of primary consumers after adjustment for fractionation; error bars are 1 SE

Figure 8.19: IsoSource results for *Caridina nilotica* from 12 Mile Brackish. Error bars are standard errors.

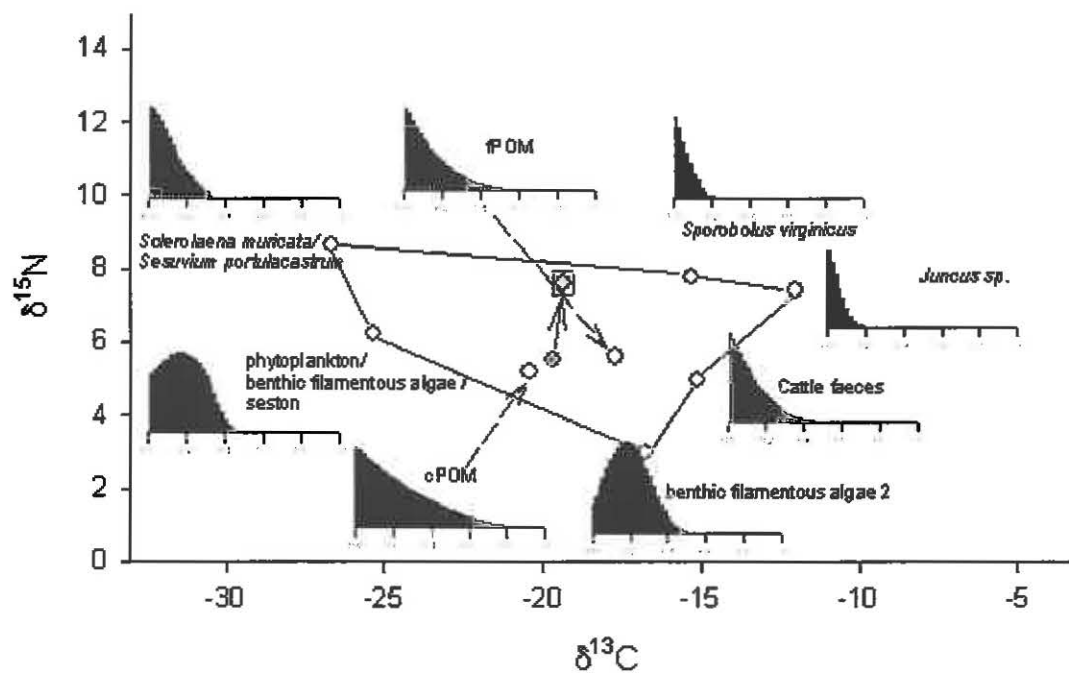


Figure 8.19. IsoSource results for *Caridina nilotica* from Twelve Mile brackish; error bars are standard errors

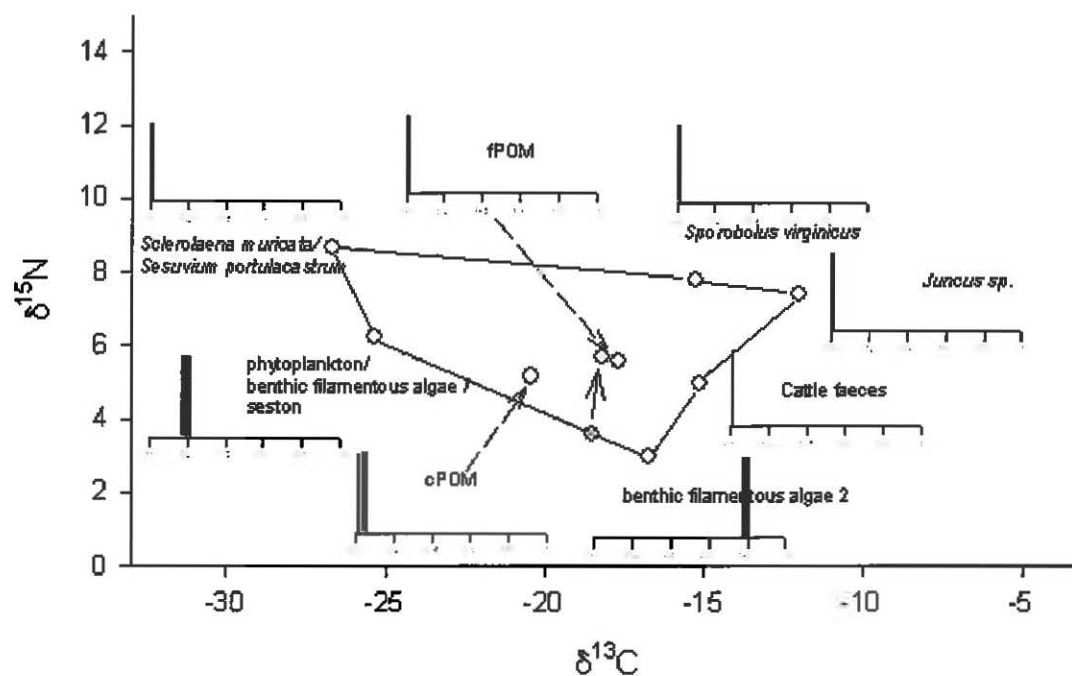


Figure 8.20. IsoSource results for small juvenile amphipods from Twelve Mile brackish; error bars are standard errors

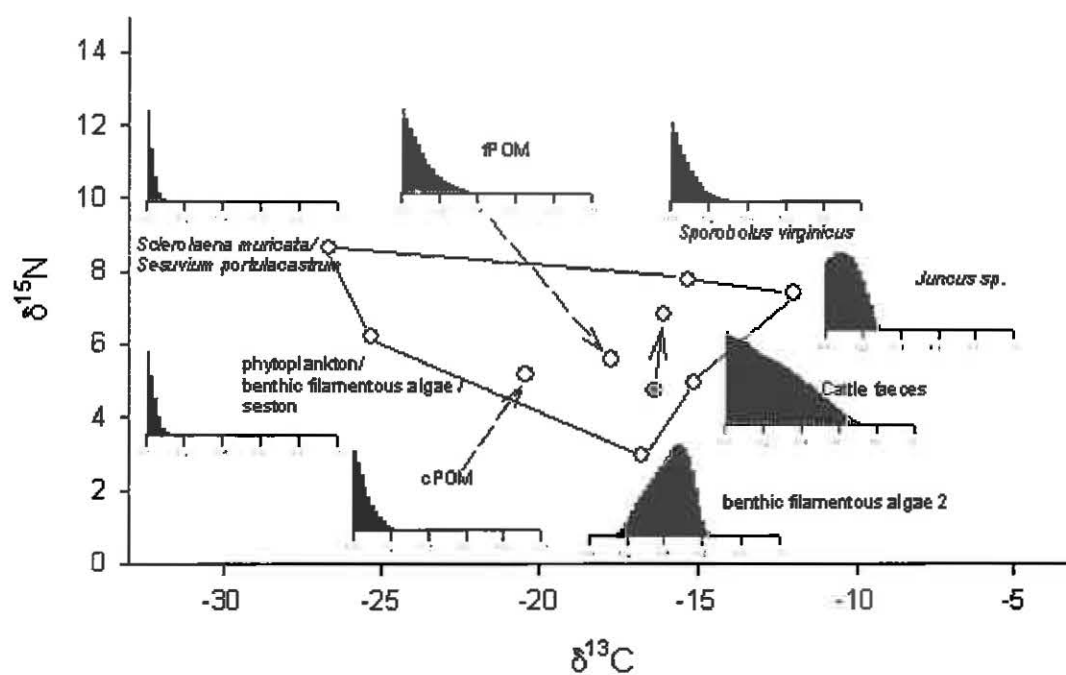


Figure 8.21. IsoSource results for *Pymanisus sp.* from Twelve Mile brackish; error bars are standard errors

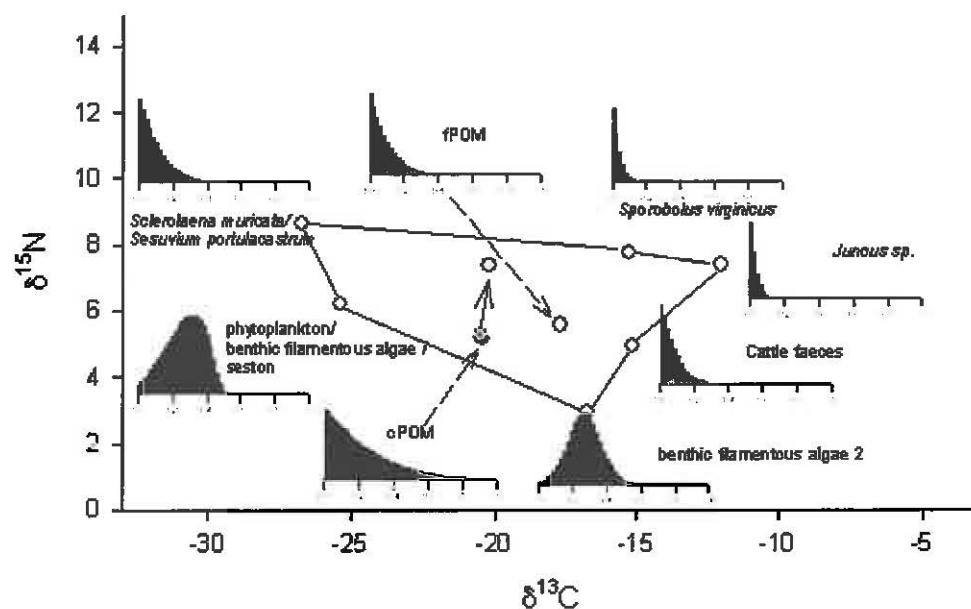


Figure 8.22. IsoSource results for *Physastra* sp. from Twelve Mile brackish; error bars are standard errors

Twelve Mile upstream

The nine producers sampled from the Twelve Mile Creek upstream pool (Figures 8.7 and 8.23) represented a quite different producer suite to that at the Twelve Mile brackish pool (Figures 8.6 and 8.11), with only five producers (seston, green filamentous algae, *S. virginicus* and *Juncus* sp.) in common. *Sesuvium portulacastrum* and seston had similar isotopic signatures so were combined for IsoSource modelling, while benthic filamentous algae was uncommon at the site and so excluded from the models.

Again the shrimp *C. nilotica* had a similar $\delta^{15}\text{N}$ signature to the phyto-detritivorous fish (Figure 8.23) but in this case was more enriched in $\delta^{13}\text{C}$, indicating a somewhat different dietary composition to the fish. IsoSource models suggest the nutrition of both fish and primary consumers at Twelve Mile upstream, *N. erebi* (Figure 18.24) and, *M. cephalus* (Figure 8.25) was based primarily on the bulrush, *Typha orientalis*, the waterlily, *Nymphaea violacea* and the saltmarsh succulent, *Sesuvium portulacastrum*, or seston, while that of the *C. nilotica* (Figure 8.26) was likely to have other components, particular the reed *Juncus* sp.

As with Twelve Mile brackish, insects and gastropod snail primary consumers (Figure 8.27) had $\delta^{15}\text{N}$ signatures lower than those of phyto-detritivorous fish. Once again a number of species had signatures too depleted in $\delta^{15}\text{N}$ for IsoSource modelling. Models for the snail *Physastra* sp. (Figure 8.28) included substantial contributions from *Nymphaea violacea* and the saltmarsh grass *Sporobolus virginicus*, and a likely minor contribution from MPBs, quite different to the models for that species at Twelve Mile brackish.

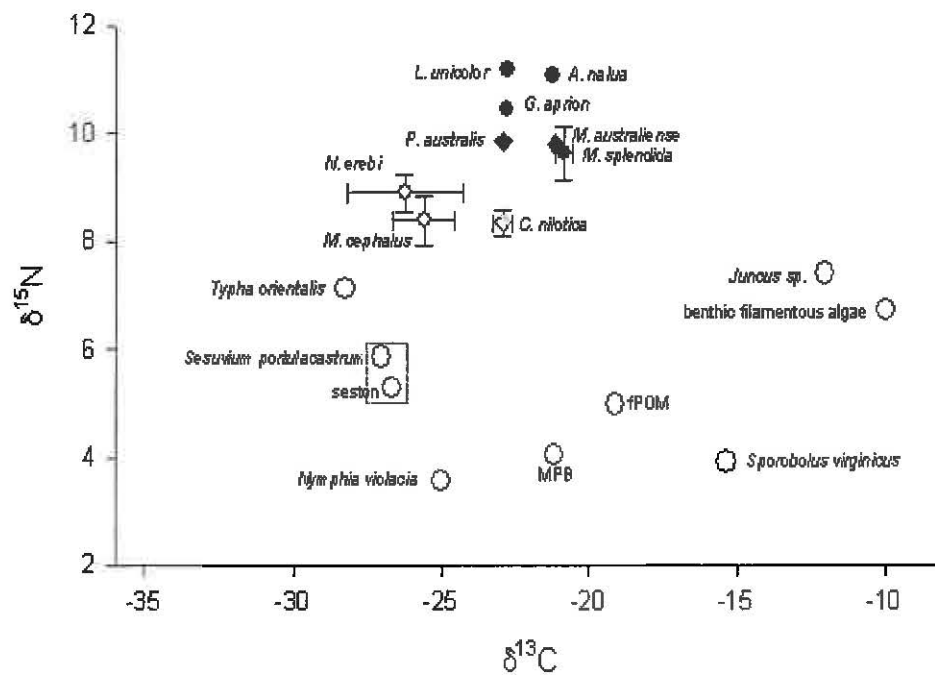


Figure 8.23. Mean stable isotope values for producers (unfilled symbols) and fish and crustacean consumers (filled symbols—grey: primary consumers; black: higher-order consumers) at Twelve Mile upstream; error bars are standard errors

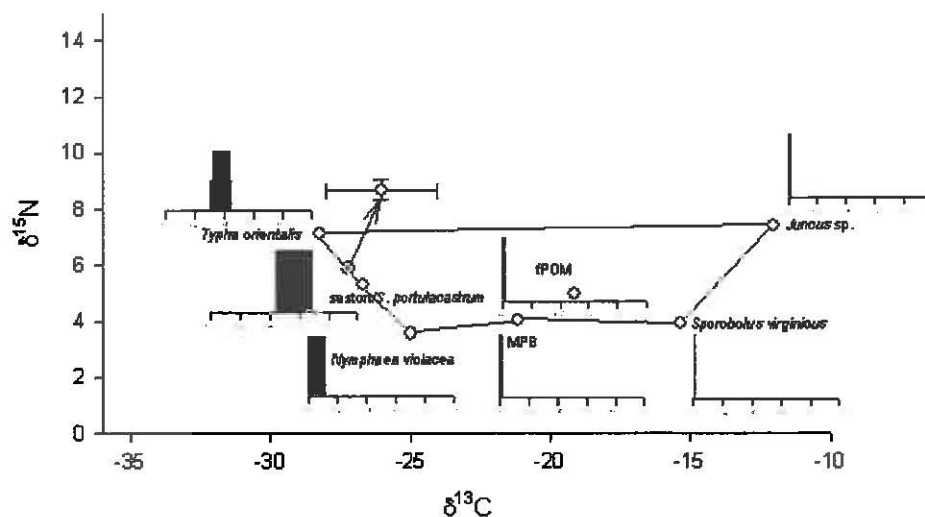


Figure 8.24. IsoSource results for *Nematalosa erebi* from Twelve Mile upstream; error bars are standard errors

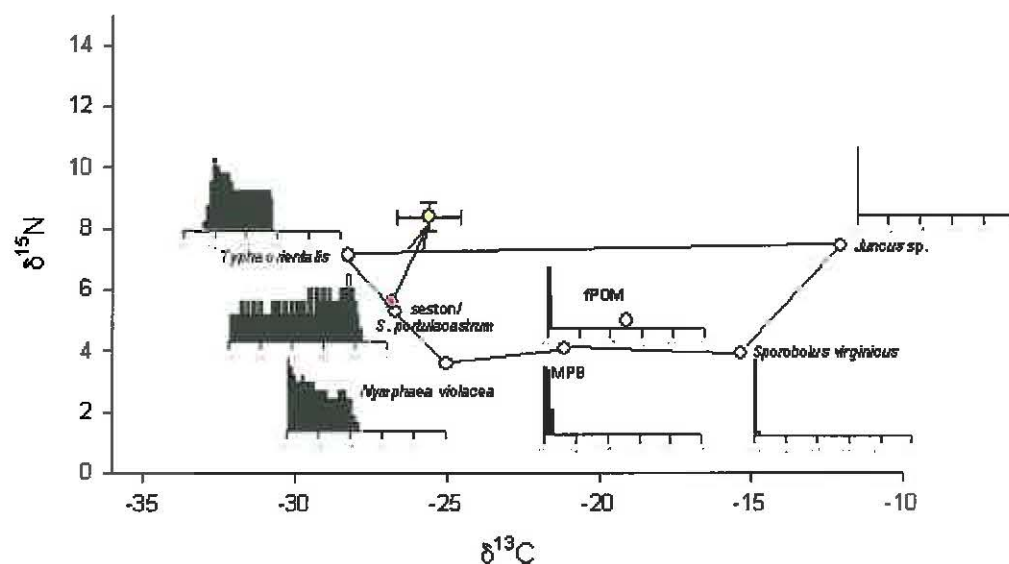


Figure 8.25. IsoSource results for *Mugil cephalus* from Twelve Mile upstream; error bars are standard errors

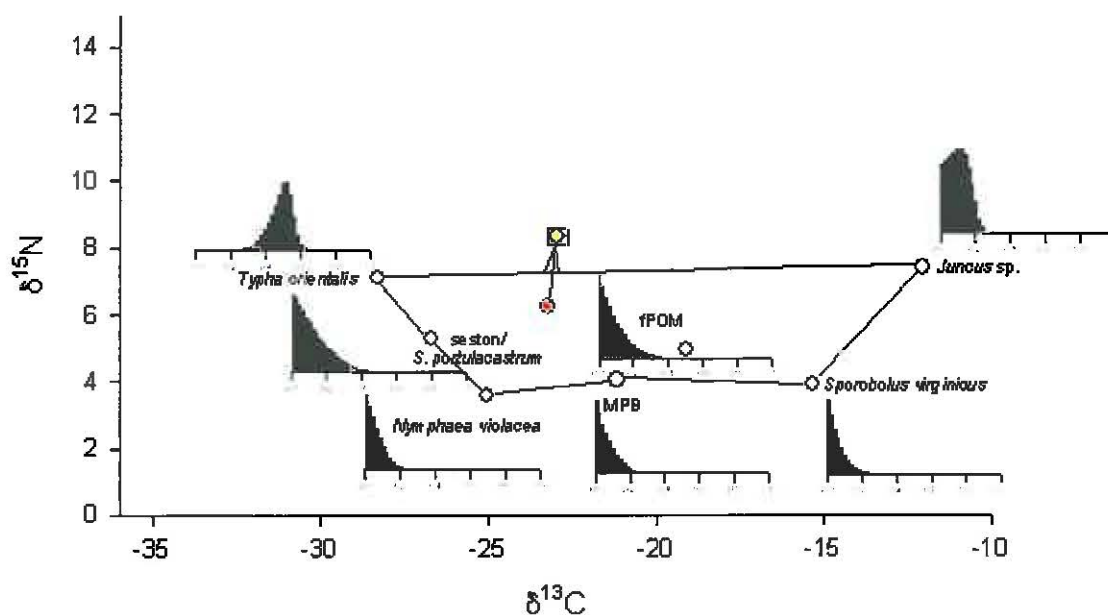


Figure 8.26. IsoSource results for *Caridina nilotica* from Twelve Mile upstream; error bars are standard errors

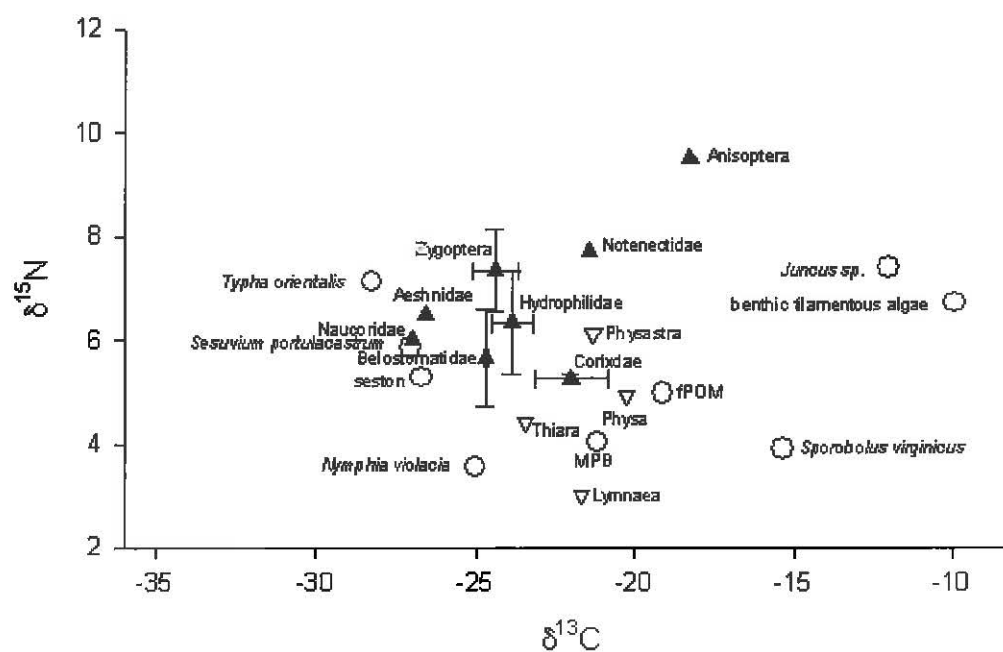


Figure 8.27. Mean stable isotope values for producers (unfilled symbols) and insects and gastropods (filled symbols—grey: primary consumers; black: higher-order consumers) at Twelve Mile upstream; error bars are standard errors

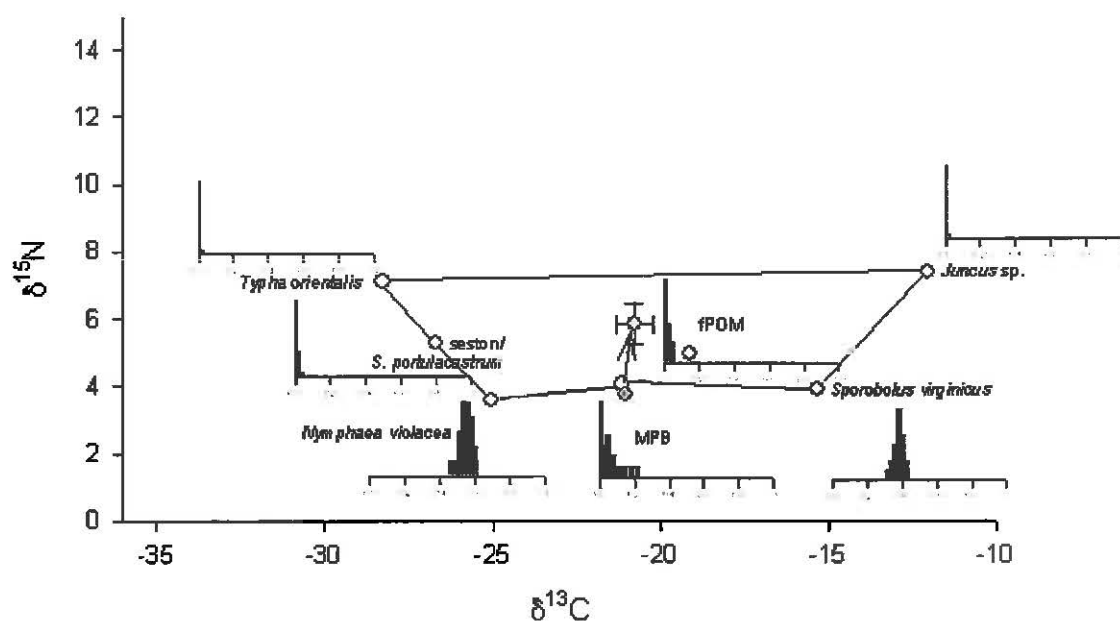


Figure 8.28. IsoSource results for *Physastra* sp. from Twelve Mile upstream; error bars are standard errors

Gonong saline

The Gonong saline pool presented a different suite of 11 possible sources of primary productivity (Figure 8.29), with only five (*S. virginicus*, *S. portulacastrum*, MPBs, POM and filamentous algae) common to the Twelve Mile Creek sites. In particular the Gonong site had a substantial presence of fringing mangroves, principally *Aegiceras corniculatum*, *Avicennia marina* and *Rhizophora stylosa*, along one bank. The mangrove *A. corniculatum* and the spreading nuthead, *Epaltes australis* had almost identical isotopic signatures, but as *E. australis* was uncommon around the pool it was omitted from analysis. Similarly the succulent saltmarsh plant *Suaeda australis* was uncommon and so also omitted. The mangrove *R. stylosa* and *Acacia* sp. had similar signatures and were combined for IsoSource modelling. *Casuarina equisetifolia* had a signature too distant from the primary consumers to have meaningful feasible contributions and was omitted.

The phyto-detritivorous fish at Gonong saline formed two distinct groups. The first (*S. multifasciata*, *Valamugil* sp.1 and *Valamugil seheli*) were in the expected position; more depleted in $\delta^{15}\text{N}$ than the fish at higher trophic levels. In contrast, the other two phyto-detritivores, *M. cephalus* and *L. subviridis*, had $\delta^{15}\text{N}$ values similar to the fish at higher trophic levels, and too high to produce feasible IsoSource models with the producer group present.

Most of the producer groups had a range of feasible contributions to IsoSource models for both *S. multifasciata* (Figure 8.30) and *V. seheli* (Figure 8.31). However, while the median of most models was close to zero, the bulk of the feasible contributions of both *S. virginicus* and green filamentous algae were greater than zero, indicating that these were probably both important contributors to the nutrition of these species. *Valamugil* sp.1. demonstrated a similar pattern (Figure 8.32), but in this case all feasible models had a moderate influence of filamentous algae and a major influence of *S. virginicus*, with little likelihood of contributions by other sources. Notably, mangroves did not appear to be likely to be important contributors to the nutrition of any of the species.

Only two invertebrates, *Sesarma* sp. and *Uca signata*, had isotopic signatures close to the primary producer groups (Figure 8.33). The IsoSource modelling for *Sesarma* sp. (Figure 8.34) indicated a substantial contribution of MPBs to all models with a likelihood of feasible contributions from *S. portulacastrum* and particularly *S. virginicus*, while *Uca signata* (Figure 8.35) was more similar to *Valamugil* sp. with a substantial feasible contribution by *S. virginicus* and a smaller, but important contribution by filamentous algae.

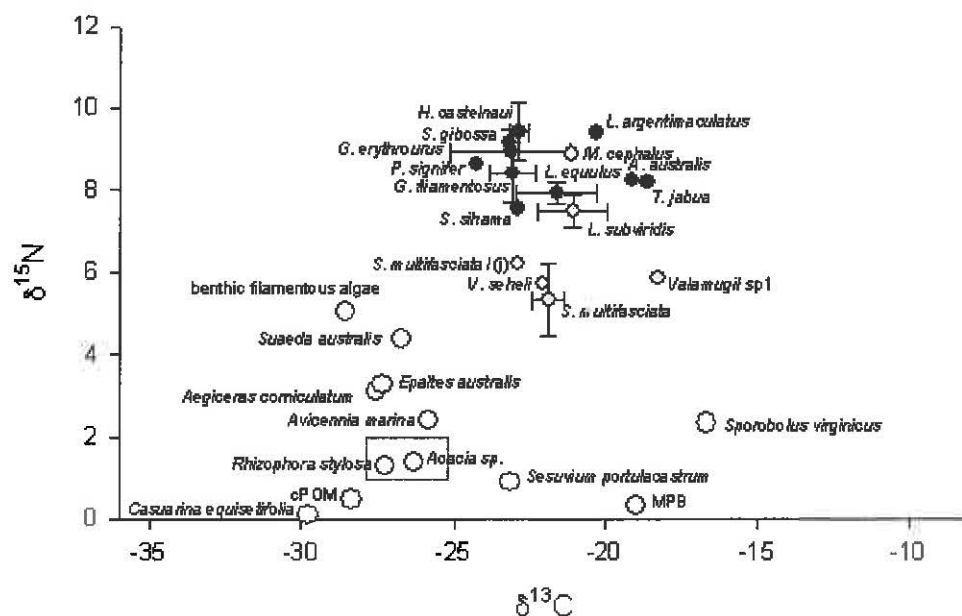


Figure 8.29. Mean stable isotope values for producers (unfilled symbols) and fish (filled symbols—grey: primary consumers; black: higher-order consumers) at Gonong saline; Error bars are standard errors; boxes indicate producers grouped for IsoSource analysis; irregular polygons indicate major consumer groups

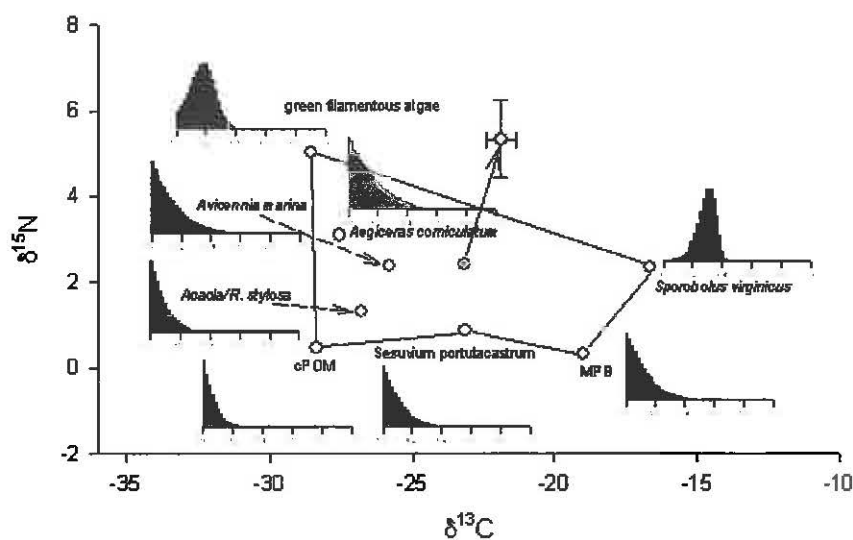


Figure 8.30. IsoSource results for *Selenotoca multifasciata* from Gonong saline; error bars are standard errors

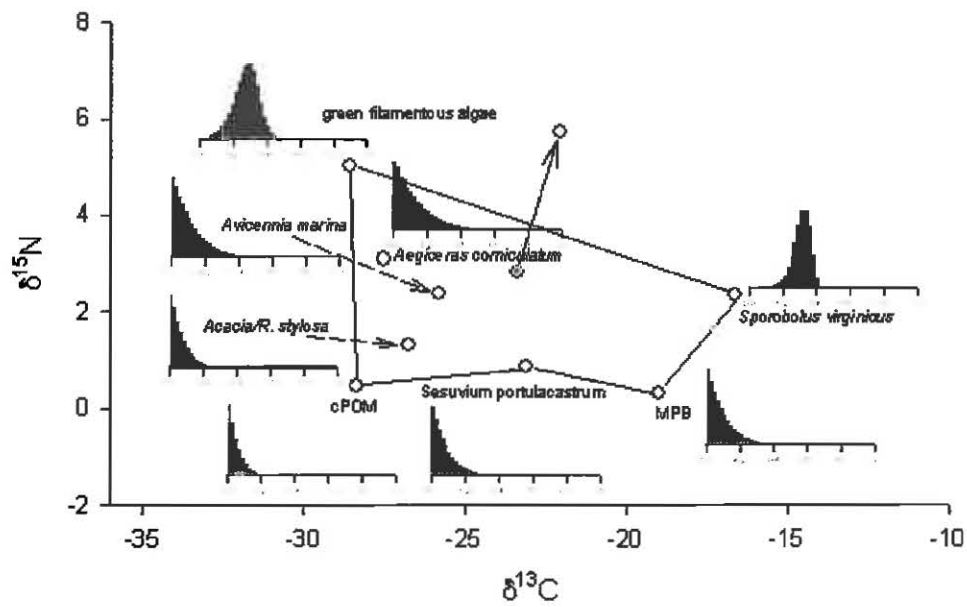


Figure 8.31. IsoSource results for *Valamugil seheli* from Gonong saline; error bars are standard errors

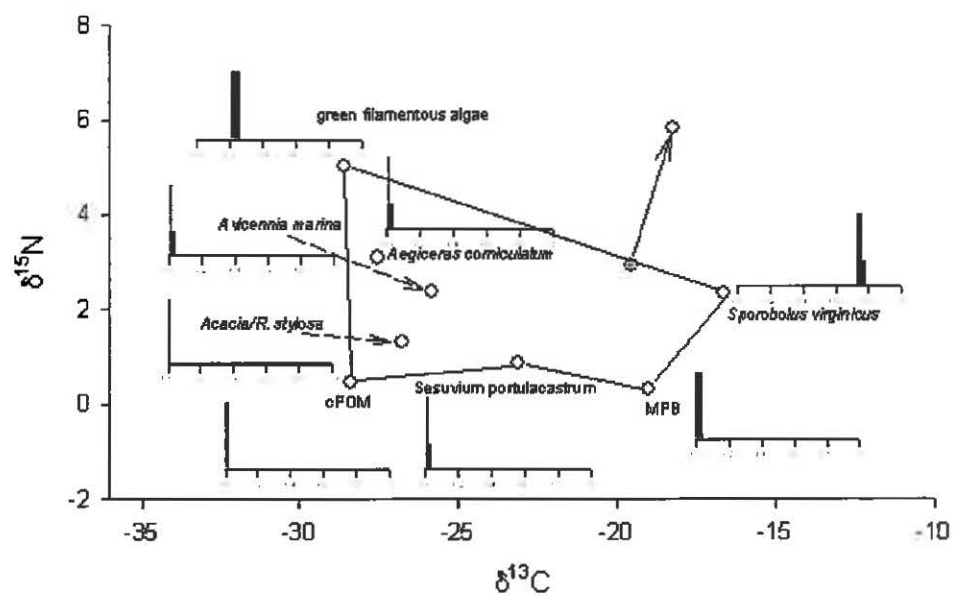


Figure 8.32. IsoSource results for *Valamugil* sp.1 from Gonong saline; error bars are standard errors

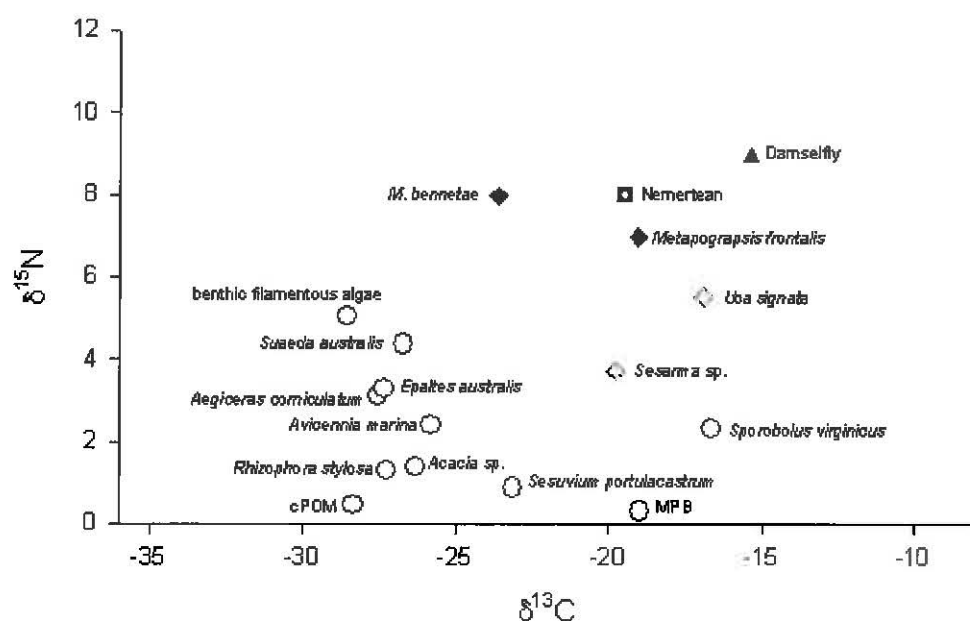


Figure 8.33. Mean stable isotope values for producers (unfilled symbols) and invertebrate consumers (filled symbols—grey: primary consumers; black: secondary consumers) at Gonong saline; error bars are standard errors

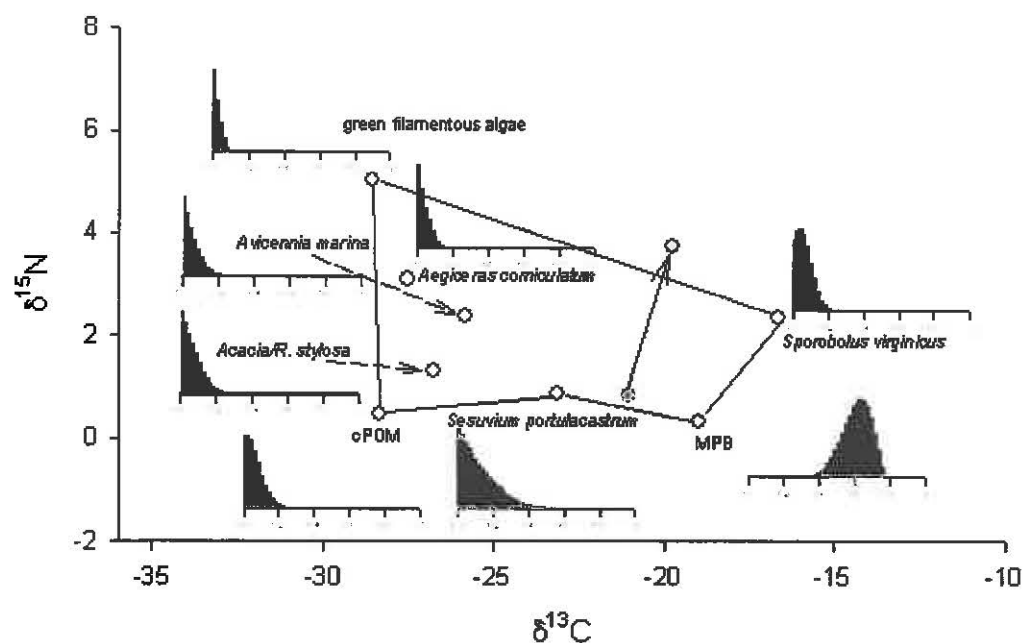


Figure 8.34. IsoSource results for *Sesarma* sp. from Gonong saline; error bars are standard errors

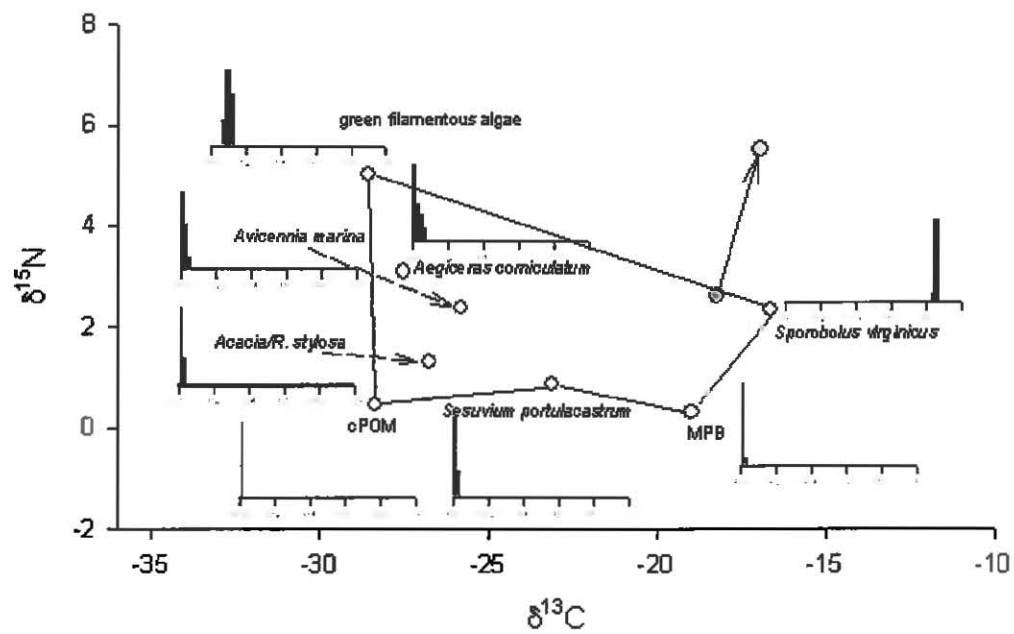


Figure 8.35. IsoSource results for *Uca signata* from Gonong saline; error bars are standard errors

Munduran saline

Eleven producer groups were collected from the Munduran saline pool (Figure 8.36). Of the primary producers collected, only *Suaeda australis* and *Epaltes australis* were omitted from IsoSource analysis due to low levels of occurrence, while the signatures of *Rhizophora stylosa* and *Acacia* sp. were very similar and so grouped.

At Munduran saline phytodetrivores occupied lower trophic positions (i.e. lower $\delta^{15}\text{N}$ values) than other fish species (Figure 8.36). However, unlike other sites, the more herbivorous species (*S. multifasciata*, *Siganus lineatus* and *Chanos chanos*) had substantially lower $\delta^{15}\text{N}$ values than did the less herbivorous mullet (*L. subviridis* and *M. cephalus*). IsoSource analysis indicated that the two mullet (Figures 8.37 and 8.38) had diets based on green filamentous algae and *S. virginicus*, with only minor contributions likely from other producers.

S. virginicus was also important for *S. multifasciata* (Figure 8.39) and *S. lineatus* (Figure 8.40), with MPBs and/or *S. portulacastrum* also likely to be important. In contrast, the nutrition of *C. chanos* (Figure 8.41) seemed to be based mainly on *S. portulacastrum*, with a minor contribution of coarse particulate organic matter, and possible MPBs.

Again it was noticeable that mangroves appear not to be feasible important contributors to the nutrition of any of the species.

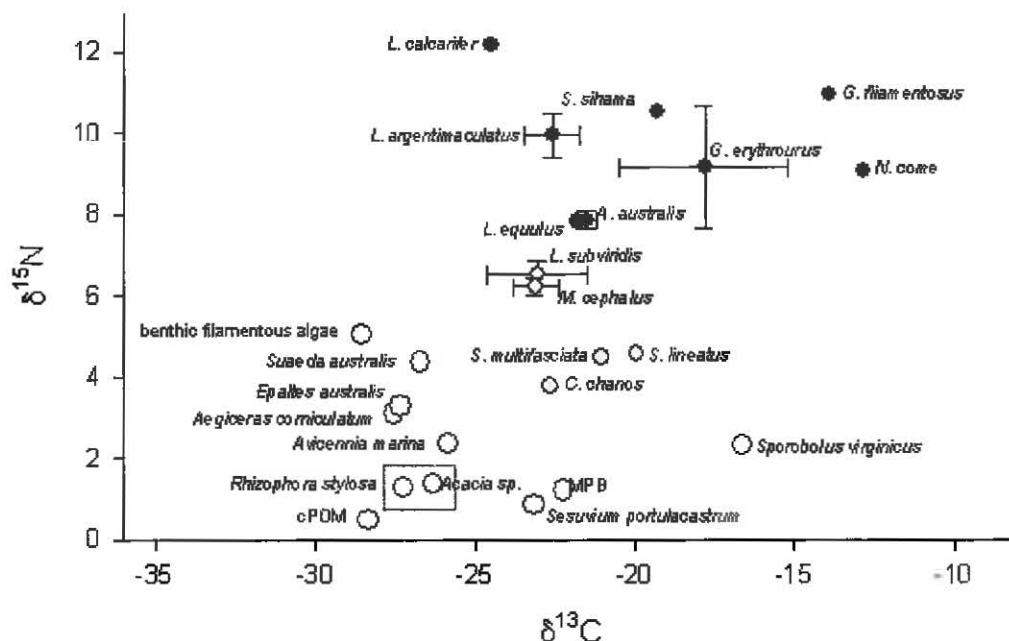


Figure 8.36. Mean stable isotope values for producers (unfilled symbols) and fish (filled symbols—grey: primary consumers; black: higher-order consumers) at Munduran saline; Error bars are standard errors; boxes indicate producers grouped for IsoSource analysis; irregular polygons indicate major consumer groups

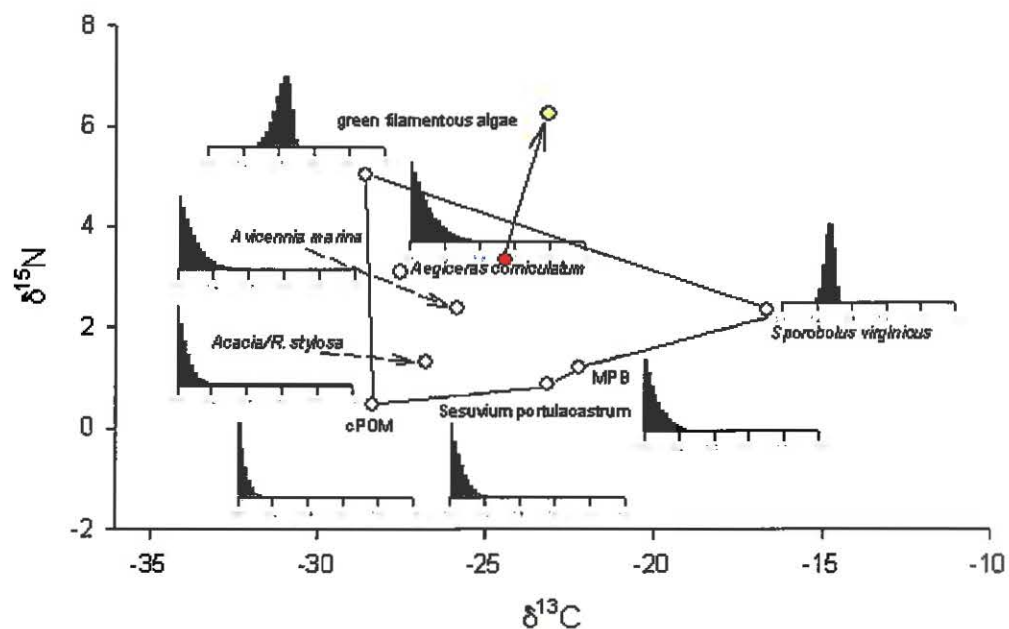


Figure 8.37. IsoSource results for *Mugil cephalus* from Munduran saline; error bars are standard errors

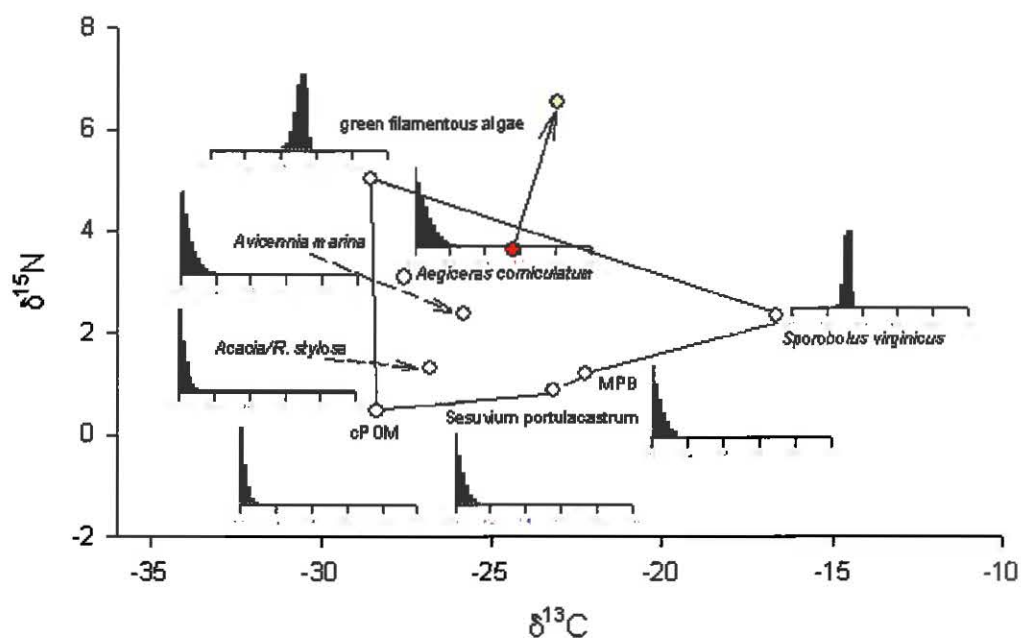


Figure 8.38. IsoSource results for *Liza subviridis* from Munduran saline; error bars are standard errors

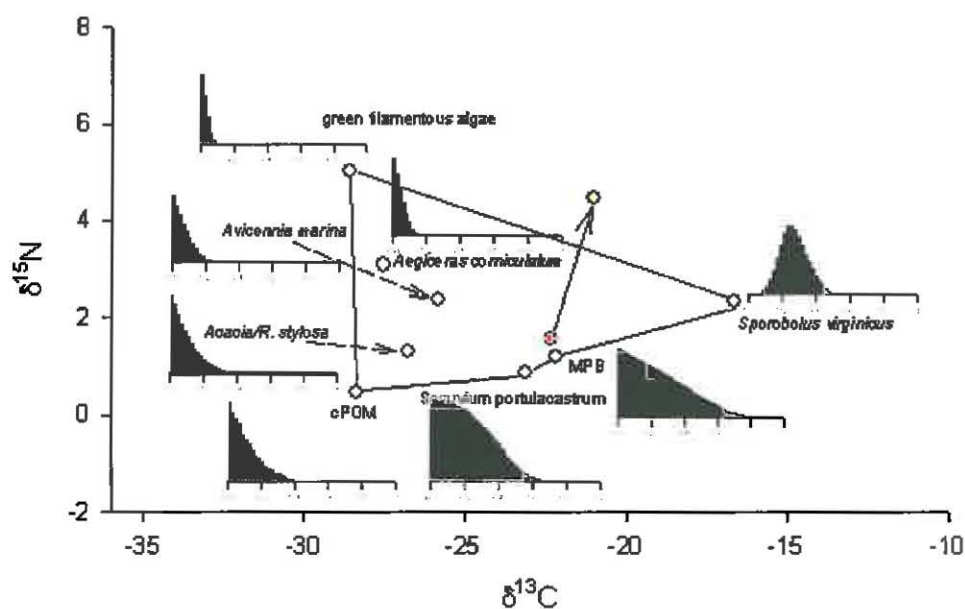


Figure 8.39. IsoSource results for *Selenotoca multifasciata* from Munduran saline; error bars are standard errors

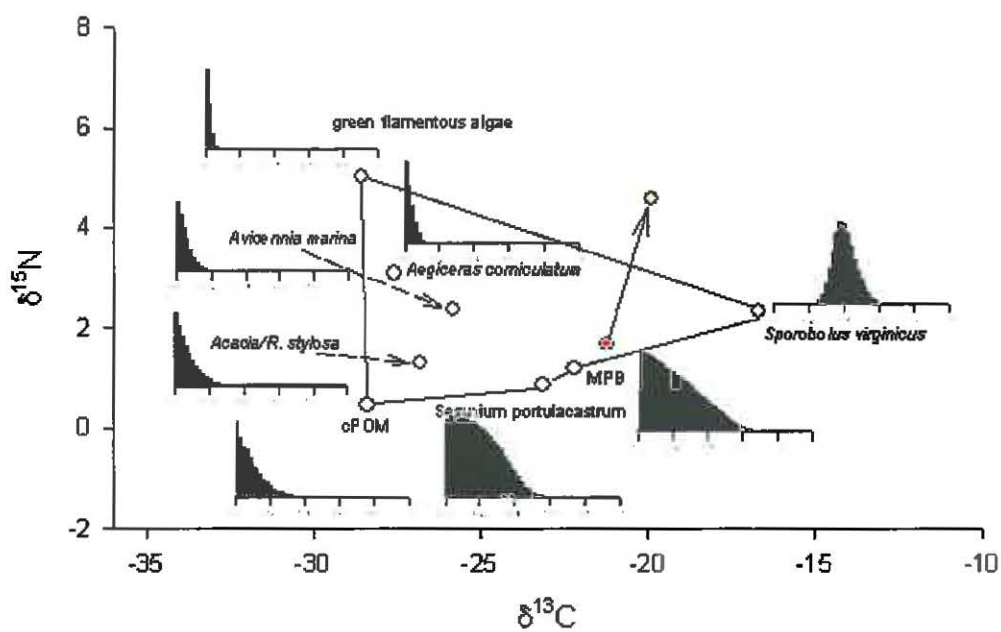


Figure 8.40. IsoSource results for *Siganus lineatus* from Munduran saline; error bars are standard errors

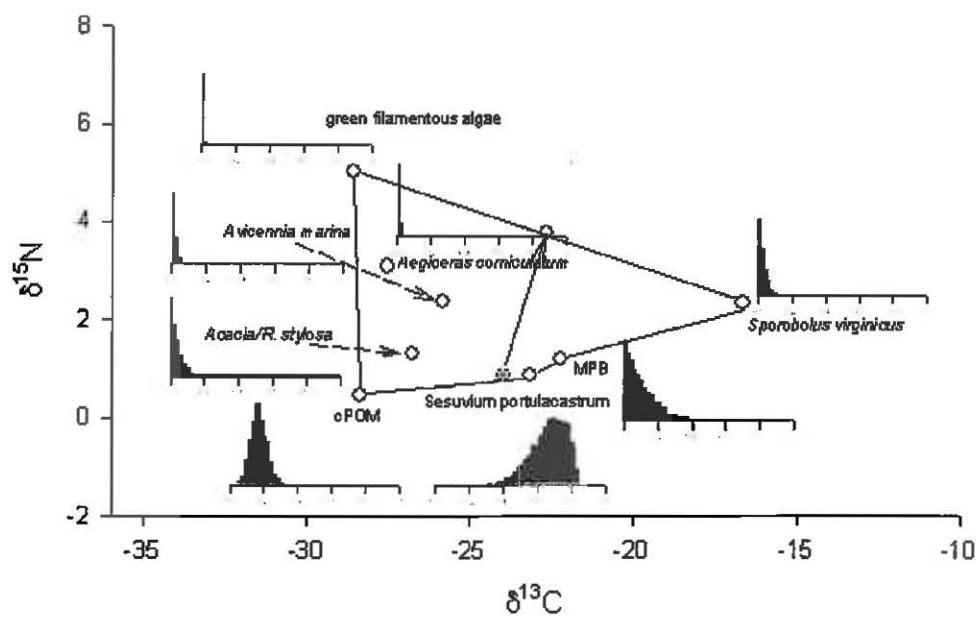


Figure 8.41. IsoSource results for *Chanos chanos* from Munduran saline; error bars are standard errors

Frogmore lagoon

Frogmore lagoon presented a smaller array of potentially important primary producers, with eight groups (Figure 8.42). Four of these (*Alternanthera* sp., *Glinus lotoides*, *Polygonum plebeium* and *Heliotropium indicum*) had similar signatures and were grouped for IsoSource analysis as 'C3 herbs'. The two phytodetritivorous fish took up lower trophic positions (lower $\delta^{15}\text{N}$) than the other fish species.

There was a broad range of feasible models for the nutrition of *N. erebi* (Figure 8.43) but all included fPOM and most included pasture grass. Many models also included C3 herbs and the green alga *Cladophora* sp. In contrast, *M. cephalus* (Figure 8.44) showed a narrow range of feasible dietary models, all of which contained a large component of fPOM and a small component of *Cladophora* sp.

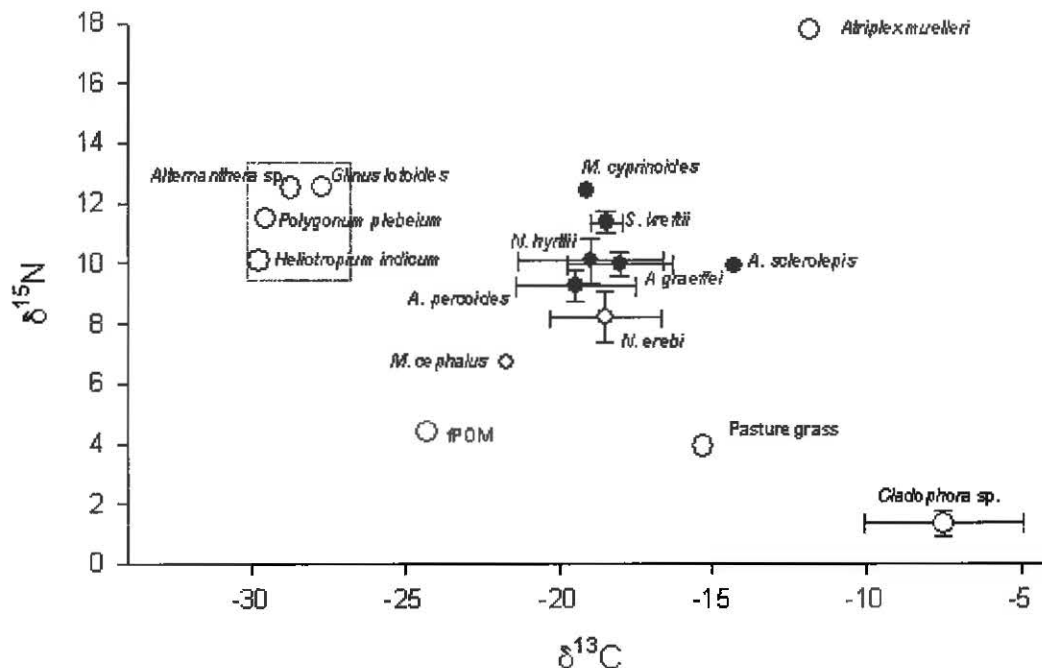


Figure 8.42. Mean stable isotope values for producers (unfilled symbols) and fish (filled symbols—grey: primary consumers; black: higher-order consumers) at Frogmore lagoon; Error bars are standard errors; boxes indicate producers grouped for IsoSource analysis; irregular polygons indicate major consumer groups

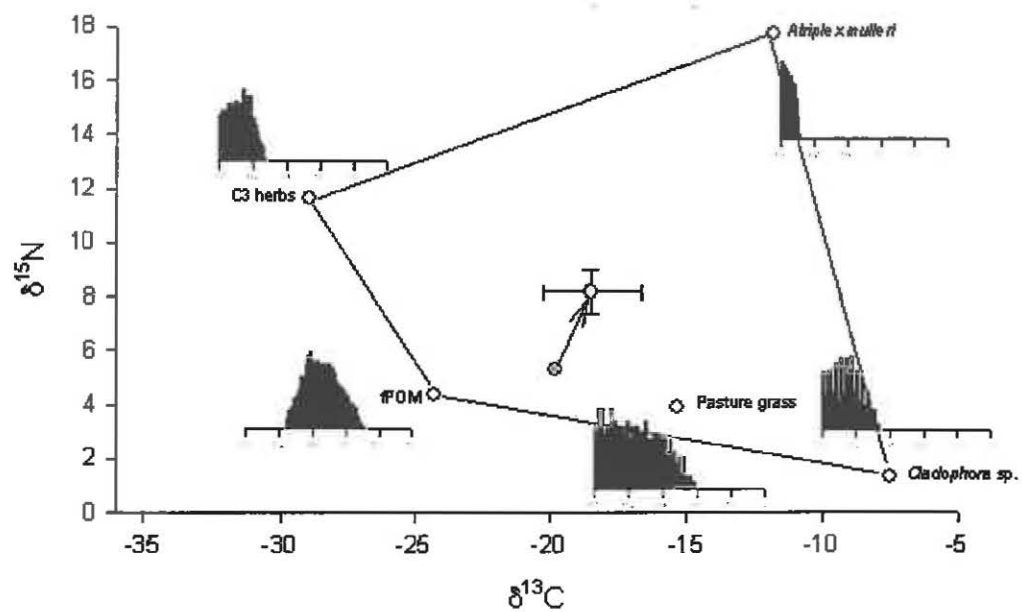


Figure 8.43. IsoSource results for *Nematalosa erebi* from Frogmore lagoon; error bars are standard errors

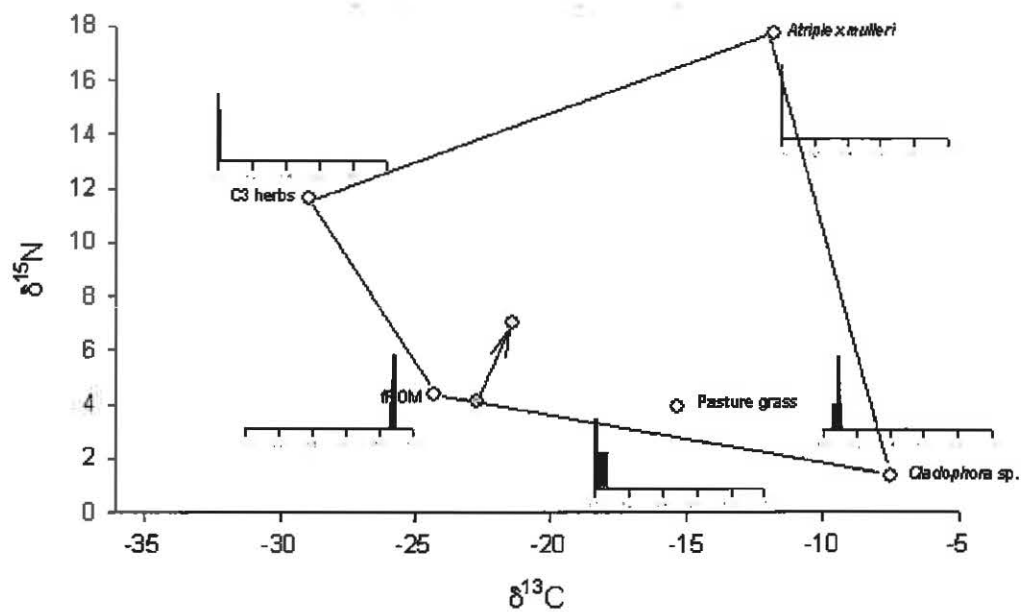


Figure 8.44. IsoSource results for *Mugil cephalus* from Frogmore lagoon; error bars are standard errors

Summary of producer importance to primary consumers

Despite considerable variations in signatures between sites, the overall pattern of importance of sources of primary production is consistent (Table 8.4). Over half the sources, including notably mangroves and terrestrial plants, had no instances where they made a major feasible contribution among the 26 IsoSource models. In contrast, green filamentous algae type 1 and the marsh plants *S. virginicus* and *S. portulacastrum* were important in most models in which they appeared. Other groups, notably MPBs (at saline sites) and *T. orientalis* (at freshwater sites), were present at only a few sites but contributed to a number of models for consumers at each site. In contrast, despite occurring in as many models as *T. orientalis*, the depleted $\delta^{15}\text{N}$ values of *N. violacea* meant it was important in few models. Similarly, *Juncus* sp. occurred in many models but was important in few.

Table 8.4. Number of IsoSource models in which each producer made a major feasible contribution. Data for *S. portulacastrum* and GFA 1 include instances where they were grouped with other producers that showed no contributions when not grouped. Empty cells indicate a lack of major feasible contributions

	<i>L. subviridis</i>	<i>M. cephalus</i>	<i>N. erebi</i>	<i>S. multifasciata</i>	<i>Malamugil</i> sp.	<i>V. scheli</i>	<i>C. chanos</i>	<i>S. lineatus</i>	<i>C. nilotica</i>	<i>Physastra</i> sp.	<i>Pymanisus</i> sp.	Amphipod juvs	<i>Sesarma</i> sp.	<i>U. signata</i>	Total
<i>A. marina</i>															
Acacia/Rhizophora															
<i>A. corniculatum</i>															
<i>A. muelleri</i>															
23 herbs															
<i>Cladophora</i> sp.															
Cattle faeces															
CPOM									1						1
FPOM		1	1												2
GFA1	1	2	1	1		1			1			1			8
GFA2									1	1	1	1			4
<i>Juncus</i> sp.	1				1										2
MPB				1				1					1		3
<i>N. violacea</i>			1												1
Pasture grass															
<i>S. portulacastrum</i>		2	2	2			1	1	1						9
<i>S. virginicus</i>	2	1		2	2	1		1						1	10
<i>T. orientalis</i>		1	1						1						3

Overall, with the exception of mangroves and *Juncus* sp., production utilised at each site seemed to reflect the common aquatic, and pool edge plants present at the site, with *S. virginicus* and *S. portulacastrum* particularly important. The lack of a strong mangrove signal also indicates little input from terrestrial trees, which being C3 plants would have signatures similar to mangroves [e.g. the similarity of *Acacia* sp. and *R. stylosa*, and the position of *C. equisetifolia* (Figure 8.29)].

In general, IsoSource models of suggested isotopic signatures were more highly aligned with original plant sources of organic carbon than POM, suggesting the POM collected from pool edges was largely refractory material, while most nutrition was obtained from 'fresh' detritus in earlier stages of decomposition, possibly found in deeper parts of the pools. This negative decomposition shift is likely due to the removal of more positive components (e.g. sugars) which are readily and easily utilised. Where sequences of pools were sampled in upstream gradients (Munduran and Twelve Mile Creeks), phyto-detritivorous fish in downstream sites (Munduran saline and Twelve Mile brackish) had very different isotopic signatures from their upstream counterparts (Figure 8.10).

Discussion

The suites of potentially important primary producers varied among sites, depending on environmental setting—pastoral, native forest, mangrove lined etc. As expected there was little variation in $\delta^{13}\text{C}$ signatures for higher plants occurring at multiple sites because carbon isotopic ratios are taxon specific depending on the plant's particular photosynthetic pathway. In contrast, $\delta^{15}\text{N}$ signatures varied greatly among sites indicating utilisation of different sources of nitrogen. While much of this difference seemed to relate to pool type (fresh vs. saline vs. brackish), a more detailed analysis of nitrogen sources may be useful to determine the extent to which these difference are a consequence of anthropogenic nitrogen entering pool food chains (e.g. from agri-chemicals).

Food chains in the Fitzroy wetland pools are quite short. Stable isotope analysis, as well as dietary studies (Chapter 7), indicate that top predators like *L. calcarifer* derived most of their nutrition from feeding directly on primary consumers (two trophic steps above producers), and omnivorous fish had $\delta^{15}\text{N}$ signatures that were unlikely to be more than three steps away from sources of primary production. Short food chains are expected in habitats like the Fitzroy pools that have relatively small areal extents (Brose *et al.* 2004). Notwithstanding this, domination of the fauna by phyto-detritivores (Chapter 5) and the importance of these in the diets of apex predators like barramundi (Chapter 7), suggests that a considerable amount of energy is transferred via this two-link food chain. This suggests efficient transfer of productivity and energy to the top of the food chain because simple thermodynamic constraints mean energy lost is proportional to the number of trophic transitions (Kaunzinger & Morin 1998).

The bases of pool food webs: isotope signatures of primary consumers

In a broad sense there was a clear split between fish and shrimp primary consumers—with nutrition based largely on higher plants—and other invertebrates that gained the bulk of their nutrition from algal sources. However, the situation with many invertebrates is unclear because they were too depleted in $\delta^{15}\text{N}$ to produce feasible IsoSource mixing models. This could be due to unrecognised sources of nutrition (e.g. microbial productivity), or could be a result of poorly defined fractionation values (see above).

While there was little change in isotopic signatures of most pool flora and fauna over time, there was considerable spatial variation, with the same species

deriving the majority of their nutrition from different sources in different pools. In fact, there were clear differences in sources of primary production among pools that transcended taxonomic differences; despite interspecies differences in sources of nutrition, there was greater similarity between different species at a site than between the same species at different sites, with species-specific signatures showing distinct clusters based on pool identity.

In general, the major sources of nutrition were derived from plants common in or close to the pools. The exception to this was mangroves which showed only low feasible contributions at both Gonong and Munduran saline, despite fringing most of one pool edge (particularly in the case of Munduran). In contrast, the saltmarsh grass, *S. virginicus*, and the saltmarsh succulent, *S. protulacastrum*, appeared to be major contributors at most sites where they occurred, similar to the situation for estuarine wetland pools in other systems (Sheaves *et al.* in review). MPBs are important in many estuary systems (Cook *et al.* 2004a,b), including the Fitzroy estuary proper (Ford *et al.* 2005), and this importance was reflected for a number of consumers in Gonong and Munduran saline pools. In contrast, MPBs had relatively low importance in the freshwater and brackish pools, probably because these pools had only small areas of shallow edge.

Material derived from higher plants seemed to comprise a major component of the nutrition of phyto-detritus-feeding fish right across the spectrum of wetland pools. These plants were either specialised still-water plants (e.g. *N. violacea*) or plants of the littoral fringe (e.g. *S. virginicus*). Detritus from such plants would be much less abundant in the main body of the Fitzroy estuary due to high tidal movement and saline conditions, and because of the much lower ratio of riparian edge. This suggests that the pools can provide a much greater level of nutrition per volume than is available in the estuary proper.

This, together with the energy-efficient short food chains, provides at least part of the explanation for the high densities (Chapter 4) and biomasses (Chapter 5) of fish in the pools. In addition, juvenile fish require much greater quantities of nutrients than adults (Yañez-Arancibia *et al.* 1994) making habitats with abundant supplies of nutrients particularly important. Thus the floodplain wetland pools probably make a much greater contribution to the nutrition of the whole Fitzroy estuary system than suggested by their areal extent, particularly in a system like the Fitzroy where estuarine waters are often heterotrophic (Ford *et al.* 2005).

Conceptual models

No conceptual models of the importance of various sources of organic matter to the support of food webs of tropical estuarine floodplain wetland pools exist. The closest analogue would be three competing models developed for large rivers and floodplain systems in temperate and subtropical areas of the United States; the *flood pulse concept* (Junk *et al.* 1989), the *river continuum concept* (Vannote *et al.* 1980), and the *riverine productivity model* (Thorp & Delong 1994) (see Box 8.2). Although the wetland pools only flow intermittently and are at a much smaller scale than the systems these models were developed for, the models form a useful starting point.

Box 8.2. Conceptual models of the importance of different sources of organic matter to the support of stream food webs

Flood pulse concept (Junk *et al.* 1989)

- Most nutrition comes from production within the adjacent floodplain, with little in-stream production
- Seen as typical of unaltered floodplain streams

River continuum concept (Vannote *et al.* 1980)

- Most nutrition comes from organic matter washed in from upstream areas (terrestrial or within upstream areas). Production within the local stream area or along its banks is of minimal importance
- Seen as more usually a feature of stream areas without a substantial adjacent floodplain

Riverine productivity model (Thorp & Delong 1994)

- Most nutrition comes from either productivity within the stream or direct inputs of leaves etc. from the riparian zone. Non-living organic carbon (POM) derived from elsewhere is present within the stream but is of a refractory nature, and so is difficult to assimilate (Thorp *et al.* 1998).

Despite differences in detail, food webs across all the Fitzroy wetland pools were supported by within-pool productivity (benthic algae) and riparian vegetation (largely *S. virginicus* and *S. protulacastrum*). There was little evidence of important inputs from upstream sources of carbon (phyto-detritivorous fish in Munduran saline and Twelve Mile brackish had very different isotopic signatures to those in upstream parts of the same systems) or from sources distant from pool edges (no evidence of inputs from terrestrial trees that were common in woodlands adjacent to most pools), making a strong match to the *riverine productivity model*. Furthermore, POM signatures were rarely important, suggesting that much of the POM was refractory, again in accord with the *riverine productivity model* (Thorp *et al.* 1998).

Under the *riverine productivity model* (RPM) the majority of organic matter supporting food webs comes from local autochthonous production (water plants and algae) or direct inputs of material from riparian vegetation. The variety of environmental settings of the Fitzroy floodplain pools means that the exact identity of the contributors varies from pool to pool (Figure 8.45) but the dominance of inputs from autochthonous and riparian production remains.

This input is likely to take two forms: (i) more or less continuous input from water plants whenever they are available and (ii) pulsed inputs from littoral vegetation (e.g. saltmarsh plants) due to rainfall or wind. Inputs from surrounding woodlands, fields etc. and upstream pools is apparently small and/or of a refractory nature. Although mangroves are an important component of the riparian vegetation of the saline pools they seem to contribute little to food webs, a situation reported from an increasing number of studies (Stoner & Zimmerman 1988; Primavera 1996; Loneragan *et al.* 1997; Schwamborn *et al.* 2002).

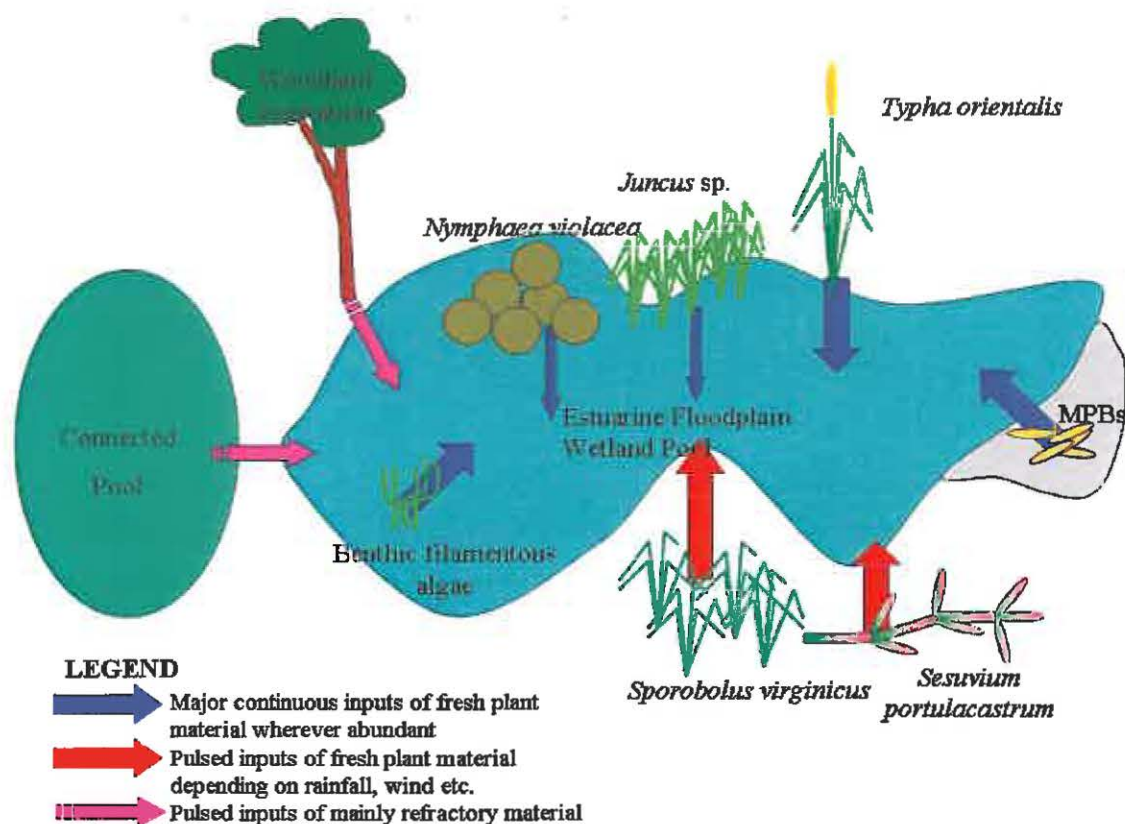


Figure 8.45. A conceptual model of inputs of organic carbon supporting food webs in tropical estuarine floodplain wetland pools

The phyto-detritivorous fish occupying the Fitzroy wetland pools are only equipped to consume live plant material by grazing (Bellwood 2003; Karpouzi & Stergiou 2003), and so are not equipped to feed on the hard tissues of living higher plants. Thus the importance of terrestrial plants in IsoSource models of all species indicates the consumption of considerable amounts of detritus, which is supported by gut content analysis (Chapter 7). Despite this, it is clear that feeding on detritus was not indiscriminate; detritivores in all pools showed a range of isotopic signatures relating to different mixtures of the available simple plants and higher plant detritus. Therefore, even though detritus would seem to be a simple, homogeneous resource, there was considerable partitioning. This partitioning could be the result of different sizes of different fish species (Chapter 5), different species feeding in specific parts of the pools (Chapter 11) or the active selection of organic particles of particular sizes or shapes during feeding (Blaber 1976).

Implications

The clear shifts to different sources of organic carbon at different pools shows that the detritus-based food webs of the Fitzroy wetland pools are adaptable and labile; they shift to utilise whatever useful sources of organic carbon are abundant at a site. From this point of view, pool food webs are likely to be resilient to many changes in vegetation type, making them adaptable to many types of agricultural, and perhaps even urban (Connolly 2003), development. However, the fact that sugar cane and invasive pasture grasses contribute little nutrition to aquatic food webs (Bunn *et al.* 1997) suggests that situations where pools become surrounded by monoculture of poor nutritional value should be avoided. The likely resilience of detritus-based food webs contrasts with herbivore-based food webs which may be reliant on specific sources of primary productivity. At least from the point of view of nutrient supply the presence of these detritus-based food webs means that the wetland pool ecosystems will be buffered from some of the possible effects of global climate change.

Despite the broad spectrum of sources of nutrition accessed, saltmarsh plants made considerable feasible contributions to most models. This could be because these are particularly nutritious or simply because they were among the most abundant plants surrounding these pools. Regardless of the reason, it is likely that one thing the pool ecosystems are sensitive to is the loss of this apparently innocuous vegetation type, with occurrences like grassfires likely to present a particular danger to ecosystem function.

Chapter 9 Food webs of Fitzroy estuarine floodplain wetland pools

Marcus Sheaves

Introduction

Together, information on the densities and compositions of pool fish fauna (Chapter 4), patterns of difference in fish biomass (Chapter 5), abundance and trophic roles of invertebrates (Chapter 6), diets of fish (Chapter 7) and investigation of the producer base of pool ecosystems (Chapter 8) provide a broad spectrum of information on the structure of food webs of the Fitzroy estuarine floodplain wetland pools.

In this chapter that information is combined to develop a general model of the structure of pool food webs and investigate the nature of food webs under four different scenarios: food webs of (1) saline pools with regular connections to the Fitzroy estuary, (2) brackish pools with irregular connections to the Fitzroy estuary, (3) freshwater pools when isolated from other pools or streams, and with *maximum water depth exceeding about 1.5 m*, and (4) freshwater pools when isolated from other pools or streams, and with *maximum water depth less than about 1.5 m*.

Results and discussion

The basic food web

The Fitzroy estuarine floodplain wetland pools comprise a diverse range of pool types, in a range of geographic settings (Chapter 2) and with a variety of levels of connectivity and trajectories of temporal change (Chapter 3). However, the food webs of these disparate pools have a common general structure (Figure 9.1) comprised of short food chains, with much of the productivity flowing through a very short, three-link food chain (detritus/detritus-feeding fish/carnivorous fish or birds). Short food chains are important in tropical mangrove estuaries (Sheaves & Molony 2000). Because a considerable amount of energy is lost at each trophic transfer (Cousins 1996), the presence of short food chains means that a great proportion of the energy derived from primary productivity is transported to the top of the food web (Sheaves & Molony 2000), providing the opportunity for high levels of export to other habitats (Deegan 1993, Sheaves & Molony 2000).

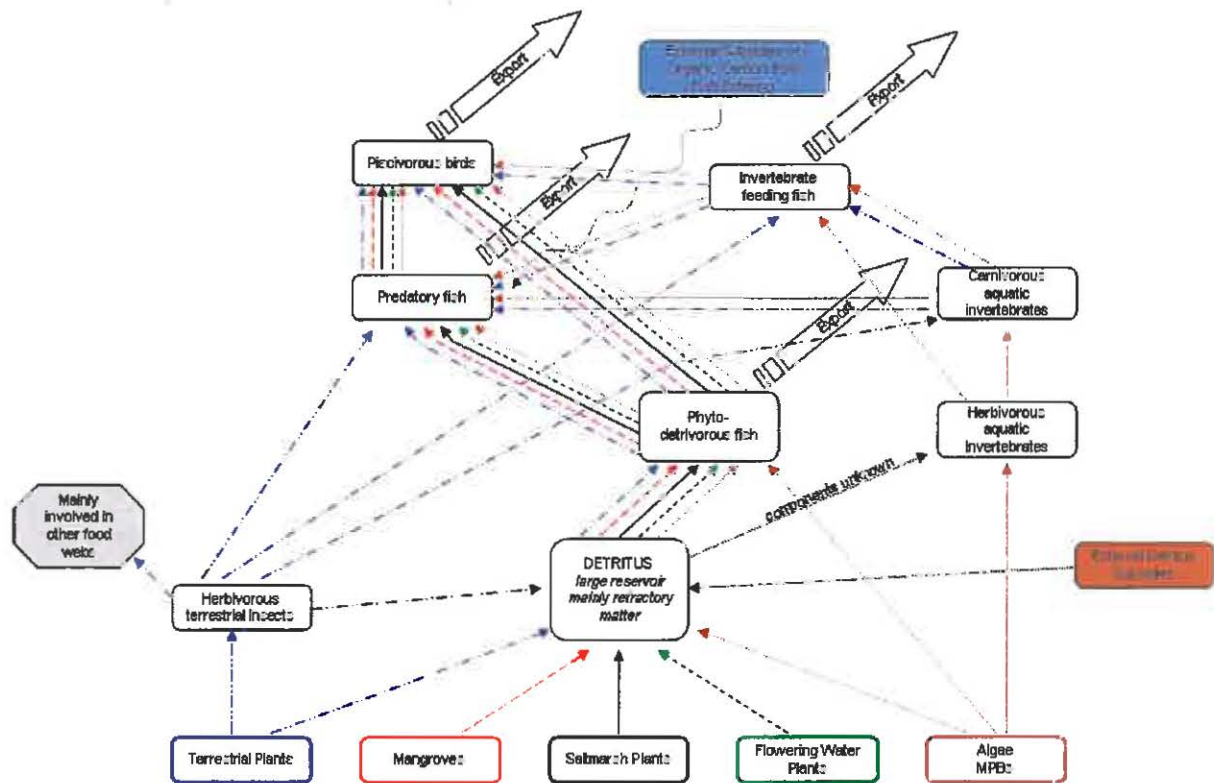


Figure 9.1. Basic structure of food webs in the Fitzroy estuary floodplain wetland pools Thin, colour-coded arrows indicate pathways from different potentially important carbon sources. The importance of external subsidies of detritus (i.e. material imported from upstream or from outside the immediate pool area) is difficult to determine but they are clearly highly variable and assumed to be minor, and so not traced through the system. Broad 'export' arrows indicate movement away from the pool to other pools or other habitats. Recycling of wastes to the detritus pool is assumed for all animal groups but is not indicated on the diagram.

Across all the Fitzroy wetland pools there are five groups of potentially important primary producers—terrestrial plants, mangroves, saltmarsh plants, flowering water plants and algae—that grow in or around the pools and, although the importance of each group varies from pool to pool, saltmarsh plants and algae are important contributors of nutrition wherever they occur. The importance of contributions from further afield is unknown because inputs from these sources are very difficult to trace. There are also periodic inputs from the Fitzroy estuary or other pools and waterways during connection events, as well as imports and exports of organic carbon in the form of the biomass of animals migrating in and out of the pools.

At times of aquatic connection the movement of animals and plant material can influence foodweb structures. In non-connection periods food webs in many pools are reasonably stable. This stability is highest in saline pools that are regularly connected with the estuary proper, meaning water levels remain fairly constant and conditions fairly stable. At the other extreme are isolated pools (e.g. freshwater Frogmore lagoon, saline German Jack's lagoon) that connect to

water bodies only infrequently, where fluctuating pool levels can produce a series of effects leading to ecosystem change (Chapter 5). Despite various levels of physical isolation from other aquatic systems, the pools are connected by the predatory activities of piscivorous birds that move freely between the pools (Chapter 12).

There are many different scenarios under which food webs could be modelled. Many are very transitory so may not be profitable to study. For example, German Jack's pool fills on very high tides then is disconnected for long periods. It is always shallow (allowing heavy predation by piscivorous birds) and dries quickly, becoming rapidly hypersaline and inhospitable to fauna. In other scenarios, it may be too difficult to collect data (e.g. on pools during flooding). For contrast, the four scenarios investigated here are either the 'usual' situation for each major type of pool (saline, brackish and fresh) or illustrate the important changes in function as pools dry out.

Scenario 1: Saline pools with regular connections to the Fitzroy estuary

Saline pools (Figure 9.2) like Gonong and Munduran saline are regularly connected with estuarine waters (Chapter 3), with some level of connection on the highest tides in most tidal cycles. This means the pools are continually close to full and tend to have relatively stable, saline conditions; with reductions in salinity due to flooding only prevailing until the next tidal connection.

Most organic carbon supporting the food web is contributed by saltmarsh plants and algae, with the contribution from mangroves surprisingly low (Chapter 8). The majority of plant material is converted to detritus and energy flows from it to higher trophic levels largely through detritus-feeding fish. There is a second important contribution from algae, with energy passing along herbivore food chains via grazing fish and invertebrates. Energy from algae grazed by herbivorous invertebrates is passed up the web mainly via invertebrate-feeding fish, including both omnivores and specialised invertebrate feeders.

Because substantial water depth is maintained by regular tidal connections, predation by piscivorous birds is not excessive. Additionally, predation within the pools is compensated for by emigration from the estuary proper. Pool productivity is exported at a low but constant level by both birds and fish and by invertebrates leaving the pool. An additional source of organic carbon comes from fish migrating into the pool during tidal connections.

Most energy supporting the food web is contributed by saltmarsh plants and algae. The majority of plant material is converted to detritus and energy derived from it flows largely through detritus feeding fish, with a smaller contribution from herbivore food chains. Contributions from mangroves is low. Algae grazed by invertebrates is passed up the web mainly via invertebrate feeding fish. Maximum water depth is maintained by regular tidal connections so predation by piscivorous birds so losses due to predation by them are compensated for by reproduction and emigration from the estuary. Pool productivity is exported at a low, but constant level both by birds and by fish and invertebrates leaving the pool. An additional source of organic carbon comes from fish migrating into the pool during tidal connections.

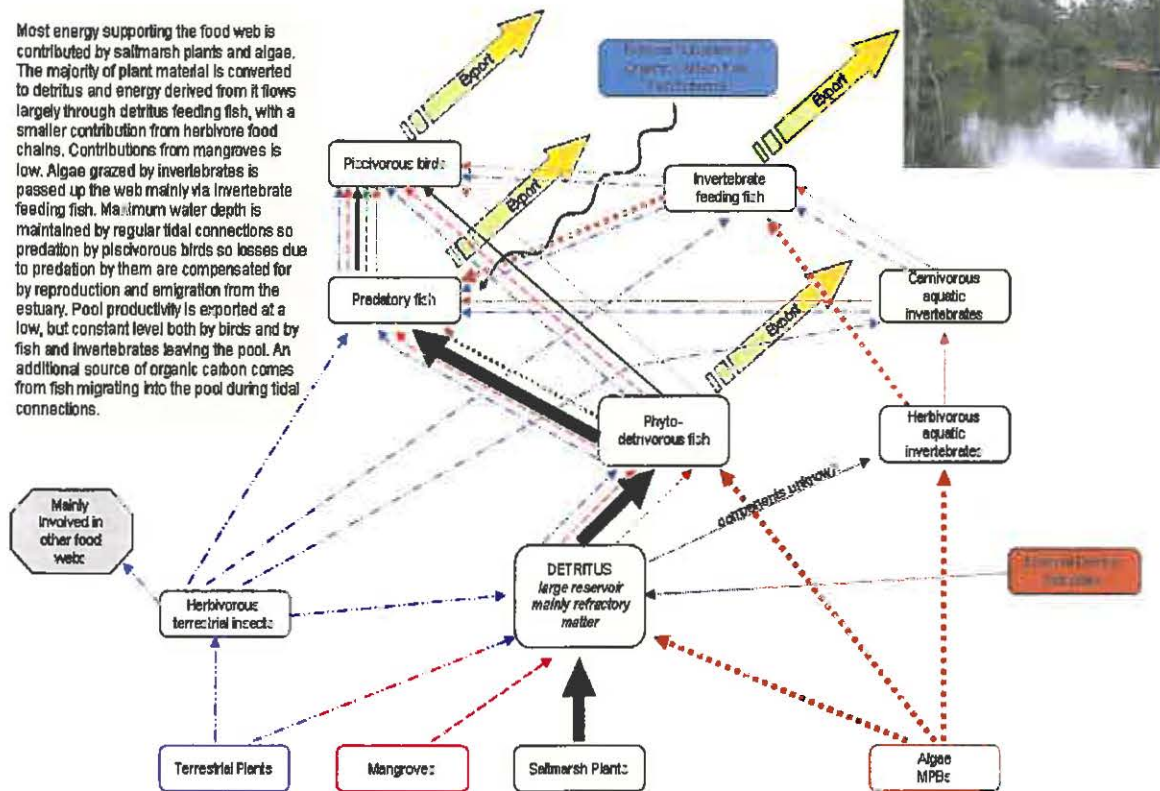


Figure 9.2. Scenario: food webs in saline pools with regular connections to the Fitzroy estuary
Export—unfilled arrows: little or no export under current conditions; yellow arrows: small percentage of total organic carbon exported; red arrows: larger percentage of total organic carbon exported

Scenario 2: Brackish pools with irregular connections to the Fitzroy estuary

Brackish pools (Figure 9.3) like the Twelve Mile Creek brackish pool are occasionally connected with estuarine waters (Chapter 3), with connection only on the highest tides of the year. Pool levels fluctuate more than for saline pools, but if they are part of a stream system, flow from local rainfall together with occasional tidal inputs mean water levels are usually reasonably high. The joint influences of fresh and salt means that brackish salinities are maintained most of the time.

As with saline pools much of the energy supporting the food web is contributed by saltmarsh plants and algae, with the majority of plant biomass converted to detritus and energy derived from it flowing largely through detritus-feeding fish. However, in contrast to saline pools, most of the grazing of live algae is by fish herbivory.

Maximum water depth rarely reaches critically shallow depths because it is maintained by irregular tidal connections as well as by downstream flows from local rainfall. Piscivorous birds are not unusually advantaged, so losses from bird predation can be compensated for by reproduction and immigration during connections to other pools and the estuary. Pool productivity is exported at a low but constant level by birds, and on occasions by fish leaving the pool during connection events. Additional source of organic carbon comes from fish migrating into the pool during tidal connection and material washed in during stream-flow events.

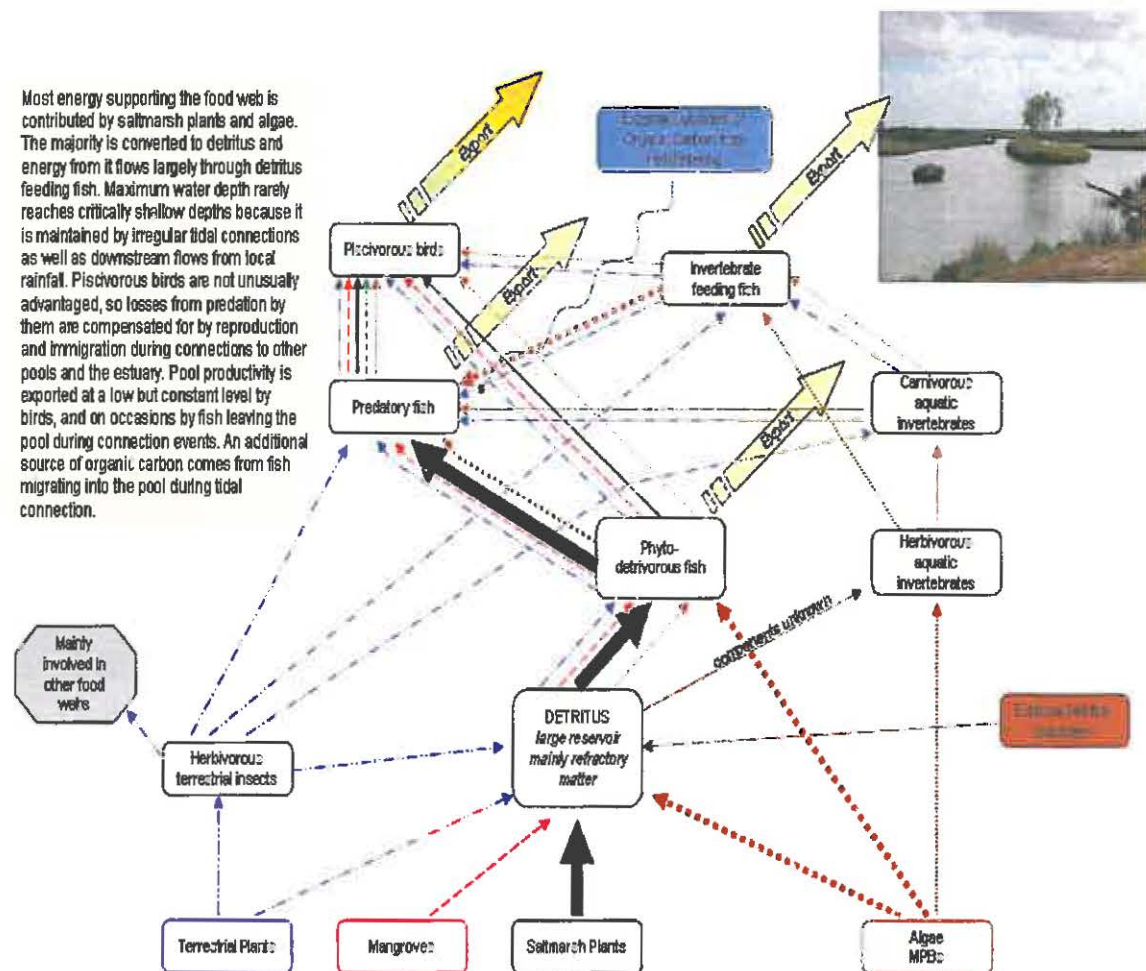


Figure 9.3. Scenario: food webs in brackish pools with regular connections to the Fitzroy estuary
Export—unfilled arrows: little or no export under current conditions; yellow arrows: small percentage of total organic carbon exported; red arrows: larger percentage of total organic carbon exported

Scenario 3: Isolated freshwater pools with high water levels

Isolated freshwater pools (Figure 9.4) like Frogmore and Woolwash lagoons are rarely connected with other freshwater systems, only rarely and indirectly connected with estuarine waters by stream flow or during major flooding (Chapter 3), and have no direct tidal connection. This means the pool water levels continually fall during disconnection periods, with the potential to dry out completely if isolated long enough. Again, most organic carbon is contributed by flowering water plants and algae, and energy from these sources is passed up the food chain through detritus via detritus-feeding fish, and directly via the grazing of fish and invertebrates. Energy from algae grazed by herbivorous invertebrates is passed up the web through both fish and carnivorous invertebrates.

When water levels are high (greater than about 1.5 m maximum depth) there is enough deep water that fish have a refuge from the heaviest predation from piscivorous birds, so losses due to bird predation do not exceed replenishment through reproduction. There is no interchange of pool fauna other than birds because of the pool's isolation from other aquatic systems. Pool productivity is only exported to other systems via birds at a low but constant level.

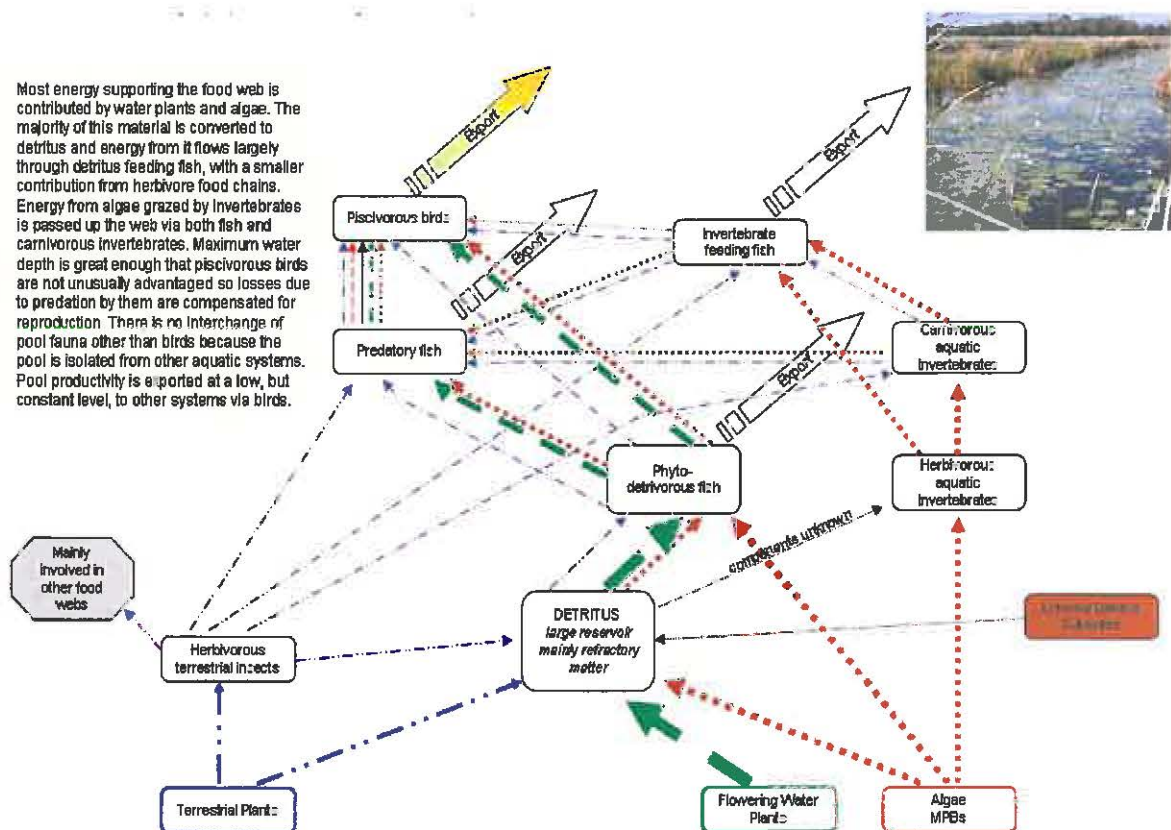


Figure 9.4. Scenario: food webs in freshwater pools when isolated from other pools or streams, and with maximum water depth *exceeding* about 1.5 m
Export—unfilled arrows: little or no export under current conditions; yellow arrows: small percentage of total organic carbon exported; red arrows: larger percentage of total organic carbon exported

Scenario 4: Isolated freshwater pools with low water levels

When maximum water depths in isolated freshwater pools fall below about 1.5 m (Figure 9.5), there is little refuge in depth and fish are forced into an ever decreasing volume of water. Piscivorous birds are greatly advantaged and congregate to take advantage of the abundant food supply. The first group to be impacted are the abundant, relatively small phyto-detritivores, and their abundance and density decreases rapidly, to the extent that they become a minor faunal component.

Phyto-detritivorous fish are the major agents through which energy stored in the detritus pool and contained in living algae is passed into the food web. Consequently, their demise severely disrupts normal trophic functioning, eventually leading to ecosystem collapse. If phyto-detritivorous fish are totally eliminated, refill by local rainfall, without reconnection to other systems, will not result in re-establishment of normal ecosystem function, which can only be restored by connected to a source from which phyto-detritivorous fish can be replenished. The large number of piscivorous birds taking advantage of the abundant supply of fish export much of the productivity tied up in fish biomass to other parts of the floodplain.

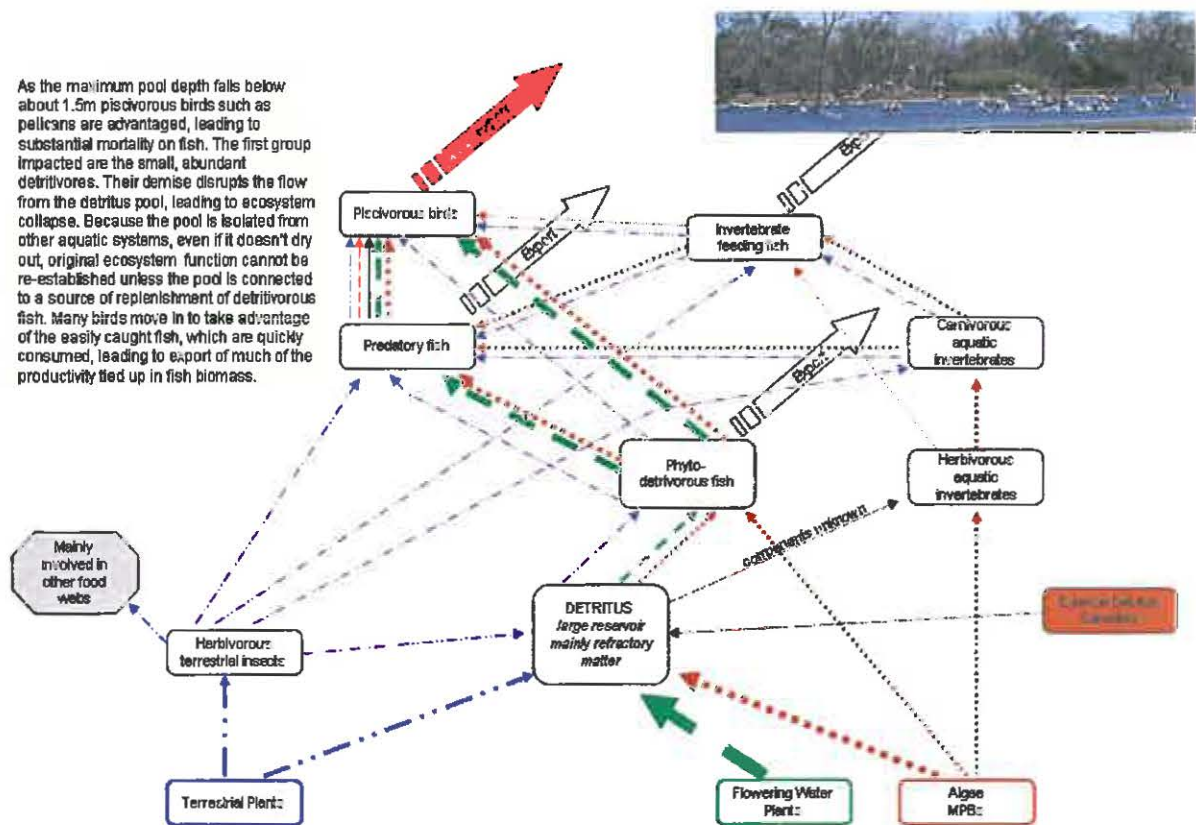


Figure 9.5. Scenario: food webs in freshwater pools when isolated from other pools or streams, and with maximum water depth less than about 1.5 m

Export—unfilled arrows: little or no export under current conditions; yellow arrows: small percentage of total organic carbon exported; red arrows: larger percentage of total organic carbon exported

Implications and uncertainties

These food chain models are not precise statements of fact, only interpretations based primarily on information in the previous chapters, so depend on the various explicit and implicit assumptions made in those chapters. However, at a general level they seem robust and sensible consequences of the combined body of information. While they probably represent the general situation reasonably well, there are many potentially important aspects glossed over due to a lack of information (e.g. the role of bacteria or the importance of organic material imported from beyond the immediate area of the pools). Obviously, more detail on temporal change and spatial differences would enhance the usefulness of the models.

A number of specific issues are also likely to be important. For instance, the role of bacteria, details of the pathways of detritus formation and the patterns of isotopic fractionation are generally unknown and difficult to determine, but are crucial to evaluating the importance of different dietary sources using stable isotopes (see Chapter 8). A second issue that needs to be addressed is the role of omnivory in foodweb structure. Omnivory is common in marine ecosystems and can introduce considerable complexity to apparently simple food webs (Polis 1991, Hall & Raffaelli 1993).

Chapter 10 Spatio-temporal patterns of fish condition

Marcus Sheaves and Ross Johnston

Summary

Standardised liver lipid vacuole area was evaluated as an indicator of sublethal changes in the health of fish in Fitzroy wetlands pools.

Estimates did not vary between pools but showed a consistent pattern of season-related temporal change, negatively correlated with water temperature.

Evaluation of lipid vacuole area suggests it has the potential to be a sensitive indicator of fish nutritional status, with the potential for development into a useful index of sublethal impacts on fish health.

Introduction

Periodic fish kills occur in both natural and constructed wetland pools. These events are catastrophic for the fauna, leading to massive decreases in abundance of ecologically important species that can then lead to substantial changes in ecosystem functioning. These changes in function can even lead to ecosystem collapse, and usually persist until the pool is again connected with a source of replacement fauna. In a broader context, fish kills often lead to greatly reduced nursery-ground function.

Fish kills also present a problem for humans in the vicinity of pools. Large numbers of rotting fish present a potential health hazard, and that, along with the odour of rotting fish, usually leads to the implementation of an expensive clean-up operation.

Fish kills are a symptom of poor environmental conditions in the pools. Some fish kills occur rapidly, with little warning (for instance when a storm causes a sudden input of water to a pool, redistributing anoxic bottom water throughout the water column, leading to low oxygen levels throughout the water column). In other cases fish kills are the end-point of slowly worsening conditions in a pool, for example, where salinity, temperature or pollution slowly increase to lethal levels. In such cases detection of degrading conditions is usually based on measured levels of physical parameters or pollutants.

Unfortunately, in most situations the lethal levels of these parameters are poorly understood. There is even less understanding of the levels at which degradation of ecological function begins, or at which the point-of-no-return is reached. Moreover, levels of physical variables and pollutants are not evenly distributed in pools, and the behavioural patterns of mobile animals such as fish can result in individuals being exposed to a greater or lesser extent than would be suggested by measured levels. On top of this, the influence of chronic, low-level inputs of pollutants or extended periods of slightly adverse environmental conditions are unknown.

At the moment management is usually reactive; cleaning up dead fish or attempting to 'save' distressed fish by translocating them to another site (there is little understanding of the effectiveness of this approach although it seems likely that many of the transported fish are already too badly affected to survive). Much more effective management could be implemented if forewarning of adverse changes was possible. However, the difficulties of linking levels of environmental parameters to faunal outcomes make it difficult to reliably detect environmental degradation before serious damage occurs. One promising option is to develop

techniques of detecting sublethal effects on the fauna itself, that is, measurements of changes in 'health' or 'condition'. Such detection could provide early warning of adverse changes before major faunal degradation occurred.

Detecting changes in the condition (health) of fish has usually relied on measures based on the length–weight relationship. However, except in extreme cases, reductions in weight at a particular length are difficult to differentiate from natural variation. Beyond this problem, the relationship between length and weight is slow to change, meaning that fish kills often occur before there is any detectable change in the length–weight relationship. Consequently, more sensitive measures of condition are required. Among the most promising of these are measurements of biochemical condition that reflect changes in the nutritional status of the fish. This approach has been demonstrated to possess the necessary attributes of rapid, sensitive response to known changes in nutritional status (Molony & Sheaves 1998a,b, Green & McCormick. 1999).

Traditionally, the measurement of biochemical condition of fish has relied on biochemical assays of the level of lipids (the main storage product of fish) in the liver (the main site of lipid storage). However, this approach is expensive and time-consuming, both in analysis and in the collection and storage of samples. A much cheaper and quicker option is to approximate lipid storage levels by estimating the relative proportion of the liver composed of lipid storage vacuoles.

While this approach has promise of providing early warnings of the development of conditions likely to lead to fish kills, it has not previously been applied to this problem. Before it can be applied successfully it is necessary to know and understand (a) the natural levels of variability within a species in one site at one time, (b) the sample size necessary to detect change, and (c) the normal, background patterns of variability due to natural (e.g. seasonal) change.

Aims

This component of study represents the initial step in developing histological evaluation of lipid storage levels as an indicator of sublethal change in fish condition in wetland pools. In particular, it investigates the extent to which the biochemical condition of fish varies between wetland pools, how it responds to seasonal and environmental change, and the extent to which it might be useful to detect recognised environmental degradation.

Methods

Study sites

Samples were collected from 10 wetland pools on the Fitzroy River floodplain: Frogmore and Woolwash lagoons, Twelve Mile brackish, Twelve Mile downstream, Twelve Mile upstream, Munduran saline, Munduran downstream, Munduran 'snake pool', Gonong saline and Little German Jack's lagoon (see Chapter 2 for pool descriptions).

Sampling

Initially, livers of all predatory fish were collected from each pool at each sampling occasion for histological preparation. A maximum of seven of each species was collected from each pool, at each time, to reduce the chance of adversely impacting the populations within the pools. At the completion of the third sampling trip (July 2004), it was clear that the abundances of predators were too low to reliably provide sufficient numbers of samples. Only two species—the barramundi, *Lates calcarifer*, and the giant herring, *Elops hawaiiensis*—occurred in reasonable numbers, and even these were abundant at only particular sites (Table 10.1). As a consequence, subsequent collections were expanded to include samples of the most abundant species in the pools, *Nematolosa erebi*, *Mugil cephalus*, and *Liza subviridis*.

L. calcarifer was captured from Twelve Mile brackish pool in all months, and *E. hawaiiensis* in all months except February 2004, allowing investigation of changes in condition over the whole study period. Sufficient samples of *N. erebi*, *M. cephalus*, and *L. subviridis* were also available from Twelve Mile brackish for meaningful analysis in November 2004, February 2005 and May 2005. Some additional samples of a number of species were also available for these months for other sites (Table 10.1).

Table 10.1. Numbers of fish collected for histological studies from Fitzroy wetland pools

		February 2004	May 2004	July 2004	November 2004	February 2005	May 2005
<i>L. calcarifer</i>	Twelve Mile brackish	5	5	6	4	1	4
	Twelve Mile fresh upstream		2	5			
	Munduran saline		1	1			
<i>E. hawaiiensis</i>	Twelve Mile brackish	8	7	7	2		3
<i>N. erebi</i>	Frogmore				5	2	4
	Woolwash					6	3
	Twelve Mile fresh downstream				3	5	4
	Twelve Mile fresh upstream				4	10	5
	Twelve Mile brackish				3	7	7
<i>M. cephalus</i>	Twelve Mile fresh upstream				2		
	Twelve Mile brackish				5	3	4
	Munduran saline				2	3	
	Frogmore				4		
<i>L. subviridis</i>	Twelve Mile brackish				3	1	5
	Munduran saline				1	8	5
	Gonong saline					2	5

Fish collected for analysis were kept in an ice-water slurry until dissection. They were returned to the laboratory as quickly as possible where the livers were dissected out and fixed in 10% Formalin for two weeks, then stored in 90% ethanol until histological processing. Two samples of each liver were placed in wax and sectioned at a thickness of 6 μm , placed on glass slides and processed using a Haemotoxin and Eocene stain.

Prepared slides were photographed at a magnification of 40x and stored as digital images, each representing an equal area of liver tissue. Lipid vacuoles appeared in the image as well defined, round-to-oval bodies of lighter colour than the surrounding tissue (Figure 10.1). The digital images were imported into the image analysis software, SigmaScan7Pro, which was used to measure the total area of each image comprised of lipid vacuoles. Image intensities between the upper and lower intensities of the vacuoles were assumed to represent lipid material.

Careful manual evaluation of 100 random images indicated that the amount of non-lipid material included between these thresholds was invariably small. Lower threshold levels used varied between 129 and 250 and upper threshold levels varied between 67 and 210. The exact threshold levels varied from slide to slide because of slight differences in the thickness of sections.

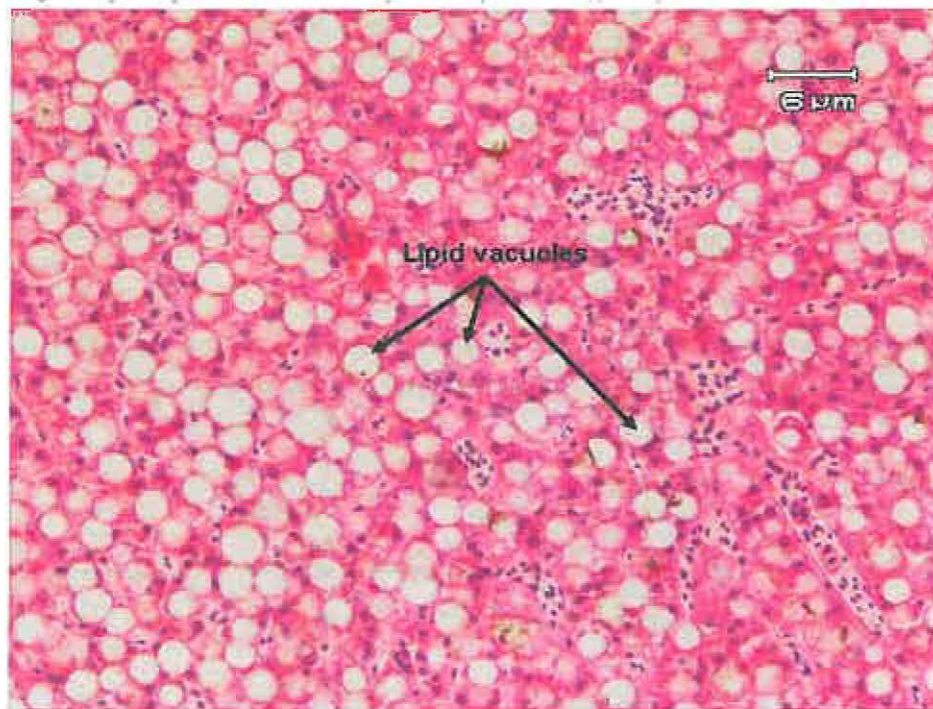


Figure 10.1. Digital image from a fish liver at 40x magnification; lipid vacuoles appear as pale white circles

To overcome any biases introduced by the use of differing thresholds, the area of vacuoles on each slide was evaluated twice, with the slides processed in random order and with each slide identified by a numeric code that gave no direct information about the species, location or time of the section. If the estimated area of the two random measurements was within 1%, the mean of the two estimates was used. If the estimates varied by more than 1%, two further estimates were made. If both of these were within 1% of either original estimate, the outlying value was discarded and the mean of the other three estimates used. If the variability was still greater than 1%, the data was discarded. The mean of the estimates from the two sections from each fish was used as the final estimate of vacuole per section for that fish.

Statistical analysis

For each species, the influence of location, trip, salinity, water temperature, turbidity, pH and dissolved oxygen (DO) on estimates of vacuole area per section was evaluated using regression trees (De'ath & Fabricius 2000). The final trees were selected under the 1+SE rule using 10-fold cross-validation (De'ath & Fabricius 2000). The relationship between the physical variables and mean vacuole area per section of *L. calcarifer* and *E. hawaiiensis* at Twelve Mile brackish was further investigated using cross-correlation.

The sample size needed to detect a difference in mean vacuole area per sections was estimated using the Power Analysis module in STATISTICA. For each species, estimation was based on detecting half the maximum difference between mean vacuole area per liver section using a t-test for independent samples (power = 0.8, $\alpha = 0.05$) observed for fish from Fitzroy wetlands pools. Estimation was conducted for the (a) highest, (b) mean and (c) lowest observed standard deviations for samples of fish comprising five or more individuals.

Results

Spatial and temporal variation in mean liver lipid vacuole area per section

The final regression trees for all species indicated that location, salinity, water temperature, turbidity, pH and DO had little influence on vacuole area, with most of the variance explained best by timing of sampling (e.g. *N. erebi*, Figure 10.2). In all cases, fish from November 2004 had the lowest vacuole areas and those from May 2004 and 2005 the highest. February samples sometimes grouped with November 2004 and sometimes with May samples.

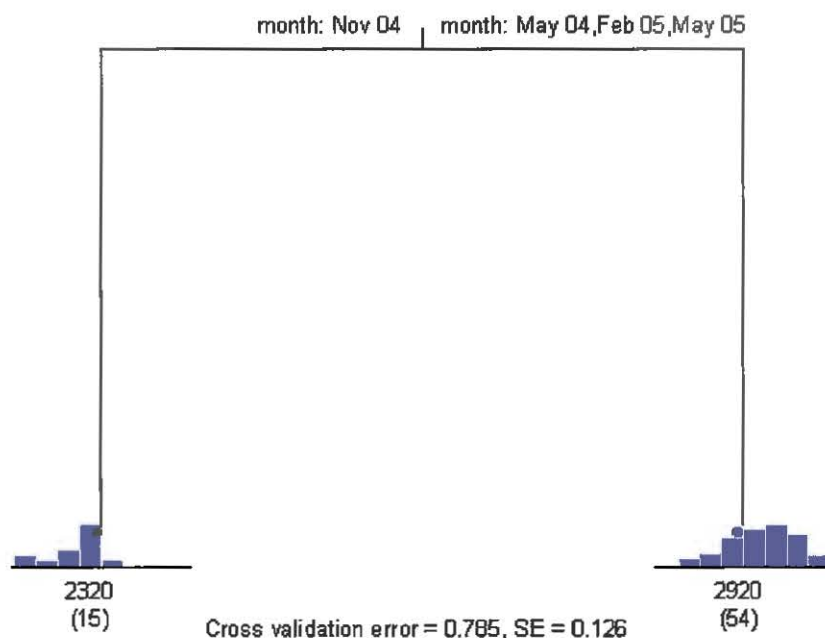
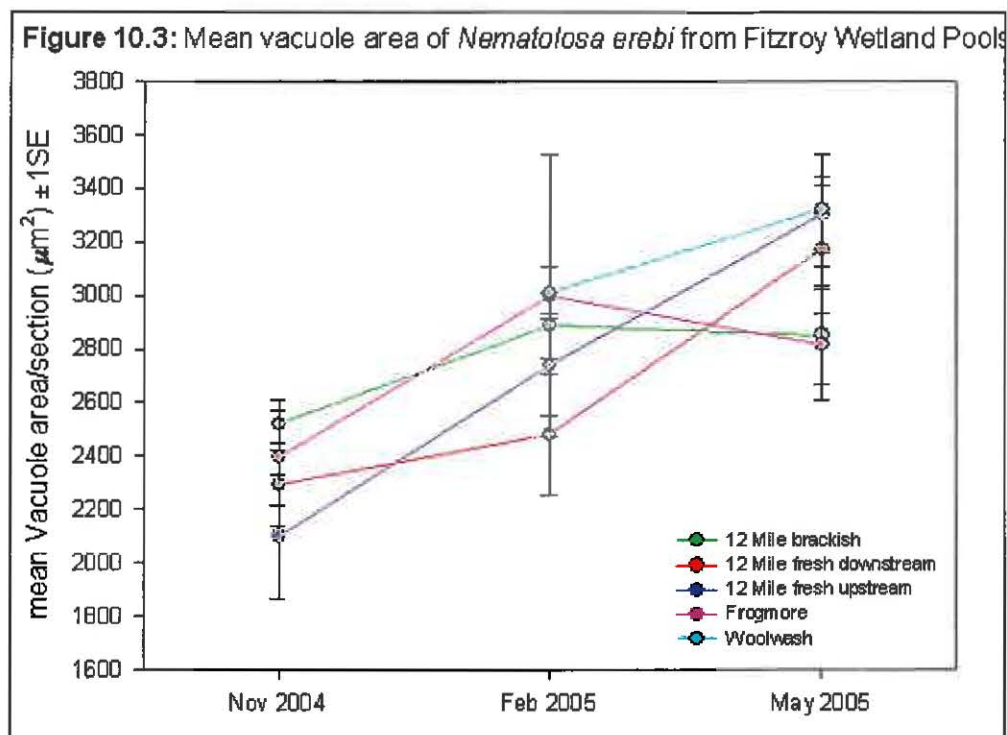


Figure 10.2. Regression tree (1+SE) for vacuole area per section for *Nematalosa erebi* from Fitzroy wetland pools, fitted under 10-fold cross-validation
Bar graphs show the distribution of samples in each branch; numbers under the bar graphs are the mean vacuole estimates; numbers in brackets are sample sizes

N. erebi showed very similar patterns of change in vacuole area from November 2004 to May 2005 at all sites where they occurred (all three Twelve Mile Creek sites, Frogmore and Woolwash lagoons) (Figure 10.3). Vacuole area was lowest in November 2004 and increased through February and into May.

Although the data are more limited, the situation was similar for *L. subviridis* (Figure 10.4) and *M. cephalus* (Figure 10.5). Where data were available, vacuole areas of fish were similar among sites at one time (the high value for *L. subviridis* in Munduran brackish should be disregarded because that value is based on data from a single fish), and increased from November 2004 through February 2005 to May 2005.

As with the previous species, *L. calcarifer* showed similar patterns in vacuole area among sites at any one time (Figure 10.6).



Figure[B3] 10.3. Mean vacuole area of *Nematolosa erebi* from Fitzroy wetland pools

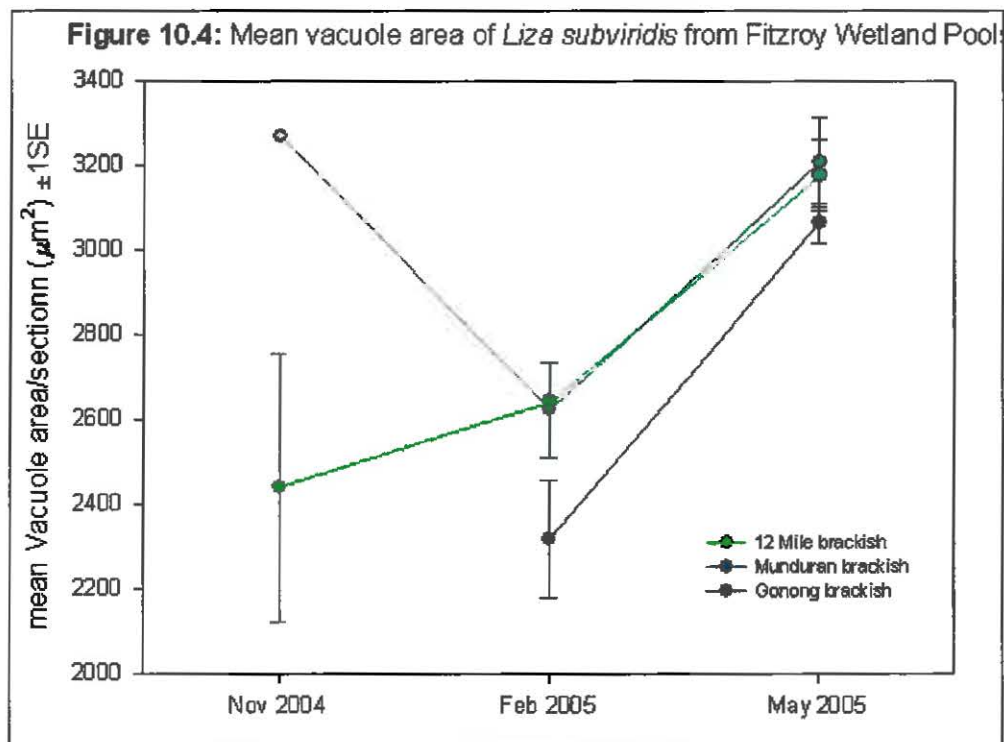


Figure 10.4. Mean vacuole area of *Liza subviridis* from Fitzroy wetland pools

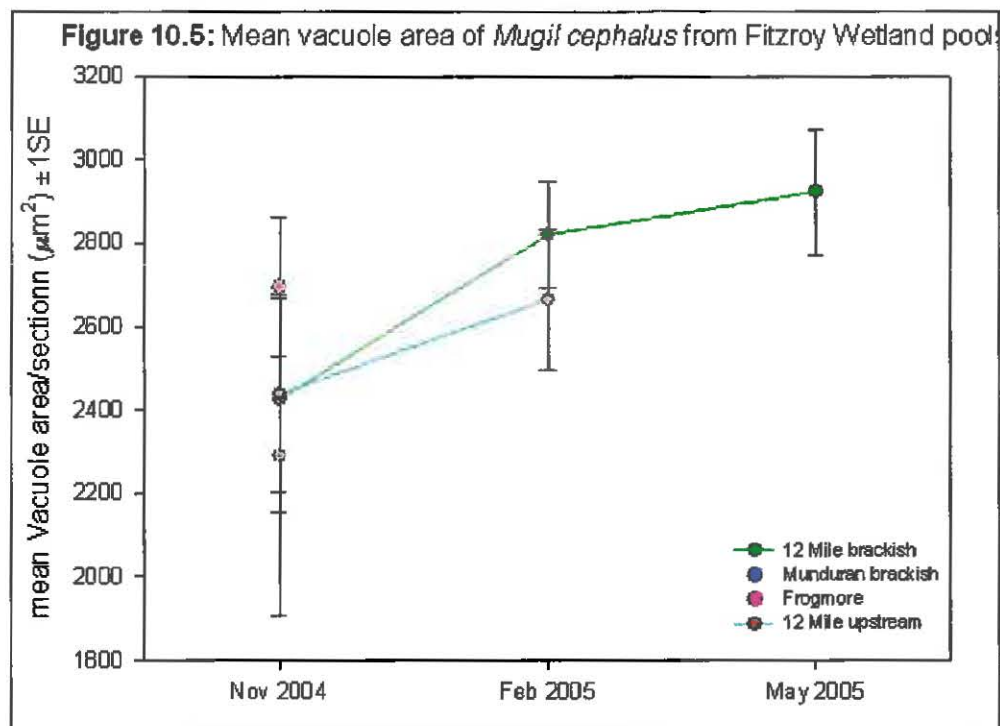


Figure 10.5. Mean vacuole area of *Mugil cephalus* from Fitzroy wetland pools

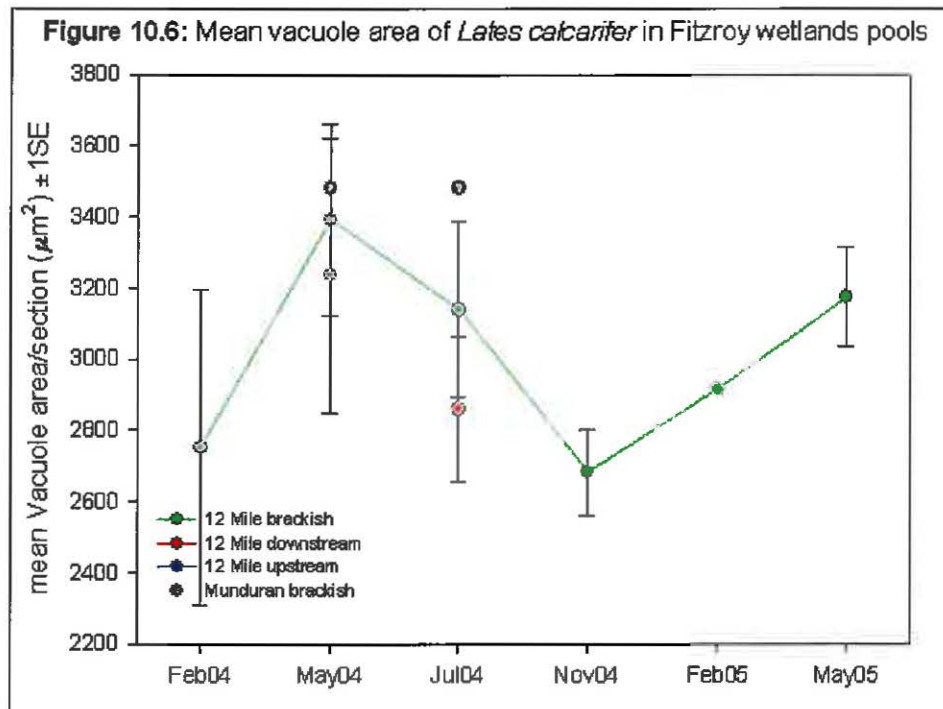


Figure 10.6. Mean vacuole area of *Lates calcarifer* from Fitzroy wetland pools

Although *L. calcarifer* was only captured in sufficient numbers to investigate temporal patterns at Twelve Mile brackish, and *E. hawaiiensis* was only captured at Twelve Mile brackish pool, they were captured in numbers at this location on all sampling occasions except February 2005 (when only one *L. calcarifer* was captured), providing a long time series of data (Figure 10.7). Again, the two species showed parallel patterns of change in vacuole area through time.

Even though regression tree analysis showed an effect of trip but no overall effect of temperature on vacuole area, the situation is different when the sequence of mean vacuole areas is cross-correlated with the sequence of water temperatures, with a clear negative correlation for both species (Figure 10.7). The greatest vacuole area corresponded to times of low water temperature and the least to times of high temperature. The cross-correlation at a lag of zero explains a substantial part of the effect of trip for both *L. calcarifer* ($r = -0.82$) and *E. hawaiiensis* ($r = -0.75$). Mean vacuole area showed no substantial cross-correlation with any other physical variable.

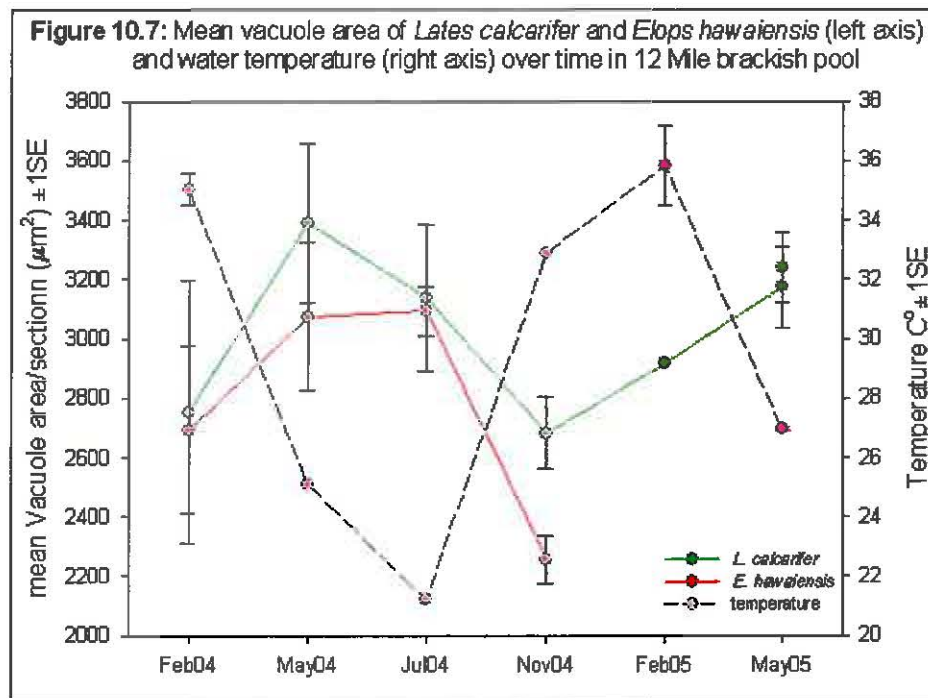


Figure 10.7. Mean vacuole area of *Lates calcarifer* and *Elops hawaiiensis* (left axis) and water temperature (right axis) over time in Twelve Mile brackish pool

Sample sizes needed to detect changes in lipid vacuole area per section

The sample sizes needed to detect a difference in mean vacuole area per section at half the maximum difference between mean vacuole area per liver section (t-test for independent samples, power = 0.8, $\alpha = 0.05$) were estimated based on observed standard deviations from sample sizes of five or more (Table 10.2). Estimated sample sizes varied between 60 (*M. cephalus*) and 14 (*L. subviridis* and *N. erebi*) for the highest observed standard deviations, down to 19 (*M. cephalus*) and 3 (*L. subviridis*), with estimated sample sizes between 36 (*M. cephalus*) and 7 (*L. subviridis*) for the mean standard deviation.

Table 10.2. Estimated sample size (N) needed to detect half the observed maximum difference between mean vacuole area per liver section using a t-test for independent samples (power = 0.8, $\alpha = 0.05$) for fish from Fitzroy wetland pools. Estimation used (a) highest, (b) mean and (c) minimum standard deviation observed for samples of fish containing five or more individuals

	<i>Elops hawaiiensis</i>	<i>Lates calcarifer</i>	<i>Liza subviridis</i>	<i>Mugil cephalus</i>	<i>Nematalosa erebi</i>
Largest mean	3239	3563	3267	2916	3432
Smallest mean	2257	2682	2066	2290	2101
Maximum difference between means	981	880	1201	625	1330

Highest stdev (n >=5)	799	603	539	601	585
Mean stdev (n >=5)	510	422	359	465	445
Lowest stdev (n >=5)	220	240	179	329	304

(a) N @highest stdev (n >=5)	43	31	14	60	14
(b) N @mean stdev (n >=5)	19	16	7	36	9
(c) N @lowest stdev (n >=5)	5	6	3	19	5

Discussion

Variation in biochemical condition of fish in Fitzroy wetland pools

Even though the Fitzroy pools represent an eclectic group of environments, differing in salinity regime, physical connectivity, location and environmental setting, there was no indication of systematic variation in biochemical condition (as measured by vacuole area per standard section of liver) between sites. Furthermore, biochemical condition showed the same distinct pattern of seasonal change across pools, with high values of liver vacuole area corresponding to times of lowest water temperature (Figure 10.7).

Experimental evidence shows that the biochemical condition of fish is strongly influenced by physiological stressors, such as poor nutrition (Molony & Sheaves 1998a,b). Thus, the similarities between diverse sites in the present study suggest that the fish, and the food webs and wetland pools that support them, were healthy and functioning within environmentally suitable limits.

This does not mean that the fish faunas of all Fitzroy wetland pools are equally healthy or that the pools and their fauna are not under threat from forces that cause degradation but do not produce changes in health. The study pools were chosen because they appeared to have no major barriers to physical connectivity, and because they could be accessed reliably. Consequently, the study cannot be taken to represent the situation in poorly connected pools or pools where conditions or landholders made access difficult—exactly the types of pools potentially likely to provide unhealthy environments for reasons such as poor exchange of water, high levels of pollution or eutrophic conditions.

Additionally, conditions such as reducing water levels may lead to less habitat space but no detectable reduction in condition, because shallowing depths make the fish more vulnerable to bird predation so keeping fish numbers in balance with the available feeding area or volume. Similarly, the study pools that did develop adverse conditions (the two German Jack's lagoons developed very hot and hypersaline conditions) likely to lead to decreased health of their faunas, were very shallow, meaning their fish fauna was consumed by piscivorous birds before conditions became extreme.

Usefulness of biochemical condition as a tool for detecting adverse faunal change

The similarity in liver lipid vacuole area between sites indicates it is a reliable, repeatable measure. The clearly detectable pattern of temporal change, strongly correlated with water temperature, an important driver of physiological processes (Begon *et al.* 1990), suggests that this measure of biochemical condition reliably reflects real physiological changes. It also indicates that this measure varies substantially and predictably, prerequisites for any useful measure of change.

The strong cross-correlations at a lag of zero further indicate that the responses are rapid. The ability to reflect seasonal change strongly suggests that lipid vacuole area should provide clear indications of adverse changes in health of fish in wetland pools because such changes should be greater than the observed seasonal change, which by definition is within natural variation. Previous studies have shown substantial changes in liver vacuolation resulting from changes in nutritional status (Green & McCormick 1999, Salhi *et al.* 1999, Caballero *et al.* 2004) and pollution (Saleh & Hamza 1986, Arellano *et al.* 1999) above those produced by seasonal effects such as temperature (Molony & Sheaves 1998a,b). These factors point to liver lipid vacuole area as a useful tool for detecting stress-induced changes in fish in wetland pools at a sublethal level, and therefore also as a potentially useful index of pool biological health. The response to seasonal change has one further consequence: any study of biochemical condition would need to account for this water temperature related variation.

Despite this potential usefulness, the lipid vacuole area of *N. erebi*, the dominant fish in all the freshwater sites, showed no difference in May 2005 at Woolwash lagoon compared to the other wetland pools (Figure 10.3). This was despite a massive reduction in numbers in Woolwash that led to fish kills beginning in September 2005. This is not surprising, because liver lipid levels reflect nutritional status (Green & McCormick 1999, Salhi *et al.* 1999, Caballero *et al.* 2004).

The reduction in numbers in Woolwash occurred when the pool level fell to a point where piscivorous birds such as pelicans, *Pelecanus conspicillatus*, became very effective (in May 2005 numbers were so low that it was difficult to collect the small number of fish needed for lipid vacuole studies). Consequently, the numbers of *N. erebi* were probably kept to a level where resources were not limiting, so unlikely to produce a response in individual fish lipid levels. Clearly, lipid vacuole area, or any other measure of biochemical condition, is an unsuitable index of pool health in such a situation. However, its ability to reliably reflect physiological change make it potentially very useful for the detection of degradation due to

effects such as pollution or low oxygen levels, in situations where events such as increased predation due to reducing water levels do not complicate the situation.

Based on the range of standard deviations observed during the study, the sample sizes needed to detect a reasonably conservative change (half the maximum change seen in the study) is manageable (between 7 and 36 samples for the average standard deviation, depending on species). The actual sample sizes needed may be even lower because the standard deviation of the estimates is likely to fall as operators become more experienced.

Conclusion

This study represents the initial step in developing histological evaluation of lipid storage levels as an indicator of sublethal change in fish condition in wetland pools. More work is needed, but the results so far indicate the approach may provide a reliable and cost-effective tool for detecting changes in the health of fish in wetlands pools, in response to such stressor resulting in changes in nutritional status, before the stresses become critical.

Chapter 11 Within-pool distribution of aquatic vertebrates

Ross Johnston and Marcus Sheaves

Introduction

The most noticeable and contentious by-products of the human development of waterways are habitat degradation and loss (Holland *et al.* 2004). As a consequence, understanding habitat preferences of fish is central to managing waterways and wetlands. Understanding how fish are distributed relative to available habitat types has another benefit; it allows sampling to be more directly focused on target species, so that population parameters (density, species richness and relative abundance) can be more reliably estimated because sampling can be tailored to best represent the range of habitats and species available in a target area. Additionally, because distribution is frequently interrelated with trophic function (Sheaves & Molony 2000), understanding distribution, in conjunction with knowledge of diet, enhances the understanding of energy flows through and within systems.

Prior wetland research in tropical Australia has examined in-stream fish assemblages while off-stream/isolated pools have been largely ignored. At best, studies have examined the compositions of fish assemblages in isolated pools and related differences in composition among pools to differences in broadscale habitat characteristics of the pools (e.g. Arthington *et al.* 2005). Globally, studies investigating spatial distributions of fish within pools have been focused on specific interactions among biota such as predator/prey relationships (e.g. Skov *et al.* 2002), have only considered a small range of habitats (e.g. Romare *et al.* 2003), were single species studies, or focused on a single spatial scale (Essington & Kitchell 1999). Studies mapping the spatial distribution of fish assemblages within lakes or pools and encompassing all habitat types and spatial scales are rare, particularly for shallow water bodies such as those on the Fitzroy River floodplain.

This component of the study examines and describes the within-pool spatial distribution of the numerically dominant fish species in the Fitzroy floodplain wetland pools. To achieve this, predictive models were developed from existing literature and tested in the Fitzroy wetland pools. Available literature predominately relates to large, deep, stratified water bodies in the northern hemisphere (e.g. Mehner *et al.* 2005). While it is unlikely that information from those systems is wholly appropriate for tropical and subtropical pools with little or no stratification, the absence of more appropriate literature models derived from these systems provide the best starting point available.

Previous literature suggests open water and deeper habitats are likely to contain a mix of pelagic planktivores (Skov *et al.* 2002), detritivores and large benthivores (Diekmann *et al.* 2005) and pelagic piscivores (Mehner *et al.* 2005). In shallower, edge-associated habitats we may expect to see pelagic planktivores (Lewin *et al.* 2004) and detritivores (Pusey & Kennard 1996) again, as well as small (Lewin *et al.* 2004) and large (Pusey & Kennard 1996) benthivores and large, site-attached piscivores (Skov *et al.* 2002). Clearly, there is substantial overlap of trophic categories across habitat types.

Moreover, different studies report different habitat preferences for the same species in different regions (Skov *et al.* 2002; Lewin *et al.* 2004). Such inconsistency in distributions within temperate regions makes biomasses and/or density distributions for tropical or subtropical systems difficult to predict. Furthermore, extrapolating from these studies to Australian tropical or subtropical systems at a taxonomic level provides little useful information.

Fortunately, fish sampling conventions in Australian freshwater studies provide some useful clues to build on. Most Australian freshwater fish studies restrict

sampling to edge habitats (e.g. Arthington *et al.* 2005), thus tacitly implying that there are few fish in deeper, more open waters. If this is the case, with the exception of pelagic piscivores (generally low-abundance species), both biomass and abundance in a given pool is likely to be concentrated around shallow edges (Figure 11.1). A model such as this is convergent with models based on the distribution of estuary fish assemblages in tropical Australia (Blaber *et al.* 1989, Johnston & Sheaves unpublished data) (Figure 11.2). Given this, these estuary models seem appropriate conceptual starting points for understanding fish distribution in the Fitzroy floodplain wetland pools.

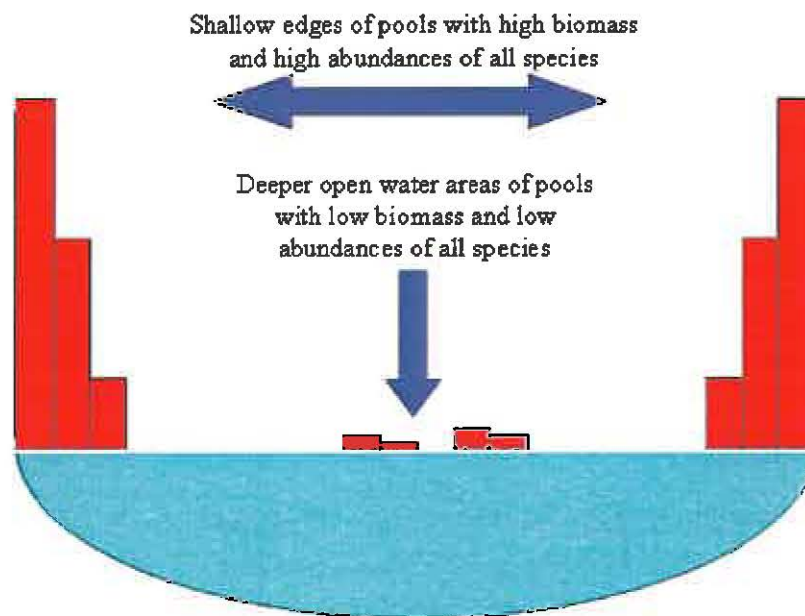


Figure 11.1. Model of fish distribution in floodplain pools developed from existing freshwater/wetland pools literature

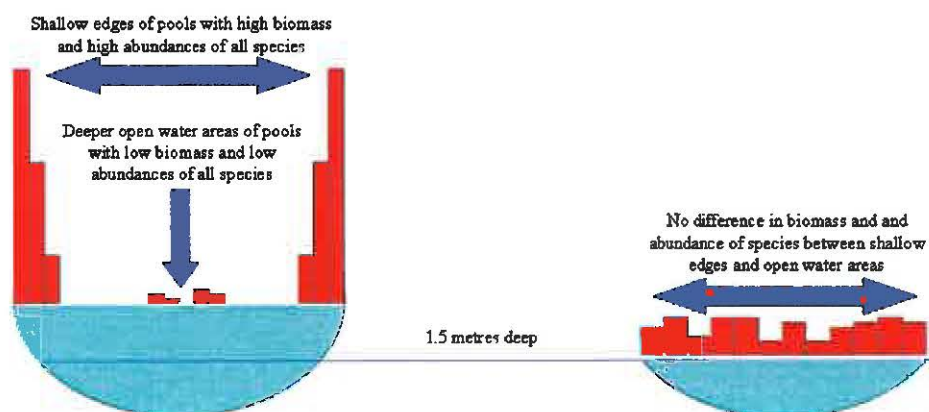


Figure 11.2. Mean model of fish distribution in tropical estuaries

Methods

Sampling gear

Cast nets (18 mm monofilament mesh; 4.29 m diameter) were used to sample fish in the pools under the net-use protocols set out in Chapter 4 and Johnston *et al.* (submitted).

Sampling design

Nets were deployed in pairs along transects across the pool. Transects were spaced approximately evenly along the navigable length of the pools, and between nine and fifteen transects (depending on pool length and depth at the time of sampling) were sampled on each sampling occasion. For Munduran and Gonong saline pools, Twelve Mile brackish and Woolwash lagoon, three pairs of nets were collected along each transect (one pair from each edge and one pair mid-pool). The greater width of Frogmore lagoon allowed the collection of five pairs of net samples spaced along each transect (one pair from each edge and one pair from quarter, one from half and one from three-quarter distance along each transect).

The sampling design was first employed in Frogmore in July 2004. Initial success led to its introduction for subsequent trips to Twelve Mile brackish, and Munduran and Gonong saline (Table 11.1). Sampling was only carried out in Woolwash lagoon on one subsequent occasion and the sampling design was also applied there. These five pools were used because they were wide enough to allow cross-pool transects to be sampled with sufficient distance between edge and middle areas to maintain the spatial independence of samples.

Table 11.1. Pools, sampling dates and total number of nets collected

Location	Pool type	Sampling dates	Total number of nets
Frogmore lagoon	Freshwater	Jul, Nov 2004; Feb, May 2005	420
Woolwash lagoon	Freshwater	Feb, 2005	66
Twelve Mile brackish	Brackish	Nov 2004; Feb, May 2005	234
Munduran Creek	Saline	Nov 2004; Feb, May 2005	174
Gonong Creek	Saline	Nov 2004; Feb, May 2005	148

Statistical analysis

Univariate classification and regression trees (C&RTs) (De'ath & Fabricius 2000) were used to examine the taxon-specific responses to the predictor variables for each of the pools. Independent/predictor variables used in C&RT analyses were: trip, longitudinal position in pool (transect), cross-pool position (coded as 0–50–100 where 0 = one bank, 50 = mid pool, 100 = the opposite bank), size class and depth. For all models, response variables (counts) were $\log(x+1)$ transformed to limit the influence of occasional nets with very high abundances (Gauch, 1982). Final C&RT models were selected using cross-validation and the 1 SE rule (De'ath & Fabricius 2000), or where the 1 SE tree only produced a single split (suggesting an overly simplistic model) the next largest tree was chosen.

Results

Frogmore lagoon

The distribution of *Nematolosa erebi* in Frogmore lagoon was primarily determined by depth, with most fish captured in water depths greater than 0.95 m; mean abundance per net 0.086 at depths less than 0.95 m and 0.37 at depths greater than 0.95 m (Figure 11.3). Although cross-pool position was highly correlated with depth, position was not an important variable for describing the distribution of *N. erebi*.

Secondary splits indicated there was little detail in the February and May 2005 samples, when few fish were recorded or for fish over 100 mm (FL) for July and November 2004. However there was a high level of detail for the smaller size classes (<100 mm FL) in the July and November 2004 samples. During those months small fish (<100 mm (FL) were more abundant in transects at the downstream end of the lagoon (transects 1–4), and generally at depths greater than 1.65 m.

The depth-related pattern of distribution of *N. erebi* remained fairly consistent in the July and November 2004 trips and in May 2005 (Figures 11.4 and 11.5). However distribution patterns were less distinct in May 2005 and possibly different in February 2005, trips when numbers of fish were quite low so any interpretation must be treated with caution.

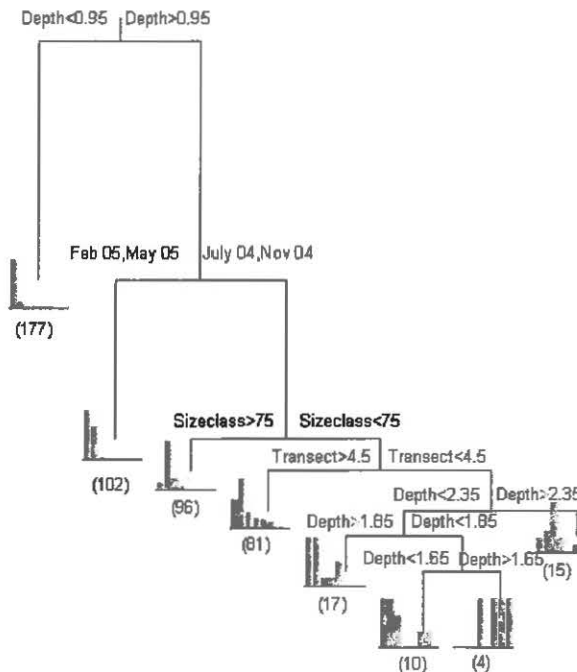


Figure 11.3. Classification and regression tree for factors affecting the distribution of *Nematalosa erebi* in Frogmore lagoon (% variance explained = 68.11)

Depths are reported in metres; response variable is $\log(1+x)$ transformed abundance; histograms show the frequency distribution of catch sizes for each terminal node; numbers in brackets show sample sizes for each terminal code

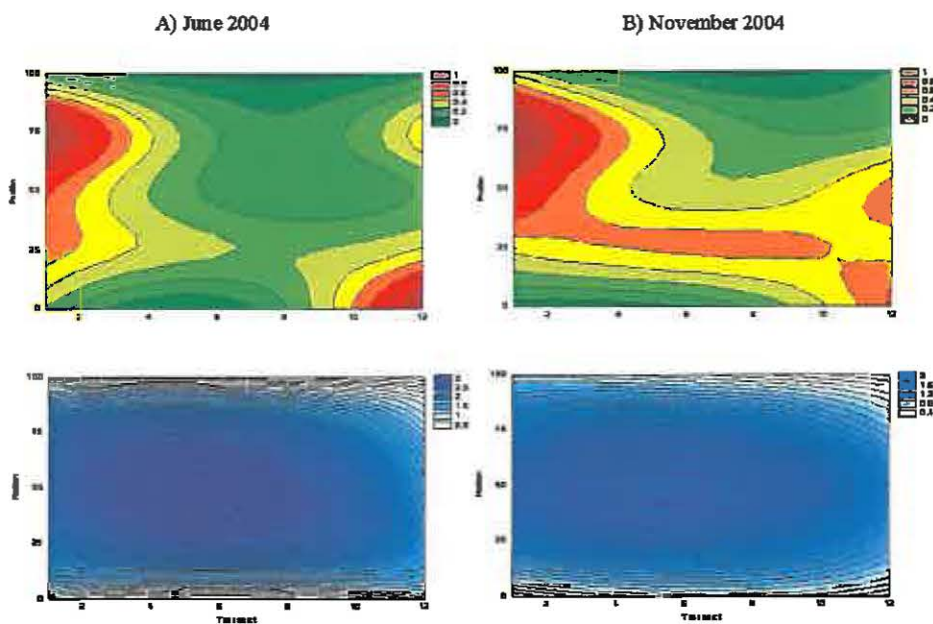


Figure 11.4. Patterns of distribution for *Nematalosa erebi* less than 100 mm (FL) in Frogmore lagoon during A) June 2004 and B) November 2004

Upper panels are distribution patterns based on abundances and lower panels show bathymetry of the pool for the corresponding months. Transect 1 is located at the downstream end of the pool. Contour lines are distance weighted least squares fit. Note: depth ranges differ between trips

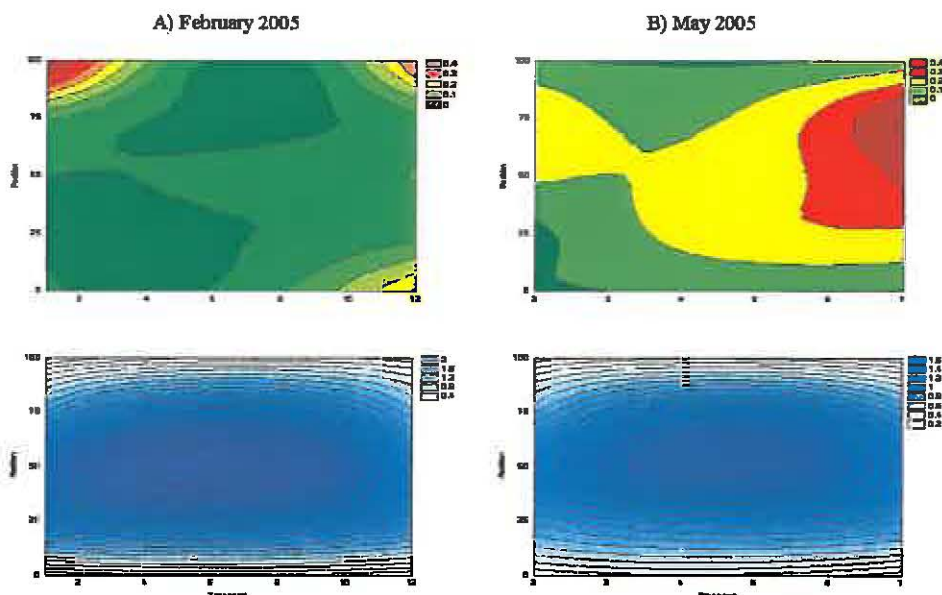


Figure 11.5. Patterns of distribution for *Nematalosa erebi* less than 100 mm (FL) in Frogmore lagoon during A) February 2005 and B) May 2004

Upper panels are distribution patterns based on abundances and lower panels show bathymetry of the pool for the corresponding months. Transect 1 is located at the downstream end of the pool. Contour lines are distance weighted least squares fit. Note: depth ranges differ between trips

Low numbers of large *N. erebi* (>100 mm FL) mean descriptions of their distribution are less conclusive than those of the small fish; however, there were clearly and consistently higher abundances recorded from the deeper water in the central part of the lagoon (Figures 11.6 and 11.7).

Depth also played a pivotal role in the distribution of *Amniataba percooides* (Figure 11.8), and the short-necked tortoise, *Emydura krefftii* (Figure 11.9). *A. percooides* were recorded in highest numbers at depths less than 0.85 m, particularly in transects associated with the highest densities of trees along the shoreline (transects 5–10). *E. krefftii* were most abundant at depths less than 0.75 m, particularly the eastern edge (positions 0 and 25) of the downstream portion (transects 1–8) of the lagoon.

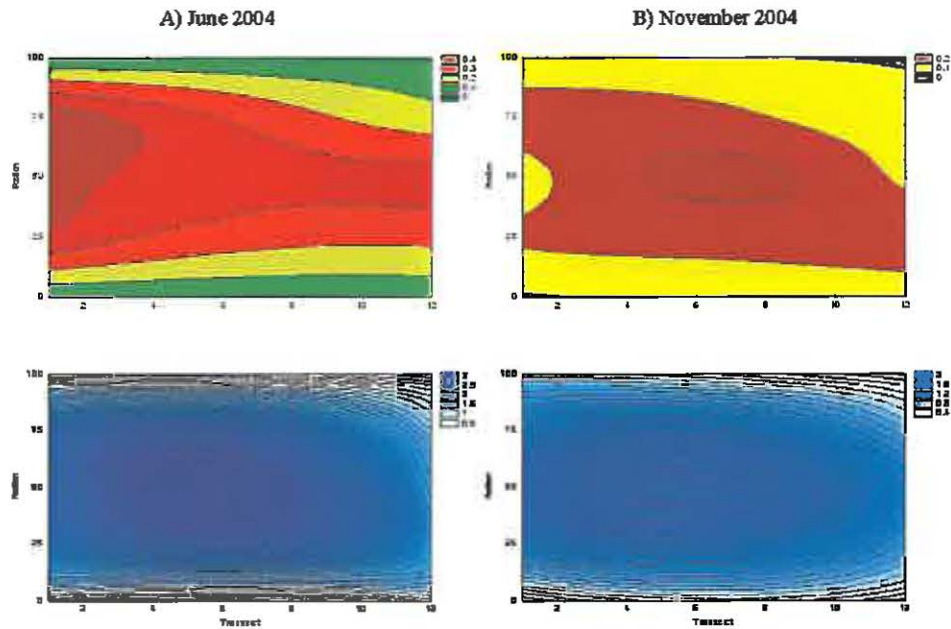


Figure 11.6. Patterns of distribution for *Nematalosa erebi* greater than 100 mm (FL) in Frogmore lagoon during A) June 2004 and B) November 2004
 Upper panels are distribution patterns based on abundances and lower panels show bathymetry of the pool for the corresponding months. Transect 1 is located at the downstream end of the pool. Contour lines are distance weighted least squares fit. Note: depth ranges differ between trips

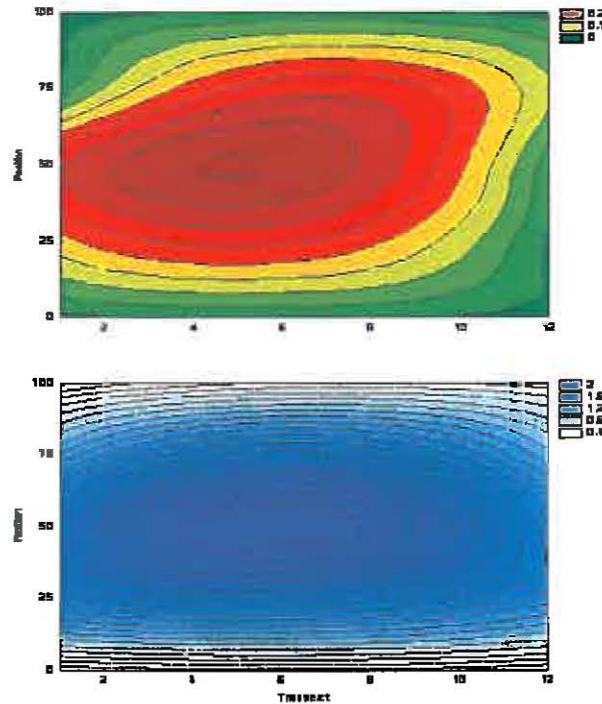


Figure 11.7. Patterns of distribution for *Nematalosa erebi* less than 100 mm (FL) in Frogmore lagoon during February 2005
 Upper panels are distribution patterns based on abundances and lower panels show bathymetry of the pool for the corresponding months. Transect 1 is located at the downstream end of the pool. Contour lines are distance weighted least squares fit.

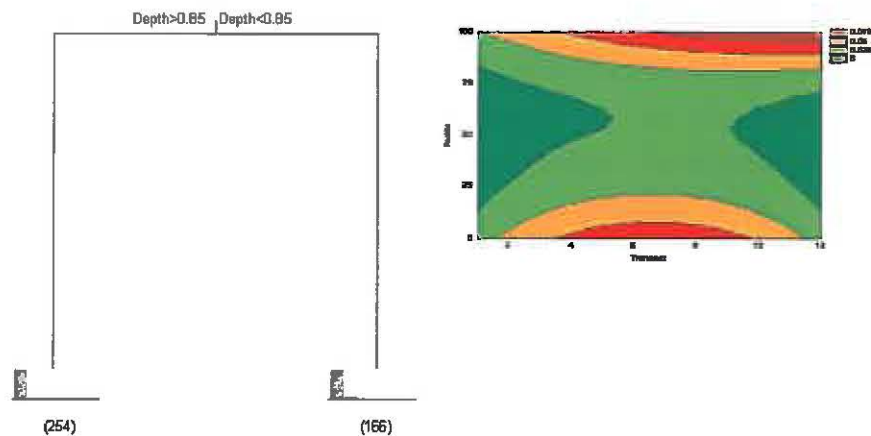


Figure 11.8. Classification and regression tree (left panel) for factors affecting the distribution of *Amniataba percooides* in Frogmore lagoon (% variance explained = 24.02)

Depths are reported in metres; response variable is $\log(1+x)$ transformed abundance; histograms show the frequency distribution of catch sizes for each terminal node; numbers in brackets show sample sizes for each terminal code. Right-hand panel shows the distribution pattern based on abundances; bathymetry of the lagoon over the sampling period can be seen in Figures 11.4–11.7.

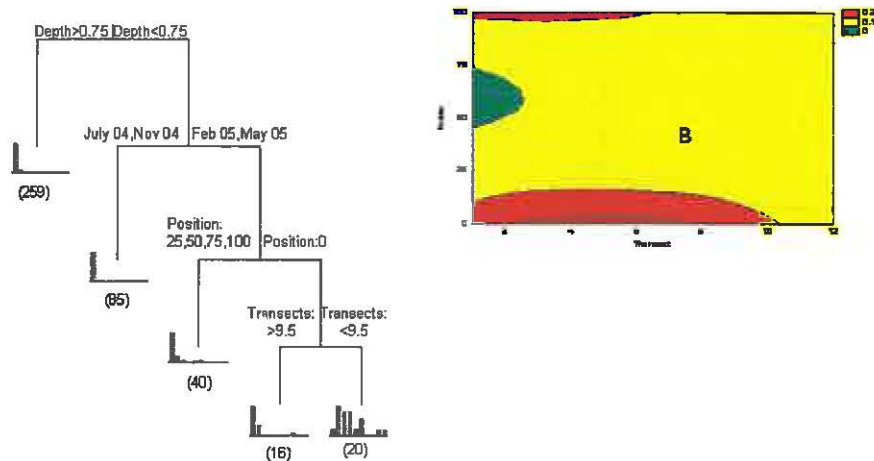


Figure 11.9. Classification and regression tree (left panel) for factors affecting the distribution of *Emydura krefftii* in Frogmore lagoon (% variance explained = 68.35)

Depths are reported in metres; response variable is $\log(1+x)$ transformed abundance; histograms show the frequency distribution of catch sizes for each terminal node; numbers in brackets show sample sizes for each terminal code. Right-hand panel shows the distribution pattern based on abundances; bathymetry of the lagoon over the sampling period can be seen in Figures 11.4–11.7.

Woolwash lagoon

The initial split in data for *N. erebi* in Woolwash lagoon separated the large (>100 mm FL) from the small (<100 mm FL) size classes (Figure 11.10). Secondary splits indicated that depth was the most important explanatory variable for the larger fish, followed by longitudinal location in the pool. Highest abundances occurred at depths greater than 1.15 m, and particularly in the downstream transects (1–7). However the lack of deep water in most of those transects meant that almost all fish were concentrated between transects 5 and 7 (Figure 11.10). Smaller fish were most influenced by longitudinal location (transect 9 had highest abundances) (Figure 11.10). The highest abundances of both large and small *N. erebi* coincided with the deepest water in the lagoon at the time of sampling; the only transects with depths over 1 m were transects 7, 8 and 9, and fish were only recorded from the middle (50) cross-pool position. There seems little doubt that depth was the reason why fish were so concentrated at the centre of the pool.

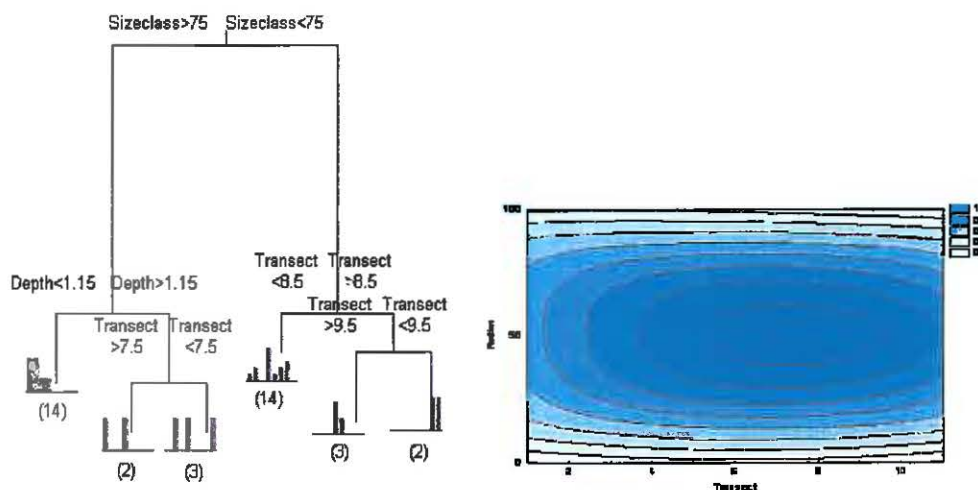


Figure 11.10. Classification and regression tree (left panel) for factors affecting the distribution of *Nematalosa erebi* in Woolwash lagoon (% variance explained = 75.04) Depths are reported in metres; response variable is $\log(1+x)$ transformed abundance; histograms show the frequency distribution of catch sizes for each terminal node; numbers in brackets show sample sizes for each terminal code. Bathymetry of the lagoon is shown in the right-hand panel. *N. erebi* were only recorded from the middle position (50) in the pool, no fish were recorded from edges (positions 0 and 100) so a least squares fit cannot be produced. *N. erebi* were recorded in all transects.

Twelve Mile brackish pool

The initial division of *N. erebi* data was based on size class, with size classes of 50 mm FL and greater placed on the low abundance left-hand tree (Figure 11.11). For the small (<50 mm FL) *N. erebi* in the Twelve Mile brackish pool, depth was the most important factor. Highest abundances were recorded from the deeper upstream transects 8-17 at depths less than 2.6 m.

Selenotoca multifasciata were initially split by size class, providing an indication that there were relatively few fish in size classes larger than 100 mm FL (Figure 11.12). For the smaller individuals (<100 mm FL), higher abundances were apparent down the western side of the pool, particularly towards the ends of the pool.

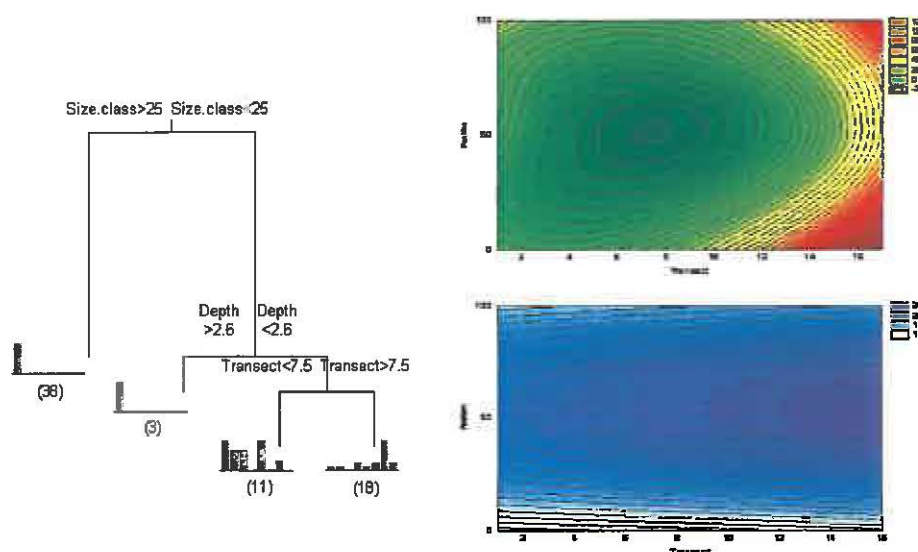


Figure 11.11. Classification and regression tree (left panel) for factors affecting the distribution of *Nematalosa erebi* in the Twelve Mile brackish pool (% variance explained = 74.6) Depths are reported in metres; response variable is $\log(1+x)$ transformed abundance; histograms show the frequency distribution of catch sizes for each terminal node; numbers in brackets show sample sizes for each terminal code. Upper right-hand panel shows the distribution pattern based on abundance, and pool bathymetry is shown in the lower right-hand panel.

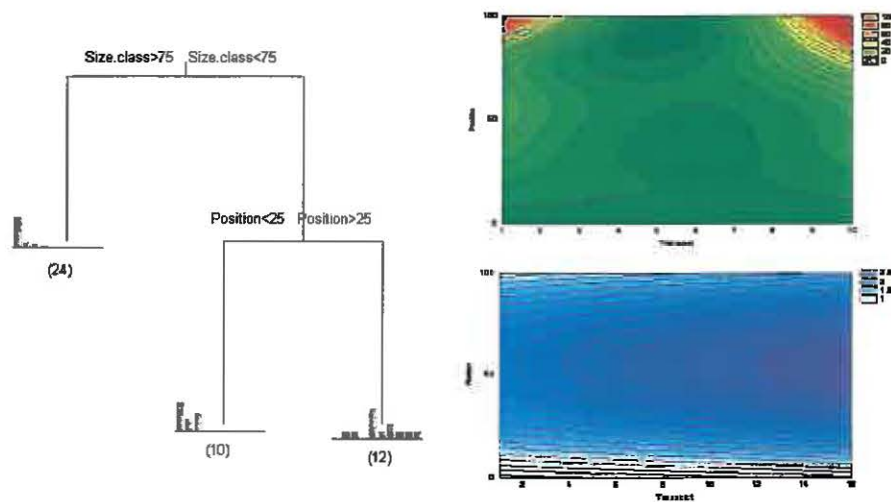


Figure 11.12. Classification and regression tree (left panel) for factors affecting the distribution of *Selenotoca multifasciata* in the Twelve Mile brackish pool (% variance explained = 75.51) Depths are reported in metres; response variable is $\log(1+x)$ transformed abundance; histograms show the frequency distribution of catch sizes for each terminal node; numbers in brackets show sample sizes for each terminal code. Upper right-hand panel shows the distribution pattern based on abundance, and pool bathymetry is shown in the lower right-hand panel.

Munduran saline pool

Few *Liza subviridis* were present in Munduran saline in February 2005 (first split), and few larger fish (>125 mm FL) were present in any trip (Figure 11.13). The smaller fish were most abundant in the downstream half of the pool (transects 1–10) and at depths less than 1.25 m. *Gerres filamentosus* distribution was most strongly influenced by depth, with highest abundances at depths less than 0.45 metres (Figure 11.14).

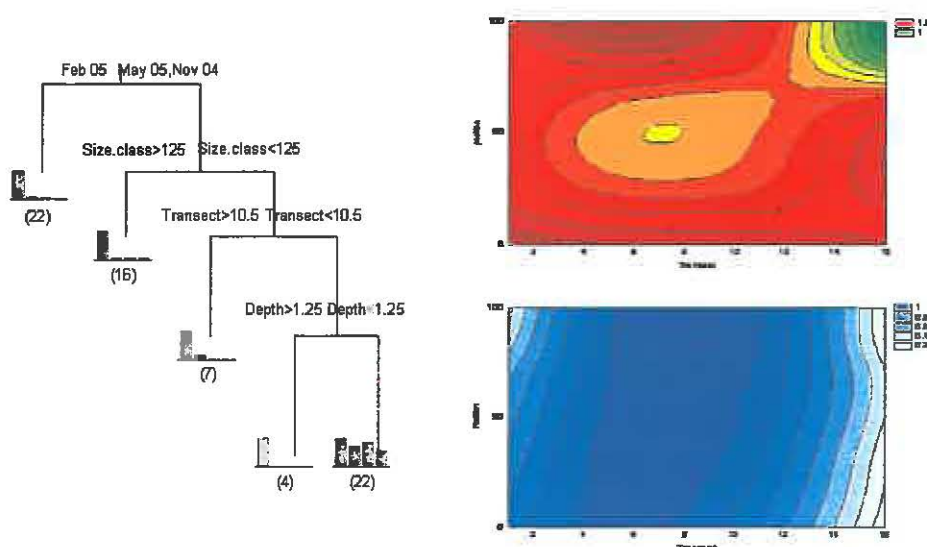


Figure 11.13. Classification and regression tree (left panel) for factors affecting the distribution of *Liza subviridis* in the Munduran saline pool (% variance explained = 55.88)

Depths are reported in metres; response variable is $\log(1+x)$ transformed abundance; histograms show the frequency distribution of catch sizes for each terminal node; numbers in brackets show sample sizes for each terminal code. Upper right-hand panel shows the distribution pattern based on abundance, and pool bathymetry is shown in the lower right-hand panel.

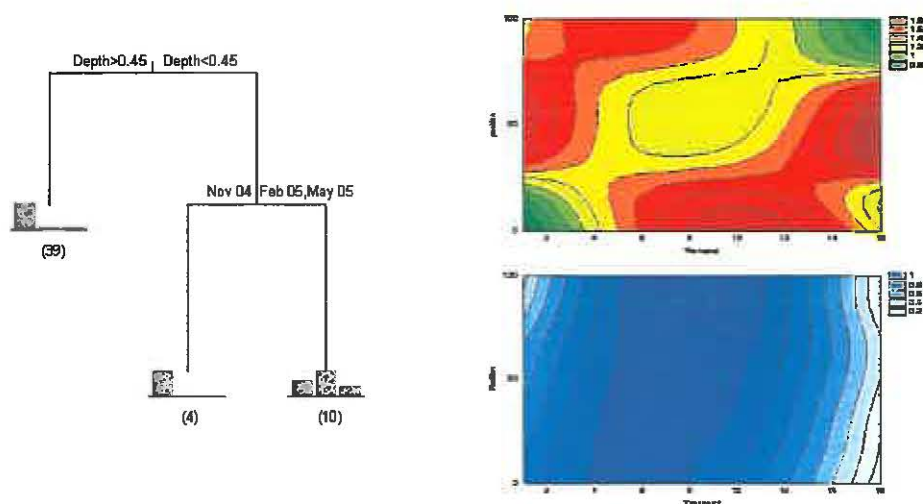


Figure 11.14. Classification and regression tree (left panel) for factors affecting the distribution of *Gerres filamentosus* in the Munduran saline pool (% variance explained = 39.73)

Depths are reported in metres; response variable is $\log(1+x)$ transformed abundance; histograms show the frequency distribution of catch sizes for each terminal node; numbers in brackets show sample sizes for each terminal code. Upper right-hand panel shows the distribution pattern based on abundance, and pool bathymetry is shown in the lower right-hand panel.

Gonong saline pool

In the Gonong saline pool, the factors with the strongest influence on the distribution of *L. subviridis* and *G. filamentosus* were not the same as in the Munduran saline pool. Depth exerted the stronger influence on the distribution of *L. subviridis* in the Gonong saline pool, with depths less than 0.25 m holding highest abundances (Figure 11.15). The principal influence on *G. filamentosus* was longitudinal position in the pool, with most fish in transects 2 and 3. Depth had a minor influence on *G. filamentosus* distribution in Gonong saline (higher abundances at depths greater than 0.45 m) (Figure 11.16), the opposite response to that in Munduran saline.

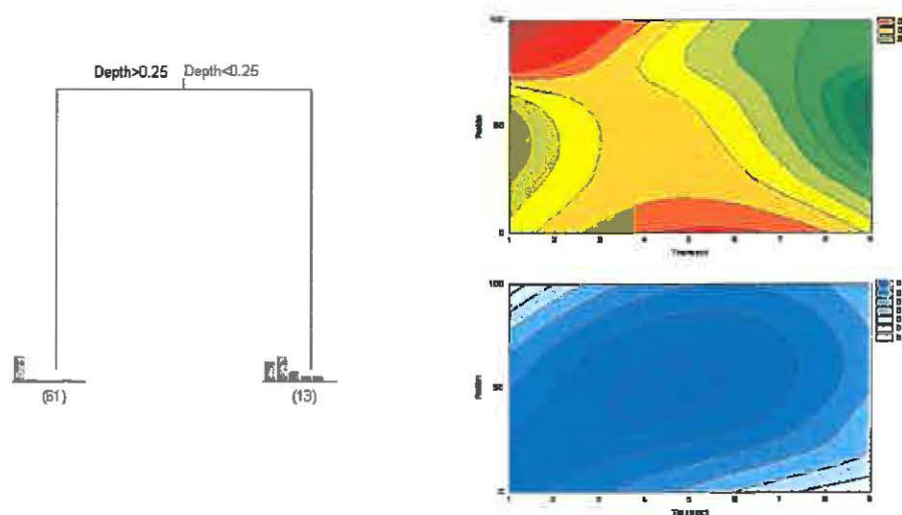


Figure 11.15. Classification and regression tree (left panel) for factors affecting the distribution of *Liza subviridis* in the Gonong saline pool (% variance explained = 22.42)
 Depths are reported in metres; response variable is $\log(1+x)$ transformed abundance; histograms show the frequency distribution of catch sizes for each terminal node; numbers in brackets show sample sizes for each terminal code. Upper right-hand panel shows the distribution pattern based on abundance, and pool bathymetry is shown in the lower right-hand panel.

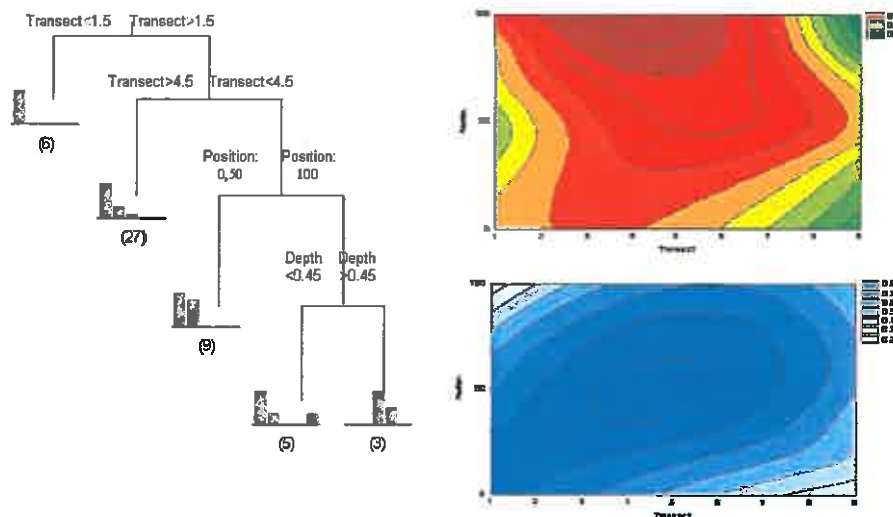


Figure 11.16. Classification and regression tree (left panel) for factors affecting the distribution of *Gerres filamentosus* in the Gonong saline pool (% variance explained = 63.97)

Depths are reported in metres; response variable is $\log(1+x)$ transformed abundance; histograms show the frequency distribution of catch sizes for each terminal node; numbers in brackets show sample sizes for each terminal code. Upper right-hand panel shows the distribution pattern based on abundance, and pool bathymetry is shown in the lower right-hand panel.

Summary of spatial factors influencing distribution and revised distribution models

Depth was the most influential factor across the range of species investigated; however, there were some inconsistent patterns for some species among pools (Table 11.2). Depth was important for small *N. erebi* in Frogmore and large and (probably) small *N. erebi* in Woolwash (moderately sloping basins, Chapter 2). Transect (position along the pool) was more important for small *N. erebi* in the Twelve Mile brackish pool. Depth was not important for *L. subviridis* in Munduran saline, but was important in Gonong saline. For *G. filamentosus*, depth was important in Munduran saline but not in Gonong saline. Transect (position along the pool) and position (cross-pool) was more influential than depth in Twelve Mile brackish, a steep-sided basin (Chapter 2) and the two erosional/depositional pools, Munduran and Gonong saline (Chapter 2).

In general, the estuary model of fish distribution (Figure 11.2) adequately described the distribution of most species of fish in each of the pools examined but there was one important deviation from the predicted model. When *N. erebi* were present in pools (freshwater and brackish pools only) they produced a strong spatial shift in the distribution of abundances and biomass; *N. erebi* dominated numbers and biomass in most pools where they were present (Chapter 5), but their preferred habitat was the deeper open water areas of pools and they were rarely recorded from shallow edges. For species other than *N. erebi*, the estuary models provide useful descriptions (Figure 11.2).

Table 11.2. Summary of the spatial factors that exerted the greatest influence on the within-pool distributions of species

Species	Location				
	Frogmore	Woolwash	Twelve Mile brackish	Munduran saline	Gonong saline
<i>Nematolosa erebi</i>	Depth	Depth	Depth		
<i>Amniataba percooides</i>	Depth				
<i>Emydura krefftii</i>	Depth				
<i>Selenotoca multifasciata</i>			Position		
<i>Liza subviridis</i>				Transect	Depth
<i>Gerres filamentosus</i>				Depth	Transect

Discussion

For many species of fish that use tropical or subtropical estuaries, the highest abundances of small individuals (<100 mm FL) are found in water less than 1.5 m deep along channel edges (Johnston & Sheaves unpublished data). Consequently, taking into consideration fish sampling conventions from Australian freshwater fish studies, a model of fish distribution was predicted for floodplain pools on the Fitzroy River delta (Figure 11.1) based largely on fish distribution patterns from tropical estuaries (Figure 11.2).

As predicted by the model, availability of shallow water was important for most species in the floodplain pools of the Fitzroy River delta. Barred grunter, *A. percooides*, and short-necked tortoise, *E. krefftii*, each had distribution patterns in line with the preliminary conceptual model (Figure 11.1), and thus similar to most estuarine fishes; they were strongly associated with shallow water along pool edges (Figures 11.8, 11.9 and 11. 11).

In the saline pools, Munduran and Gonong, mullet, *L. subviridis*, and whip-fin silver biddy, *G. filamentosus*, were influenced by different factors in each pool (Figures 11.13–11.16). Such inconsistency in results could indicate that those two species were not responding to any of the factors analysed. Previous studies have shown that in tropical estuaries both species occur in high abundances in water less than 1.5 m deep along channel edges (Johnston & Sheaves unpublished data). However, because there were few areas in either Munduran or Gonong saline where water depth exceeded 1.5 m (Chapter 2), it is likely that depth-related distribution patterns break down and alternative factors influence distribution.

In contrast to the other species, and not predicted by the conceptual model (Figure 11.1), bony bream, *N. erebi*, showed a clear preference for deeper water in Frogmore (>0.95 m) and Woolwash (>1.15 m) lagoons (Figures 11.3–11.7 and 11.10). That deeper water association was evident across the spectrum of fish size classes, although depth appeared to be less important for small (<100 mm FL) *N. erebi* in Woolwash lagoon. However, *N. erebi* in Woolwash were only found in the small remaining area of deeper water (maximum depth 1.4 m). Although this is not a definitive argument for a depth effect, few fish were present in water less than 1 m deep. Although depth was not the most influential factor for *N. erebi* in all pools where they were present, the contour plots indicate that they are rarely recorded from water less than 1 m deep. Moreover, it was clear that the preference of *N. erebi* for deeper water was consistent among pools and over time.

Depth was important for small *N. erebi* (<50 mm FL) in Twelve Mile brackish, but whether this result indicated a preference for shallow or deep water was not clear (Figure 11.11). The C&RT analysis indicated a preference for water less than 2.6 m deep; however, the Twelve Mile brackish pool differs structurally from the other pools where *N. erebi* were present because this pool is a steep-sided basin (Chapter 2) that lacks extensive areas of shallow water. Given this, if shallow water was the preferred habitat of *N. erebi* there should be high abundances of small fish in the shallow water that is available. This was not the case, and high abundances were concentrated in the deeper upstream end of the pool. Examination of more complex tree models than the model presented indicated that small *N. erebi* are most abundant at depths between 0.8 and 2.6 m.

It is often stated that shallow water provides an advantage for small fish because shallow water excludes large piscivorous fish (Morton *et al.* 1987; Patterson & Whitfield 2000). The preference for deeper water indicates that *N. erebi* probably do not use shallow water as a refuge from piscivorous fish. However, there are indications that *N. erebi* populations may be susceptible to high mortality from piscivorous birds when deep water is not available. By the concluding months of this study Woolwash and Frogmore lagoons had dried out to a point where there was little water over 1 m deep remaining in the pools (Chapter 3).

Once water levels reached those low levels, abundances of *N. erebi* dropped markedly (Chapters 4 and 5) and that drop in abundance coincided with the presence of large flocks of pelicans (Chapter 12). Because pelicans feed from the water surface (Derby & Lovvorn 1997, Kaeding 2002) it appears that fish can gain refuge from predation by pelicans by remaining in deep water (Pusey *et al.* 2004), because substantial declines in abundance were only recorded once

maximum pool depths dropped to a little over 1 m (Chapter 3). Consequently, if predation risk is an important factor in determining the distribution of *N. erebi*, it appears that refuge from piscivorous birds is more important than refuge from piscivorous fish.

The preference *N. erebi* has for deeper water also raises the possibility that their relative abundance has been underrepresented in earlier studies because fish sampling was frequently limited to pool and stream edges. Had sampling been confined to edges in the present study the number of *N. erebi* recorded would have been substantially lower. Failure to adequately represent a species that had such a major contribution to pool faunas (*N. erebi* dominated both numbers and biomass in pools where they were present) would have major implications for interpretation of assemblage composition, trophic structure and foodweb dynamics.

Conceptual models of fish distribution in floodplain pools

The distribution of fish in the floodplain pools of the Fitzroy River delta can be described by relatively simple models, with initial separation of the models based on the presence or absence of *N. erebi* (Figures 11.17–11.19). For most species depth was the most important factor in determining where fish occurred in a pool (Table 11.2). Consequently, pool profile (Chapter 2) is also an important consideration because it interacts with the availability of different depths within a pool. In response to this, models are included to account for the different pool profiles.

Species other than *Nematolosa erebi* (Figure 11.17)

Pools with shallowly sloping, steeply sloping and erosional/depositional profiles tend to have highest abundances and highest biomass of most species in the shallow edge habitats and few fish in deeper, open-water areas. In addition, biomass and abundance of most species is higher along depositional (lower angled) banks than on erosional banks when pools have erosional/depositional profiles. However, this pattern is disrupted when pools lack extensive areas deeper than 1.5 m. Irrespective of pool profile, when depths are less than 1.5 m, fish abundance and biomass are likely to be relatively evenly distributed around the pool because species with a strong shallow-water preference may disperse more generally throughout the pool.

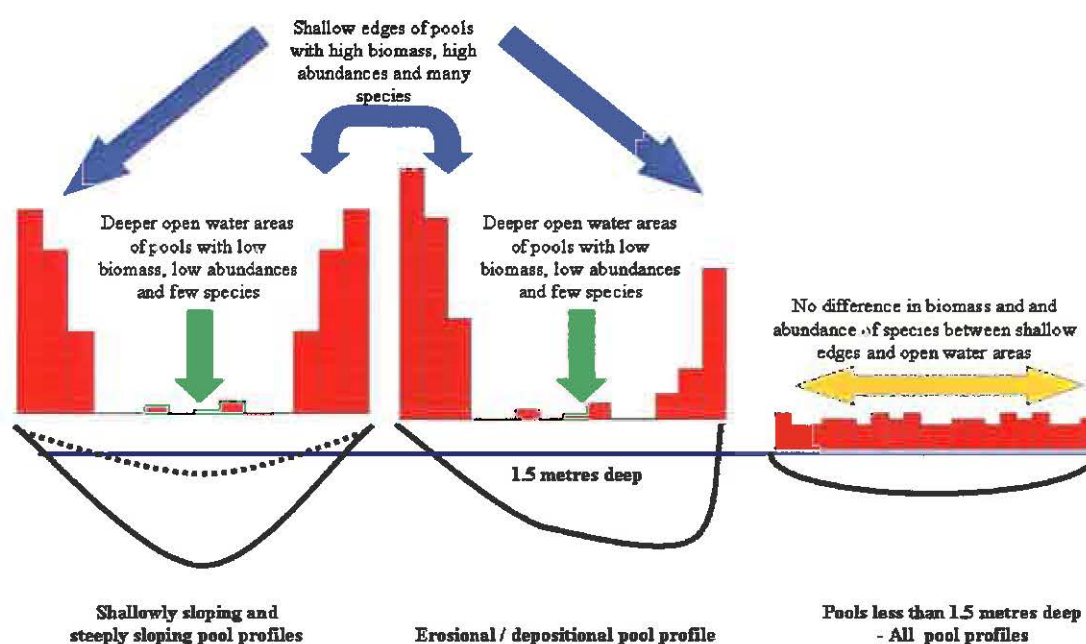


Figure 11.17. Models of the distribution of fish species other than *Nematolosa erebi*
Descriptions of pool profiles are contained in Chapter 2

***Nematolosa erebi* (Figure 11.18)**

The spatial distribution of *N. erebi* differed markedly from the predicted model which suggested highest abundances and biomass would be associated with shallow edges (Figure 11.2). Instead, *N. erebi* abundances and biomass were concentrated in the deeper, open-water areas of shallowly sloping and steeply sloping pools (Chapter 2). However, *N. erebi* were also recorded from pool edges in steep-sided basins where deep water was available up to the edge; thus it was clear that spatial distribution was driven by depth rather than being a preference for open water. Consequently, should a pool have an erosional/depositional profile then highest abundances and greatest biomass should occur towards the steeper/deeper erosional bank.

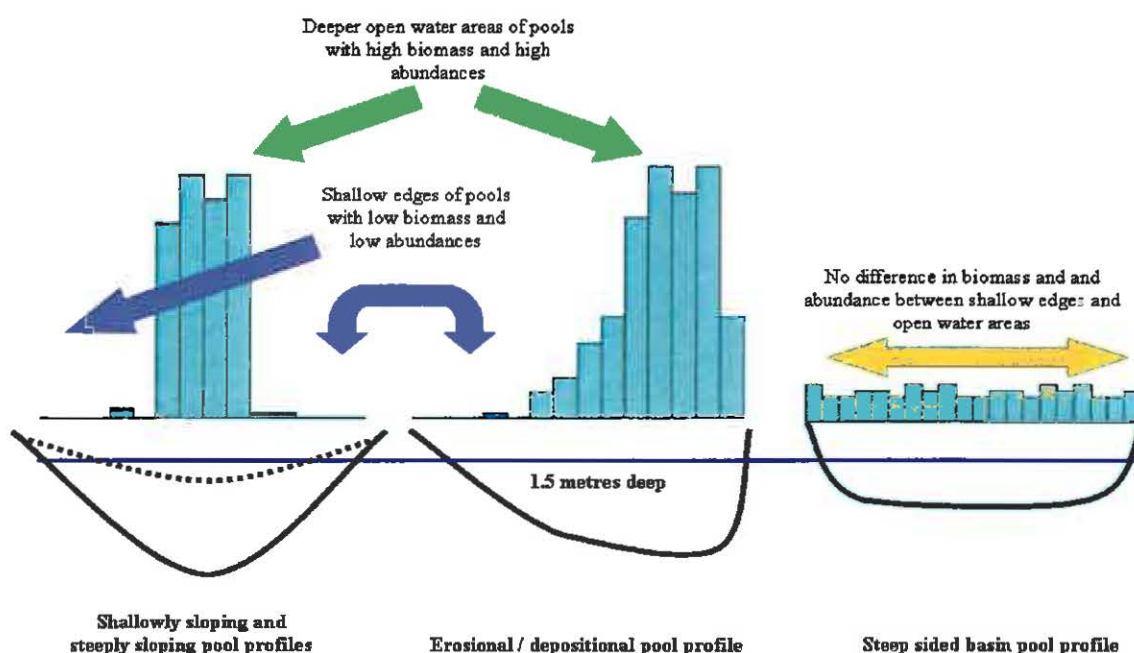


Figure 11.18. Models of the distribution of *Nematolosa erebi*
 Descriptions of pool profiles are contained in Chapter 2

Pools with a species mix that includes *N. erebi* (Figure 11.19)

N. erebi usually dominated both numbers and biomass when they were present in pools. Therefore, because they have a strong preference for deeper water, pools that hold populations of *N. erebi* have highest abundances and highest biomass in deeper water. This means shallow and steeply sloping basins have peak abundance and peak biomass around the middle of the pool, or towards the erosional bank in erosional/depositional pools. However, those deeper habitats are likely to be low in species diversity compared to the shallower edge habitats.

When the pool profile is a steep-sided basin and deeper water is available up to the edges (e.g. Twelve Mile brackish pool), *N. erebi* distribution patterns become less distinct. As a consequence, abundances and biomass are likely to be more evenly distributed around such a pool. Moreover, in the absence of shallow water, species with a shallow-water preference may also disperse more widely than they would when shallow water is available. It is also probable that shallow-water or edge-associated species will be concentrated in any areas of shallow water that are present in the pool but this is unlikely to have much influence on the overall model because of the extent to which *N. erebi* usually dominate abundances and biomass and because of the relatively small area of shallow water.

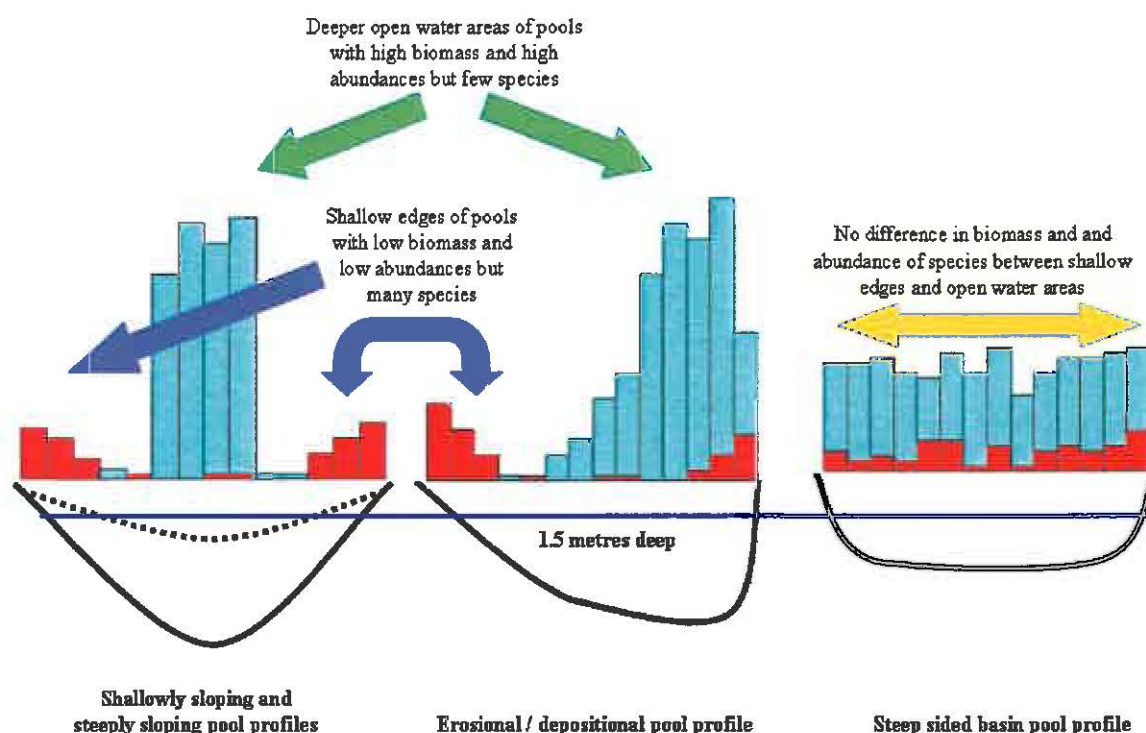


Figure 11.19. Models of the distribution of fish in wetland pools with a species mix that includes *Nematalosa erebi*
Descriptions of pool profiles are contained in Chapter 2

Chapter 12 Assessment of the role of bird predation on fish assemblages within floodplain wetlands of the lower Fitzroy River

Wayne Houston

Introduction

Bird piscivores (birds that use fish for food) have the capacity to be a major pathway for consumption of freshwater fish stocks and the assessed importance of this consumption in removal of economic fish stocks ranges from high (e.g. Madenjian & Gabrey 1995, Veldkamp 1995, Johnson *et al.* 2002) to a relatively minor impact (e.g. Nilsson & Nilsson 1976, Linn & Campbell 1992, Hebert & Morrison 2003). There has been extensive debate as to the importance of bird piscivores as significant consumers of fish stocks and the assumptions upon which many studies are based (e.g. Draulans 1988). In Europe, cormorants are thought to contribute positively to ecosystem functioning by keeping eutrophic waters free from dense fish stocks (Van Eerden *et al.* 1995).

Bird piscivores may have an important role in export and movement of fish biomass from floodplain wetlands to other ecosystem components (e.g. Bulla *et al.* 1990, Hebert & Morrison 2003, Stevens & Montague 2005). Such movements provide trophic linkages that may be important to the ecology of the ecosystems within which they occur and are likely to be of intrinsic value in ecosystem functioning over and above any detrimental impacts on fish stocks.

Substantial populations of waterbirds occur in association with lower Fitzroy River floodplain wetlands (including river backwaters), and numbers around 30 000 have been found in two surveys (October 1994 – Houston and McCabe 1996; October 2003 – Jaensch 2004). These waterbirds included several piscivore species, including pelicans, raptors, grebes, darters, cormorants, terns, egrets and herons. Some of these species were abundant (populations >100) and would be capable of causing heavy losses in single wetlands.

However, the impact of birds on wetland fish populations is likely to be highly temporally variable at any single wetland and spatially variable across the wetlands within the region (over one hundred wetland sites have been identified, Houston and McCabe 1996). As an example, cormorants have been found to be highly aggregated at all scales of observation and were associated with short-term patches of food and therefore patterns of abundance follow boom-bust

cycles linked to their prey (Dorfman & Kingsford 2001). Thus, it is unlikely that direct observational techniques on fish predation by bird piscivores would be likely to succeed in quantifying the impact of bird predation on fish populations. It is possible, however, to link patterns of fish abundance within wetlands to patterns of bird piscivore abundance (Kushlan 1976, Bulla *et al.* 1990, Stevens & Montague 2005) and this approach will be used in this study as a tool for assessing the importance of bird predation on fish stocks.

Another approach for assessing the importance of bird piscivores to fish consumption is to use traces such as droppings or regurgitated pellets to assess the diet of target species. Fish 'hard parts' within both droppings and pellets such as otoliths have been used extensively in bird piscivore dietary studies enabling fish species composition and relative abundance to be quantified (Blaber & Wassenberg 1989, Marquiss & Leitch 1990, Platteeuw & Van Eerden 1995, Veldkamp 1995, Johnson & Ross 1996, Johnson *et al.* 2002, Casaux 2003). Current isotopic studies by other CRC researchers using strontium and/or carbon isotopes may also contribute to an understanding of bird diets and origin of primary production upon which they depend.

The broad aim of the study is to contribute to a better understanding of the ecology of delta floodplain wetlands in tropical Queensland and their role in supporting fish stocks important to barramundi production. Objectives are:

1. To provide an improved basis for understanding the ecology of bird piscivores associated with delta floodplain wetlands;
2. To provide a quantitative basis for estimating bird piscivore abundance, seasonality and habitat usage in delta floodplain wetland habitats during the late dry to post-wet season corresponding to usage of these wetlands as nursery areas for barramundi;
3. To provide a basis for estimating relative importance of bird piscivores as fish consumers, their ecological role and contribution to potential fish consumption rates within these habitats;
4. Collect droppings and pellets (regurgitated hard parts) which will then be available for colleagues to determine their potential for identifying species and relative abundance of fish eaten, for example, by identification of hard parts such as otoliths, or by isotopic analysis (strontium and carbon);
5. Develop a model describing the ecology of the wetlands and associated bird piscivores.

Literature review

Waterbird assemblages present within the lower Fitzroy River wetlands including delta floodplain wetlands were surveyed in October 1994 and October 2003 (Houston & McCabe 1996, Jaensch 2004). Both studies reported about 30 000 waterbirds and 70 species of waterbirds from around 60 sites, although sites surveyed varied as a consequence of differences in sites with and without water.

Two broad ecotypes were sampled during these Fitzroy River floodplain surveys – freshwater wetlands above tidal influence and delta wetlands bordering the estuarine section of the river representing an area of overlap between freshwater and marine wetlands (Fitzroy delta floodplain wetlands). These wetlands were characterised by Wright (1968, p. 134) as 'extensive back plains traversed by a dense network of distributary channels and discontinuous linear depressions'. Several wetlands in this sector were created by damming drainage lines at the head of tidal influence.

The importance of the Fitzroy delta floodplain wetlands is demonstrated by a substantial contribution to waterbird abundance in both the 1994 and 2003 censuses (25% and 16% respectively). Contribution by piscivorous species was similar in both studies (14% to 15 %) and restricting analysis to the Fitzroy delta wetland component in 2003 showed that 11% of waterbirds were piscivores. Most abundant piscivores were Australian pelicans, little black cormorants and little pied cormorants, with substantial contributions also from gull-billed terns, white-faced herons, white-necked herons, Australasian grebes, great egrets, intermediate egrets, darter and brolga.

A post-wet season study targeting egret distribution and abundance on floodplain wetlands was carried out in May 1996 to complement the dry season censuses (Houston & McCabe 1996). Great egrets doubled in numbers compared with October 1994 while intermediate egrets increased five-fold, indicating their potential to be significant piscivores under favourable seasonal conditions. Great egrets were largely concentrated on shallowly inundated floodplain swales in open water and in drainage lines connecting deeper wetlands, and were probably targeting fish moving upstream. Intermediate egrets were largely concentrated on shallowly inundated floodplain wetlands with emergent vegetation where frogs were abundant.

Relevant findings from these studies were:

- The large area and numbers of wetlands present in the lower Fitzroy River region (over 150 sites comprising in excess of 10 000 ha);
- The relatively large pool of waterbirds present within the region including substantial populations of piscivores (at least 4000 to 5000);
- The importance of seasonal triggers such as inundation events following good wet season rains in influencing waterbird abundance;
- The substantial interannual variation in the extent of the wet and dry seasons in this region; and
- The dominance of piscivore assemblages by Australian pelicans and little black cormorants.

An assessment of the potential for direct predation of bird piscivores on barramundi was undertaken. Only one Australian study reported predation on barramundi by bird piscivores—white bellied sea-eagles (Breedon & Wright 1990). Examination of overseas literature showed one Australian-occurring species with barramundi in their gut contents—darter in India (Mukherjee 1969). Clearly, direct predation on barramundi is not likely to comprise a significant impact by bird piscivores on barramundi stock.

Predation on fish stocks that comprise barramundi food fish by bird piscivores is the most likely impact by reducing the food supply for fish piscivores such as barramundi. Many common fish species within target wetlands in this study (Marcus Sheaves unpublished data) were also reported from stomach analysis studies of feeding habits of waterbirds in Australia. Fish species found most frequently in gut contents of bird piscivores commonly found in central Queensland were the genera *Carassius* (goldfish), *Anguilla* (eels), *Nematalosa* (bony bream), *Melanotaenia* (rainbow fish), *Acanthopagrus* (sea bream), *Neosilurus* (catfish) *Leiopotherapon* (grunter) plus *Mugilidae* (mullet) (Table 12.1).

Seasonal variation in dietary composition was demonstrated in little black cormorants associated with inland lagoons in New South Wales (Miller 1979). Little black cormorants preyed primarily on goldfish (*Carassius auratus*) during late summer and autumn with crustaceans (yabbies *Cherax destructor*) and fry of redfin perch (*Perca fluviatilis*) dominating in spring and early summer. Resource partitioning was demonstrated with little black cormorants and little pied cormorants targeting different prey species during the same season (Miller 1979). These species also fed in different parts of wetlands with little black cormorants mostly in more open deeper water than little pied cormorants that fed mostly in shallow vegetated wetland margins.

Table 12.1. Fish genera found in stomachs of common waterbird piscivores in the study area

[sourced from HANZAB (Marchant & Higgins1990, Marchant & Higgins 1993, Higgins & Davies1996)]

Species	Gerres	Mugil	Nematalosa	Liza	Valamugil	Carassius	Chanos	Selenotoca	Megalops	Lates	Elops	Glossamia	Strongylura	Lutjanus	Melanotaenia	Arius	Acanthopargus	Neosilurus	Bidyanus	Anguilla	Amniataba	Leiopotherapon	Frequency of prey species
Australasian grebe																							0
Darter	1	1	1			1				2		1			1		1	1				1	10
Little pied cormorant												1			1	1		1				1	5
Pied cormorant																							0
Little black cormorant												1										1	2
Great cormorant																							0
Australian pelican						1																1	2
White-faced heron																							0
Little egret																		1					1
Eastern reef egret																							0
Great egret			1			1							1					1					4
Intermediate egret						1														1			2
Striated heron																							0
Black bittern																							0
Black-necked stork																				1			1
Brolga																							0
Osprey																							0
Whistling kite																	1			1			2
Brahminy kite		1														1	1						3
White-bellied sea-eagle		1				1				1						1	1			1			6
Swamp harrier																				1			1
Gull-billed tern			1																	1			2
Caspian tern		1	1												1								3
Whiskered tern						1									1								2
Azure kingfisher						1																	1
Sacred kingfisher						1																	1
Frequency food group recorded	1	4	4	0	0	8	0	0	0	2	0	3	1	0	4	3	4	4	0	6	0	4	

Size of fish taken as food was crudely estimated by examination of the HANZAB review compilation (Marchant & Higgins 1990, 1993, Higgins & Davies 1996). Most species took prey fish up to 18–23 cm length: cormorants, darters, Caspian terns and great egrets. Exceptions were larger waterbirds capable of taking larger fish prey such as Australian pelicans, great cormorants, whistling kites and probably storks, boobies and sea-eagles (Table 12.2). Some species took smaller fish up to about 8–12 cm, for example, herons, little and intermediate egrets, whiskered terns, and probably grebes. However, for all species where data on average size is available, preferred prey size, as indicated by average size data, was skewed towards the lower end of the size range of fish prey taken; for example, darter average size range is 3–11 cm compared with 2–20 cm size range of fish caught, and little black cormorant average size is 4–13.5 cm compared with 2–22 cm (Table 12.2).

In order to provide an estimate of fish consumption rates by bird piscivores, a review of fish predation studies was also undertaken (Table 12.2). Estimates of the percentage body weight that an average sized individual of a species consumed daily varied widely. For example, estimates for great cormorants varied from 9.5% to 21%, and Draulans (1988) noted that much variation was due to problematic assumptions being made. Barlow (1995) reviewed daily intake of fish in cormorants and found a similar range in variation for European studies of great cormorants to that found by Draulans (11.4% to 27%). Estimates for another cormorant species—double-crested cormorants in North America—ranged from 8% when feeding chicks to 15% during the non-breeding season (Johnson *et al.* 2002).

As some of the Australian estimates (Table 12.2) were comparable to the figure of 20% daily consumption of body weight in food stated by Barlow as the best estimator of food consumption for cormorants, that figure has been used in this study to estimate potential consumption of fish stocks. However, given doubt regarding the derivation of these rates of food intake, they should be treated with caution and provide a guide only.

For larger birds such as pelicans, no Australian data were available and so overseas estimates were used. For African great white pelicans, estimates of percentage body weight consumed per day ranged from 8.8% to 11.5% (Guillet & Furness 1985, Shmueli *et al.* 2000). Guillet and Furness (1985) suggest that a figure of 10% is appropriate for larger piscivores and this has been applied here. For smaller birds, only one estimate for little terns was available (Brenninkmeijer *et al.* 2002) and this was 32% so a figure of 30% has been applied to smaller piscivores.

Table 12.2. Information used to estimate fish consumption rates of common waterbird piscivores in the study area

[sourced largely from Birds Australia HANZAB (Marchant & Higgins 1990, Marchant & Higgins 1993, Higgins & Davies 1996) plus (1) Mukherjee 1969, (2) Trayler *et al.* 1989, (3) Miller 1979, (4) DEFRA 2005, (5) Gremillet *et al.* 2003, (6) Lowe 1983, (7) Mukherjee 1971, (8) Dostine & Morton 1989, (9) Blaber & Wassenberg 1989]]

Species	Weight range and midpoint	Fish capture method	Water body depth	Main food	Range in average size of prey	Range in size of prey	Fish consumption per day	Mean weight of stomach contents	% of body weight consumed per day	% of body weight used to estimate fish consumption
Australasian grebe	100–230 g, 165 g	Diving, dipping		Fish, snails and aquatic arthropods						30
Darter	0.9–2.6 kg, 1750 g	Diving	>60 cm	Mostly fish, some insects, occasionally turtles, incidental vegetable matter	3.1 to 10.8 cm	2 to 20 cm	43 g per meal, 6 meals per day = 258 g/day (1)		14.7% (1)	20
Little pied cormorant	410–880 g, 645 g	Diving, dipping	1 to 2 m deep	Mostly freshwater crayfish & other crustaceans plus fish	4.0 to 18.5 cm	2 to 25 cm		24.3 g (2)		20
Pied cormorant	1.3–2.2 kg, 1750 g	Pursuit-diving	1 to 2 m deep (p. 822) & >2 m deep	Mostly fish with a few crustaceans	5.9 to 14.2 cm	2 to 45 cm (9)				20
Little black cormorant	520–1210 g, 865 g	Pursuit-diving	1 to 2 m deep (p. 833)	Mostly fish plus freshwater crayfish & other crustaceans	4.0 to 13.5 cm	2 to 22 cm	9 in Vic	64.3 g (2); 58.4 g/day (based on Fig. 12.2 in paper average of all points) to 185 g/day (based on max estimate in Fig. 12.2) (3)	6.8% to 21.3% (3)	20
Great cormorant	2–2.5 kg, 2250 g					Up to 43 cm	Scotland (modelled data): summer 303 & winter 401 g/day (4); 672 g/day (5)		9.5–12.5% (4) to 21% (5) based on weight of European population of 3200 g	20
Australian pelican	4–6.8 kg, 5200 g	Mainly surface plunging & scooping but also surface diving	Usually <1 m but up to 2 m	Mostly fish		Nestlings were fed fish 6 to 25 cm				10

Species	Weight range and midpoint	Fish capture method	Water body depth	Main food	Range in average size of prey	Range in size of prey	Fish consumption per day	Mean weight of stomach contents	% of body weight consumed per day	% of body weight used to estimate fish consumption
White-faced heron	550 g	Most food taken when wading or walking slowly through water or by standing and waiting		Aquatic invertebrates & vertebrates		2.5 to 10 cm		23.9 g (6)		20
Little egret	300 g	Standing & waiting, crouching & waiting, slow or quick walking, running, wing-flicking, foot-stirring		Mainly fish but also frogs, insects		1 to 10 cm				20
Eastern reef egret	330–450 g, 390 g									20
Great egret	700–1200 g, 950 g	Standing & waiting, slow walking		Mainly fish but also frogs, insects & small birds		1 to 17.5 cm (7)				20
Intermediate egret	400 g	Standing & waiting, gleaning, peering or foot-stirring		Mainly fish but also frogs, lizards & grasshoppers		1 to 12 cm (7)				20
Striated heron	200–250 g, 225 g									30
Black bittern	300–420 g, 360 g									20
Black-necked stork	6000 g (one measurement only of an immature at 4000 g)	Slow walking		Fish, crustaceans, insects, snakes						10
Brolga	3.7–8.7 kg, 6200 g									10
Osprey	1–1.5 kg, 1250 g									20
Whistling kite	700–850 g, 775 g	Snatch fish from water, robbing		Carrion & live prey including mammals, birds, fish & insects		12 to 35 cm				20
Brahminy kite	500–630 g, 565 g	Take live fish from water surface, robbing		Carrion, insects, fish						20

Species	Weight range and midpoint	Fish capture method	Water body depth	Main food	Range in average size of prey	Range in size of prey	Fish consumption per day	Mean weight of stomach contents	% of body weight consumed per day	% of body weight used to estimate fish consumption
White-bellied sea-eagle	2.5–4.2 kg, 3350 g	Plunge-diving for surface swimming fish and snakes, slow circling followed by dive, robbing		Birds, reptiles, fish, mammals, crustaceans & carrion						10
Swamp harrier	630–850 g, 740 g	Slow quartering, hover & drop, dive-attack		Mammals, birds, eggs, large insects, frogs, fish & reptiles			Average daily intake of 722 g adult was 112 g; of a 635 g juvenile between 104 g & 148 g	Single feed of adult was 240 g	32%	20
Gull-billed tern	265 g	Dipping from water surface, plunging (rare)		Insects, fish & small vertebrates						30
Caspian tern	680 g	Shallow plunging		Fish		Up to 18 cm*				20
Whiskered tern	80 g	Plunging (hover & dive), dipping		Insects, crustaceans, fish, frogs	2.0–7.0 cm	1 to 8 cm	(1 male had 19 <i>A. agrammus</i> (8))			30
Azure kingfisher		Shallow-plunging, diving		Small fish, crustaceans & aquatic insects						30
Sacred kingfisher		Plunge-dive		Mainly insects, plus annelids, crayfish, crabs, spiders, fish, frogs & tadpoles						30

* 3 to 23 cm for crested tern (Blaber & Wassenberg 1989)

Some general paradigms on waterbird abundance and environmental factors have been found:

- A relationship between waterbird abundance and inundation following rainfall triggering breeding events (Halse & Jaensch 1989, Kingsford & Norman 2002);
- Waterbirds in the tropics breed predominantly in the wet season in association with increased food abundance (Kingsford & Norman 2002);
- Size of wetland—larger sized wetlands supported higher densities of waterbirds (Breininger & Smith 1990, Kerekes *et al.* 1994);
- Relationships between wetland vegetation structure and waterbird species assemblage composition (Hoyer & Canfield 1994, Halse *et al.* 1993).

Bellio *et al.* (2004) noted that food supply, weather, habitat, predators and pathogens, nesting site availability and competition were all possible ecological drivers of waterbird population dynamics. Kushlan (1976) in a study of bird wader piscivores (including great egrets) in shallow marsh wetlands in Florida found a relationship between water depth and wader density. Wader aggregations increased greatly once pools were isolated and water depth fell below 0.75 m. Kushlan identified draw-down periods during the dry season as key drivers for increasing fish availability to piscivores and subsequent increases in wader density and fish consumption rates.

Similar findings were found in South American tropical wetlands with large increases in waterbird piscivore abundance as pools dried out (Bulla *et al.* 1990).

Studies of saltmarsh wetlands in Florida identified marsh flooding as a consequence of tidal connection to the estuary and/or surface runoff from rainfall as key ecological drivers (Stevens & Montague 2005). These connection events allowed fish migration into the marsh followed by a peak in bird piscivore density. Stevens and Montague, like Kushlan, also identified draw-down of water levels below a certain depth causing concentration of fish in shallow waters as contributing to peaks in bird piscivore density although the relationship was not as strong as the initial connection to the estuary.

Two studies have found a direct relationship between fish numbers and piscivore bird densities in lakes (Whitfield 1978, Kerekes *et al.* 1994).

Methods

Waterbird habitat usage

Six sites were selected (Figures 12.1–12.8) to coincide with fish study sites (Marcus Sheaves pers. comm). These were classified according to level of connection to the estuary:

- *Lower*: with frequent connection to the estuary (Gonong and Munduran Creeks);
- *Middle*: with infrequent connection to the estuary during large tidal events (Twelve Mile Creek and German Jack's lagoon); and
- *Upper*: with rare connection to the river, usually only during larger flood events (Frogmore and Woolwash lagoons).

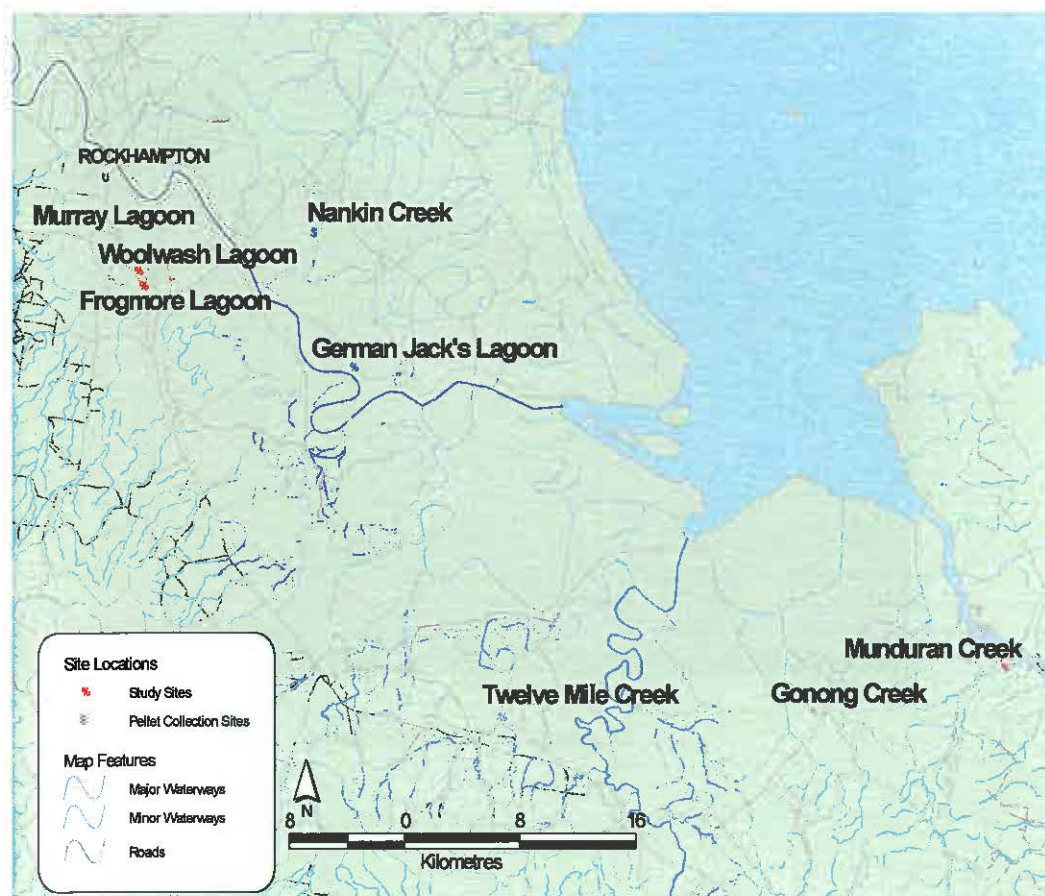


Figure 12.1. Location of study sites

Waterbird species and composition was surveyed in the last week of each month from August 2004 to April 2005 and then again in July 2005 to encompass the late dry, wet and post-wet seasons coinciding with breeding and nursery usage by barramundi. An exception was January 2005 when German Jack's lagoon was inaccessible due to weather conditions. Waterbird surveys at the two lower estuary sites (Gonong and Munduran Creeks) were discontinued after January 2004 as waterbird numbers were consistently low at these two sites reflecting differences in ecology to the other sites.

When possible, salinity was measured using a field refractometer (BS Ellipse) and the percent active wetland area (defined as the percentage of the wetland's full level that is holding water, including the muddy margins) recorded. The latter is a surrogate for water depth.



Figure 12.2. Munduran Creek



Figure 12.3. Gonong Creek



Figure 12.4. Twelve Mile Creek – brackish pool



Figure 12.5. German Jack's in October–November showing extensive draw-down and relatively gentle gradients. Note the dead coolabahs



Figure 12.6. Waterbirds perching at the Woolwash. Note the relatively steep sides



Figure 12.7. Frogmore lagoon showing elongated shape and relatively steep sides



Figure 12.8. Dead mussels exposed during draw-down period at Frogmore lagoon in February–March 2005

Pellet collection

In the 2005 wet season, searches for nesting piscivores were undertaken and two sites identified, one at Nankin Creek for darters and little pied cormorants and one at Murray lagoon for egrets (great, intermediate, little and cattle egrets). Circular flat pods lined with small-meshed shade cloth (0.6 to 0.8 m diameter) (Figure 12.9) were suspended under darter and little black cormorant nests at Nankin Creek and initially were checked daily for pellets and/or droppings but thereafter every second day over a fortnight (Table 12.3).

At the egret colony at the Botanic Gardens, tarpaulins were suspended below target species (Great Egrets) but these were unsuccessful at collecting the target species samples.

Pellets and droppings (Table 12.3) were sent to Marcus Sheaves for further analysis (not reported here).



Figure 12.9. Pellet-collecting device suspended under a darter nest, Nankin Creek

Table 12.3. Pellets and droppings collected at Nankin Creek from collecting pods

Tree & nest code	Species	No. eggs	Day						
			1	2	4	6	8	10	
1-1	LPC	3			P (2)		D	D	
1-2	Darter	1			PP	D		PP/EF	
1-3	Darter	3	D	D	D/EF		P/D		
2-1	LPC	3		PP	P				
2-2	Darter	3	D	D			D		
3-1	Darter	4	P		P	D	P	P	
3-2	LPC	5			P	PP	PP	PP	PP
3-3	LPC	5			PP		PP	PP	PP

P = pellet, PP = partial pellet, D = dropping, EF = eggshell fragment

Analysis

Piscivores were classified according to their mode of feeding:

1. Divers – darters, cormorants and grebes
2. Scoopers – pelicans
3. Waders – egrets, herons, brolgas and storks
4. Plungers – terns and kingfishers
5. Raptors – white-bellied sea-eagle, osprey, brahminy kite, whistling kite.

Months were classified into seasons based on long-term rainfall average data (BOM 2004):

1. Dry season – August to November 2004, April 2005 and July 2005
2. Wet season – December 2004 to March 2005.

Fish consumption rates for waterbirds were based on body size (see literature review):

1. Small: <300 g – 30% of body weight per day (small terns and kingfishers)
2. Medium: 300–3000 g – 20% of body weight per day (cormorants, darters, egrets, herons and most raptors)
3. Large: >3000 g – 10% of body weight per day (Australian pelican, brolga, black-necked stork and white-bellied sea-eagle).

Ordination was used to graph relationships among sites based on waterbird composition and abundance. An ordination technique known as non-metric multi-dimensional scaling (NDMS) was used (Clarke & Gorley 2001) to group sites based on their similarity. To remove the excessive influence of abundant species on similarity measures (Clarke 1993), abundance data were transformed (square-root) and sites compared using a Bray-Curtis similarity index (Clarke & Gorley 2001).

This type of analysis produces a scattergram where the distance between sites represents their dissimilarity and sites closer together are more similar than sites further apart. The scattergram is considered interpretable in two dimensions if the stress level of the iterative process is <0.20 (Clarke & Gorley 2001).

Combined with the ordination, a numerical classification (based on the same similarity index and appropriate transformation as used in the ordination plus group-average sorting) was used to define site groups (Clarke & Warwick 1994). Cluster analysis aims to find groupings of sites such that sites within a group are more similar to each other than to sites in different groups (Clarke & Warwick 1994).

A multivariate equivalent to analysis of variance, 'analysis of similarity' (ANOSIM, Clarke & Gorley 2001), was used to test for effects of site group and season on waterbird species abundance assemblages.

Results

General

Fifty-eight waterbird species of which 27 were regarded as piscivores were found during the study. Greatest waterbird and piscivore abundance was at German Jack's lagoon while both Munduran and Gonong Creeks had very low waterbird abundance, piscivore abundance (all surveys <10) and species richness compared with the other sites (Figure 12.10). Waterbird species richness reached peaks of 25 – 30 species for all four middle and upper estuary sites. German Jack's had the greatest range in abundance and species richness with few waterbirds present in October and November 2004.

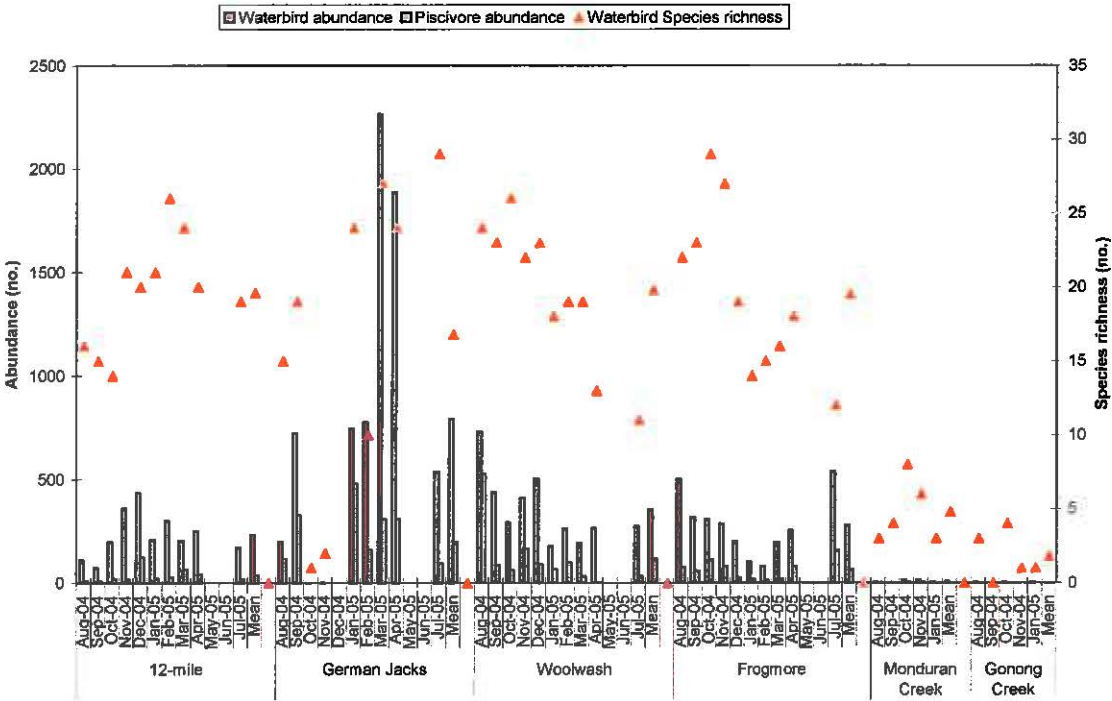


Figure 12.10. Monthly waterbird abundance, piscivore abundance and species richness at all sites

Divers were the most abundant guild (44% of total piscivore abundance) followed by scoopers. (30%), plungers (13%), waders (10%) and raptors (3%) (Figure 12.11).

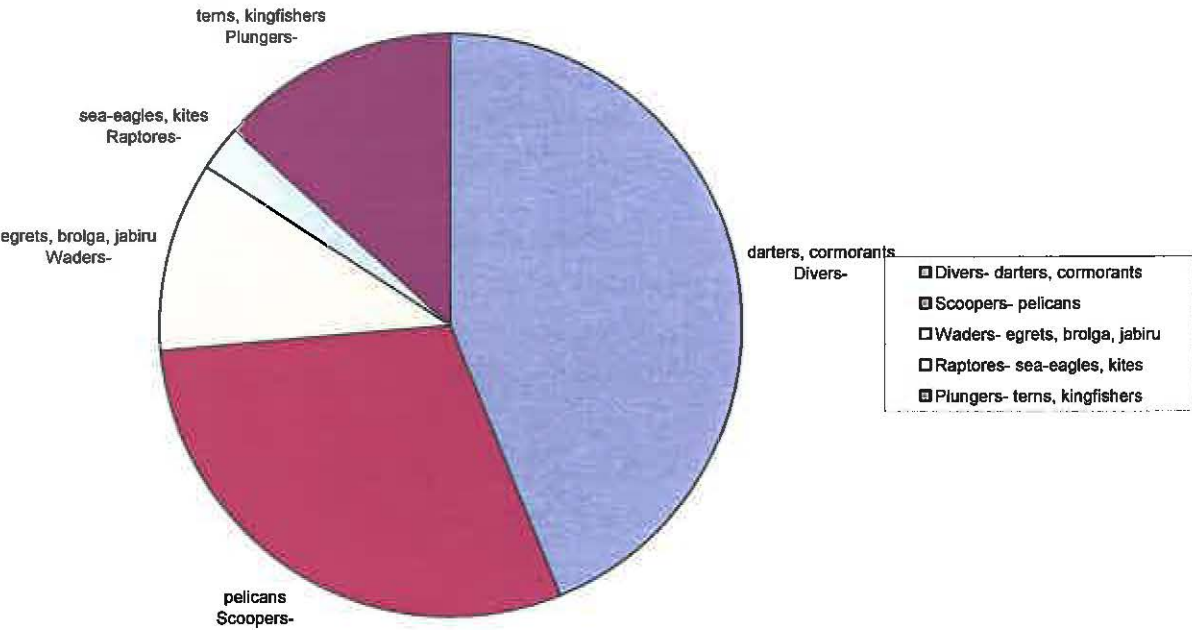


Figure 12.11. Guild composition of piscivores in the Fitzroy delta wetlands (% composition of total piscivore abundance)

Scoopers and divers were the two dominant guilds within the middle and upper sites while lower sites were dominated by either raptors (Gonong Creek) or raptors and plungers (Munduran Creek) (Figure 12.12).

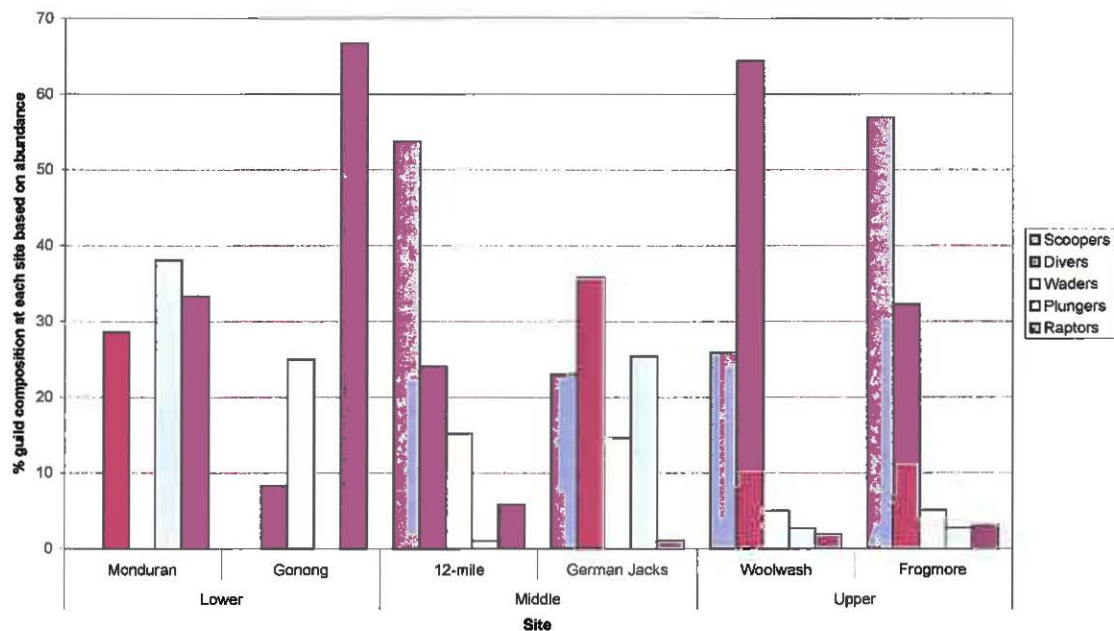


Figure 12.12. Guild percentage composition of total abundance at each site

Waders were important only at the two middle sites and this corresponded to wetlands that had large areas of relatively shallow edges making fish more accessible to this guild. The substantial contribution of waders at Gonong Creek is misleading as it represents three mangrove herons only out of a total abundance from four surveys of 12 piscivores.

Excluding the two lower floodplain sites (Gonong and Munduran Creeks), Australian pelican and little black cormorants were found in greatest average monthly abundance (approximately 30 per site) (Figure 12.13). All remaining species averaged <10 per site (Figures 12.13–12.16) with little pied cormorants, pied cormorants, darters, great egrets, gull-billed terns and Caspian terns averaging >4 individuals per site. Of the raptors, whistling kites and white-bellied sea-eagles were the most abundant (average of <2 individuals per site).

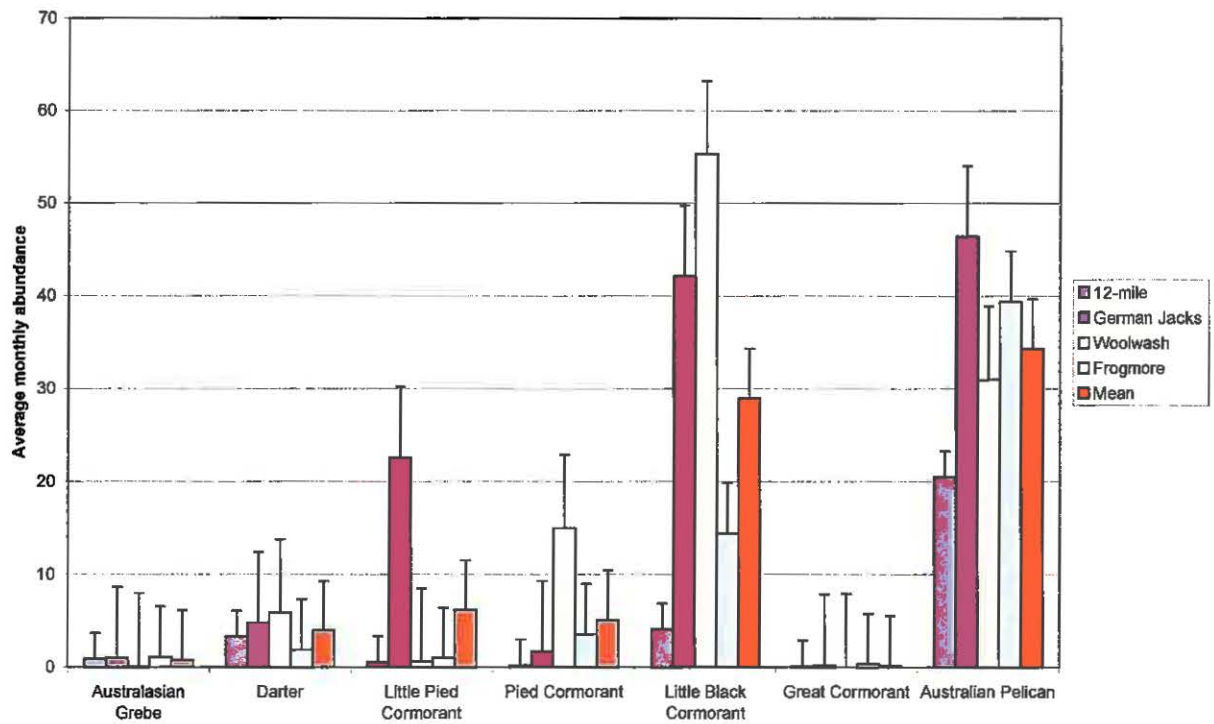


Figure 12.13. Average monthly abundance of scooper and diver guild species at each middle and upper site

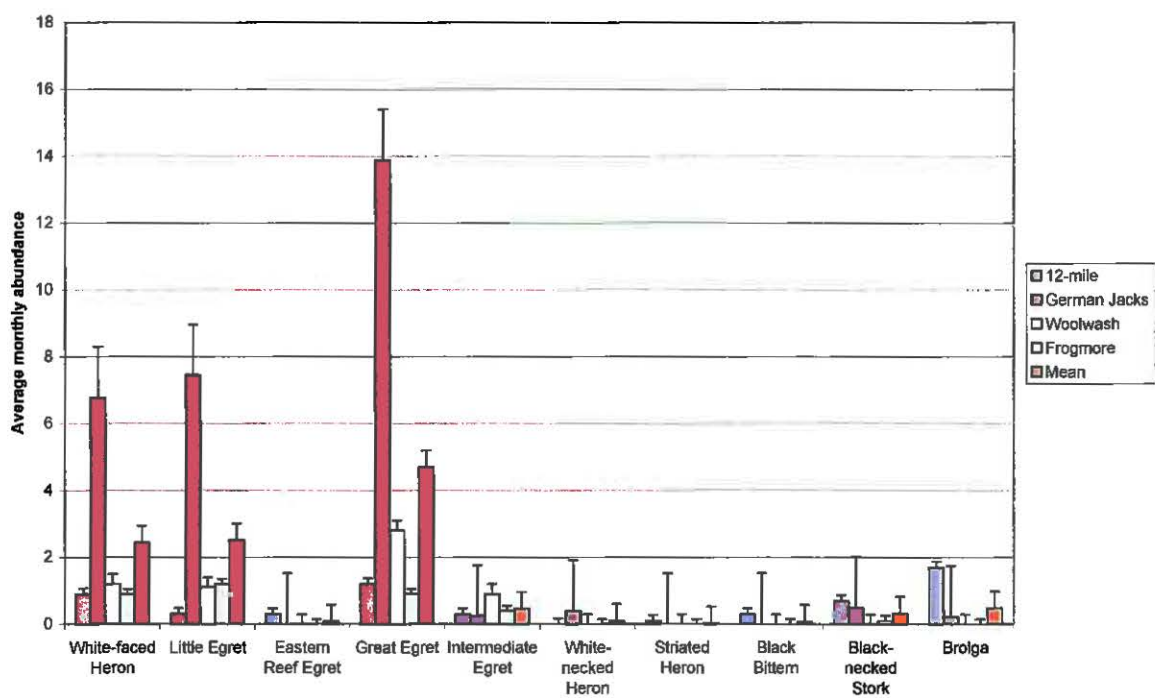


Figure 12.14. Average monthly abundance of wader guild species at each middle and upper site

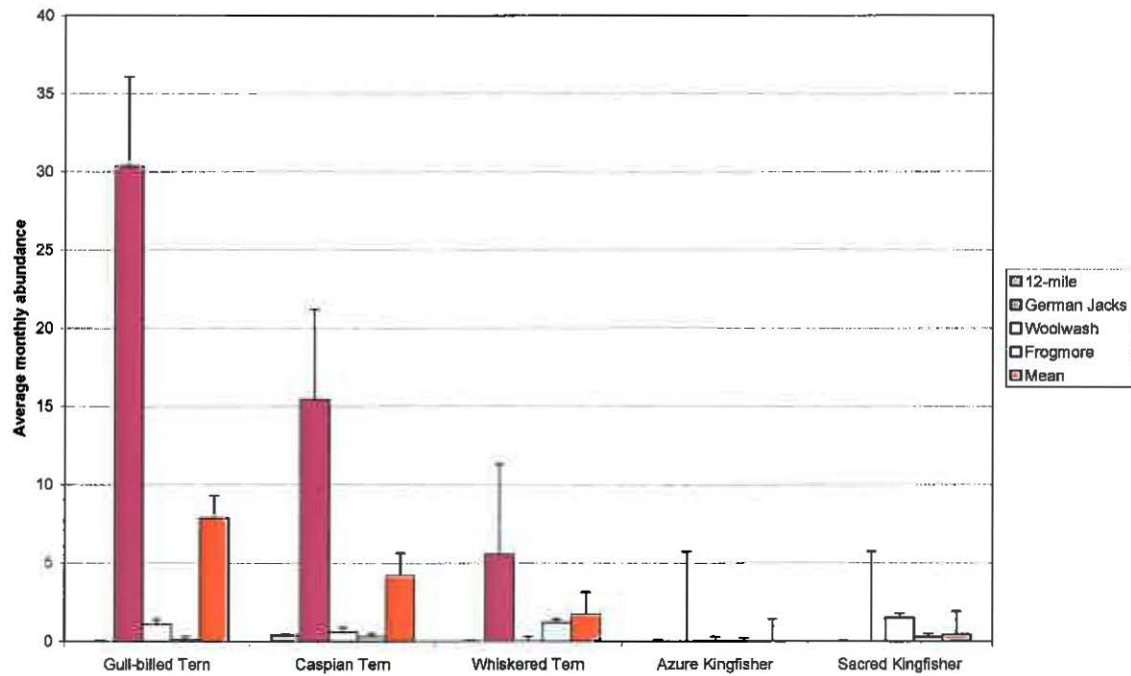


Figure 12.15. Average monthly abundance of plunger guild species at each middle and upper site

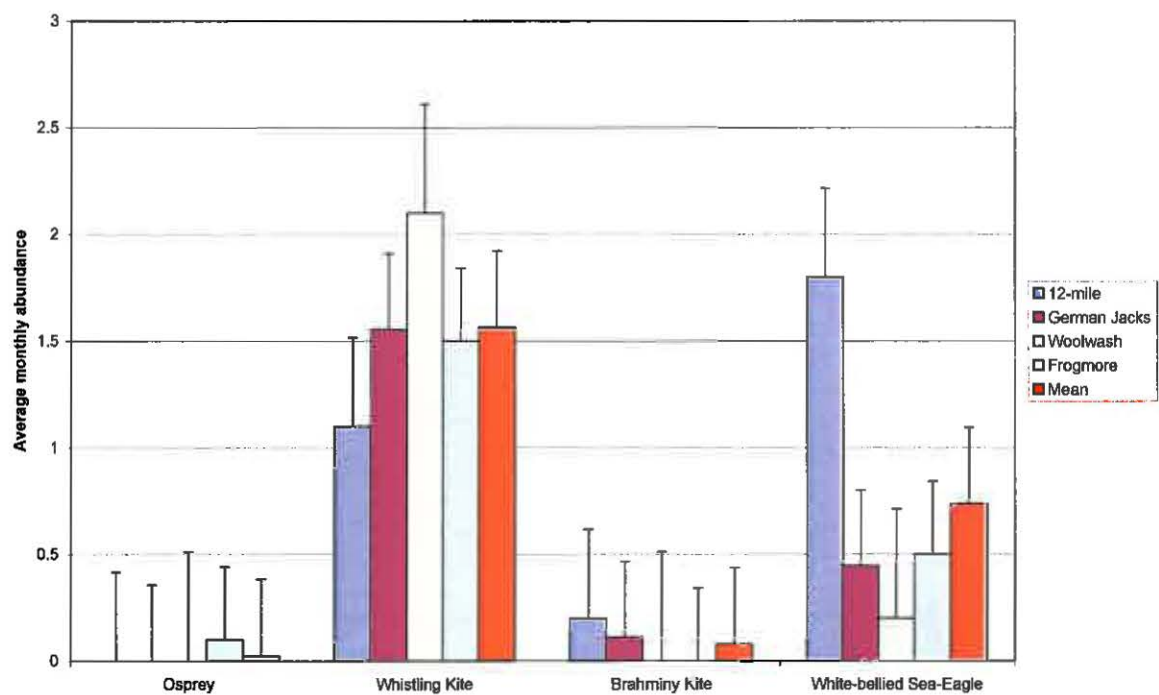


Figure 12.16. Average monthly abundance of raptor guild species at each middle and upper site

Population ecology

Of the dominant species (i.e. those with combined monthly totals for all sites >20) (Figures 12.17–12.31), only a few showed relatively constant monthly total numbers: darter, whistling kite and white-bellied sea eagle. The majority of species fluctuated in numbers from month to month. This does not necessarily mean that these species left the region, as these species may have remained in the region but had moved to non-target wetlands.

Three species had a seasonally significant change in abundance when abundances during wet and dry season months were compared: Australian pelicans and Australasian grebes were in greater abundance during the dry season while pied cormorants were more abundant in the wet season (t-test, $P < 0.05$). Reasons for these patterns are not fully understood but may relate to breeding patterns and changes in habitat requirements when breeding.

Some species were either largely confined to a single site or were dominant at a single site:

- German Jack's: little pied cormorants, gull-billed tern, Caspian tern, great egret, little egret and white-faced heron
- Woolwash: pied cormorant, sacred kingfisher.

The relatively greater number of species mostly restricted to German Jack's reflects the unusual conditions provided at this site including:

1. Relatively greater proximity to the sea
2. The relatively greater shallowness of this system compared with upper sites and therefore it has a greater expanse of shallow waters <1 m providing greater accessibility for waders to their food
3. Greater salinities encountered at this site meant that it shared more in common with lower estuary sites.

Little black cormorants were extremely variable in their abundance with two peaks of >300 birds with remaining months <100. This partly reflects this species feeding ecology whereby it forms large feeding flocks. This species remained relatively abundant within the region with reports of several sightings of feeding aggregations in excess of 100 at non-target wetlands in the area (Robert Black, Rob McFarlane, Allan Briggs unpublished data).

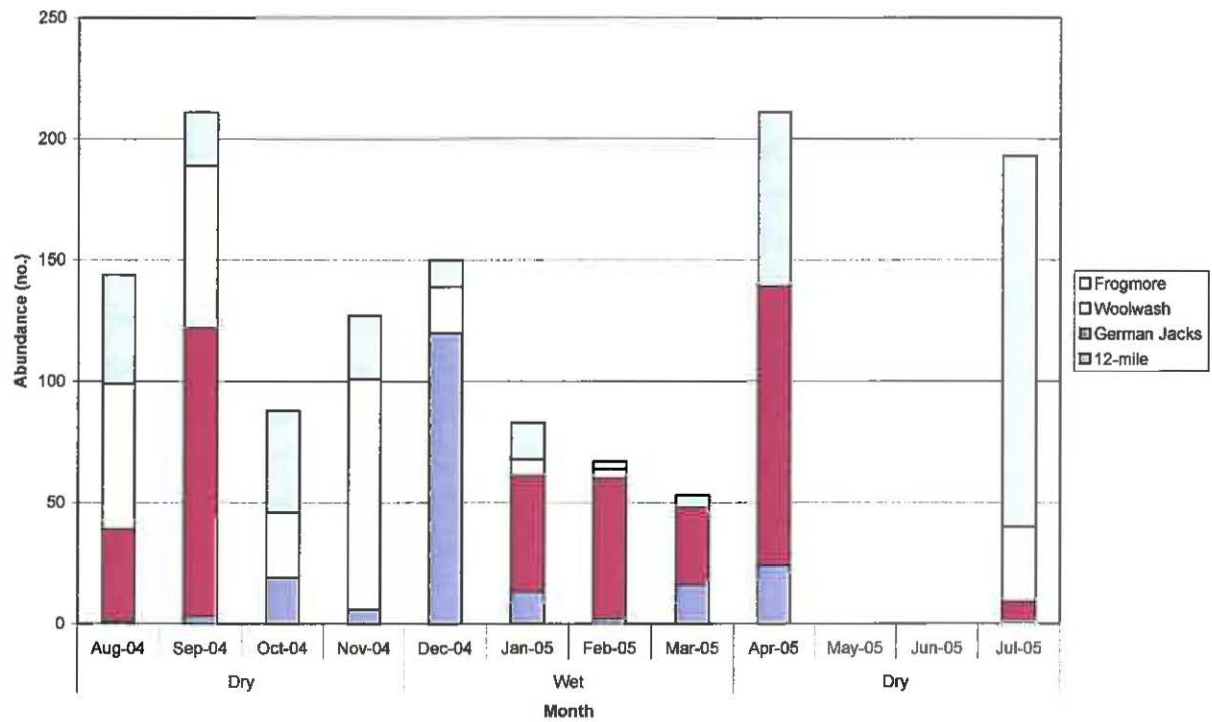
Scoopers (Figure 12.17)

Figure 12.17. Monthly counts of Australian pelicans (scoopers) at each middle and lower site

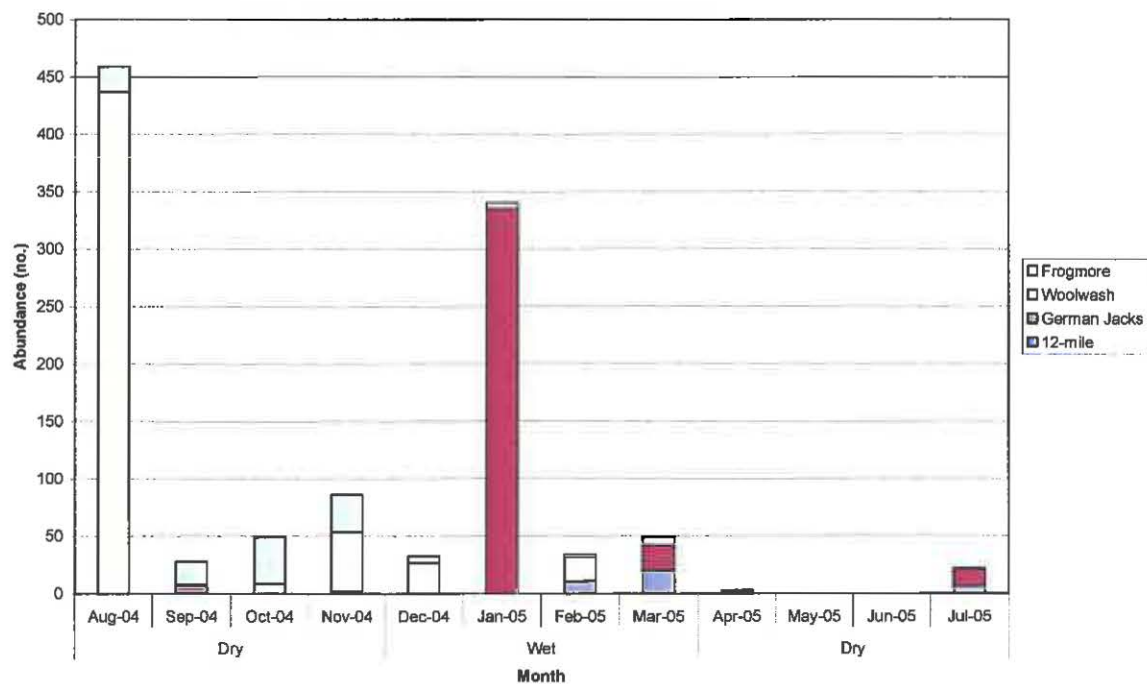
Divers (Figures 12.18–12.22)

Figure 12.18. Monthly counts of little black cormorants (divers) at each middle and lower site

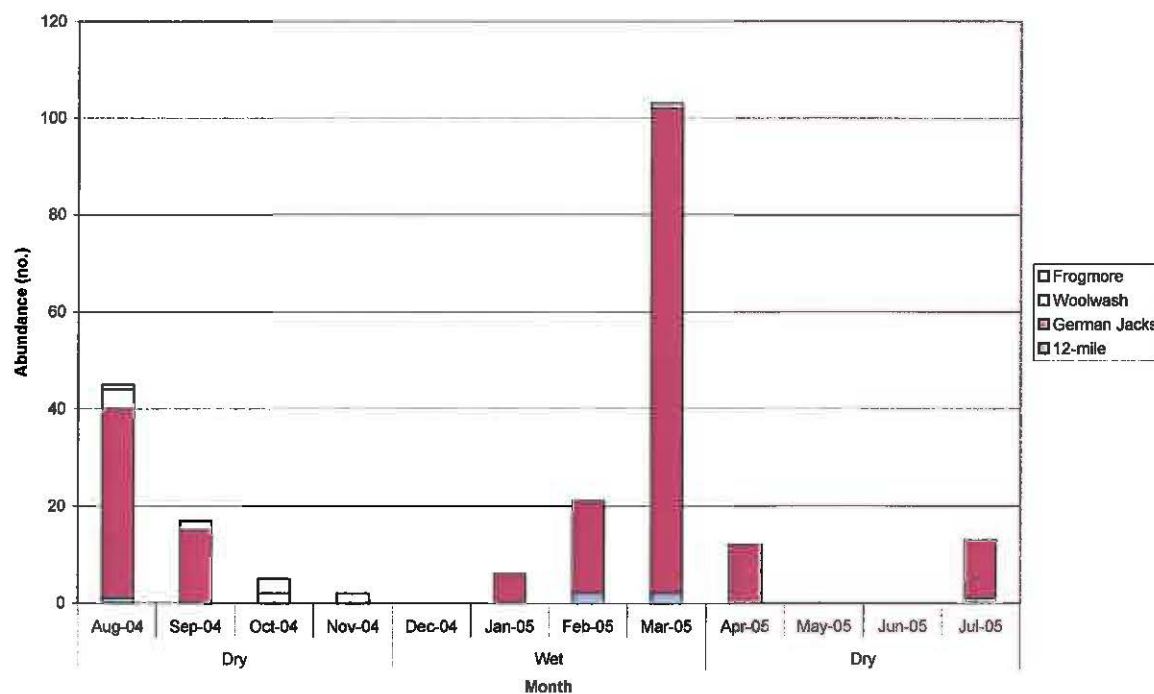


Figure 12.19. Monthly counts of little pied cormorants (divers) at each middle and lower site

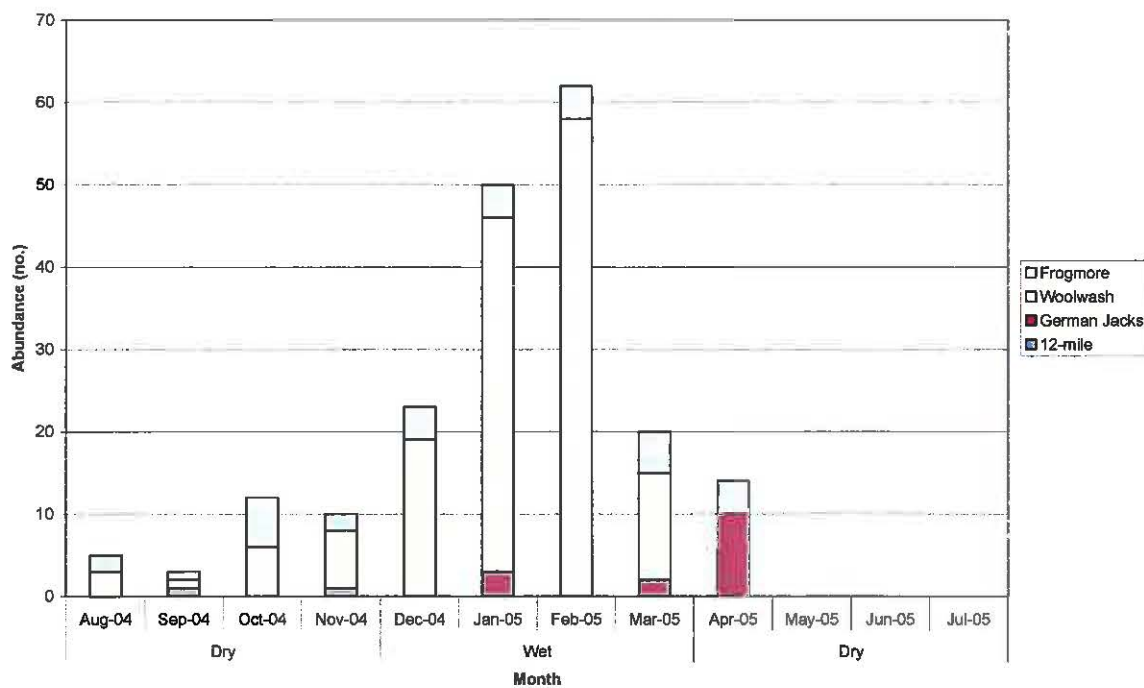


Figure 12.20. Monthly counts of pied cormorants (divers) at each middle and lower site

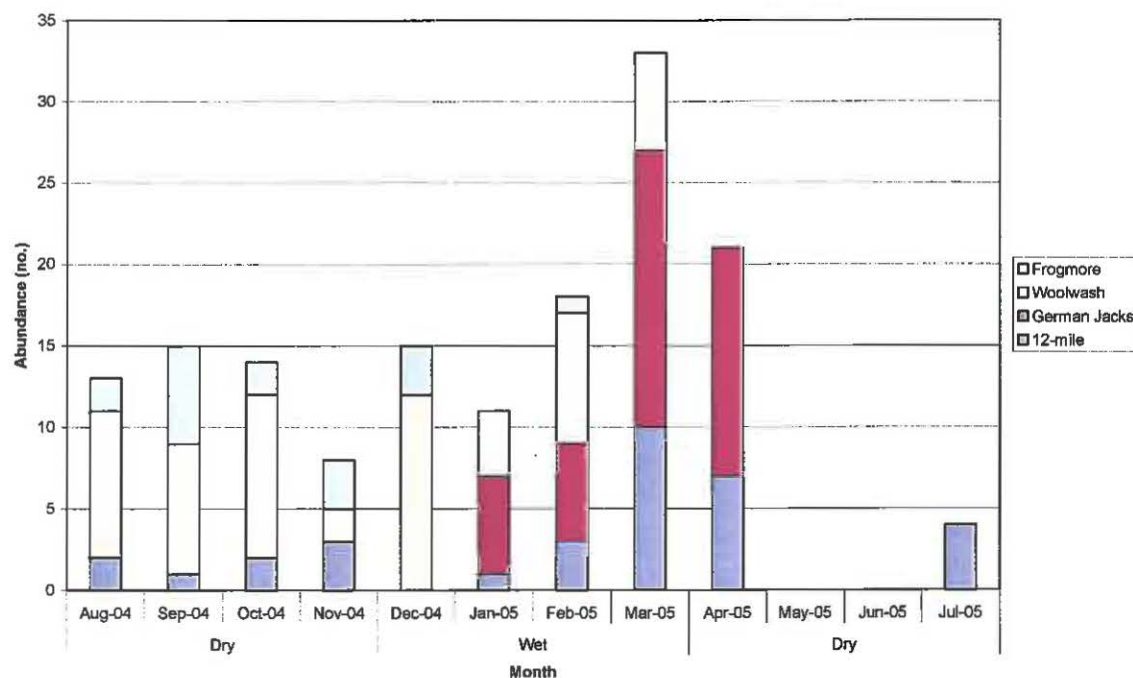


Figure 12.21. Monthly counts of darters (divers) at each middle and lower site

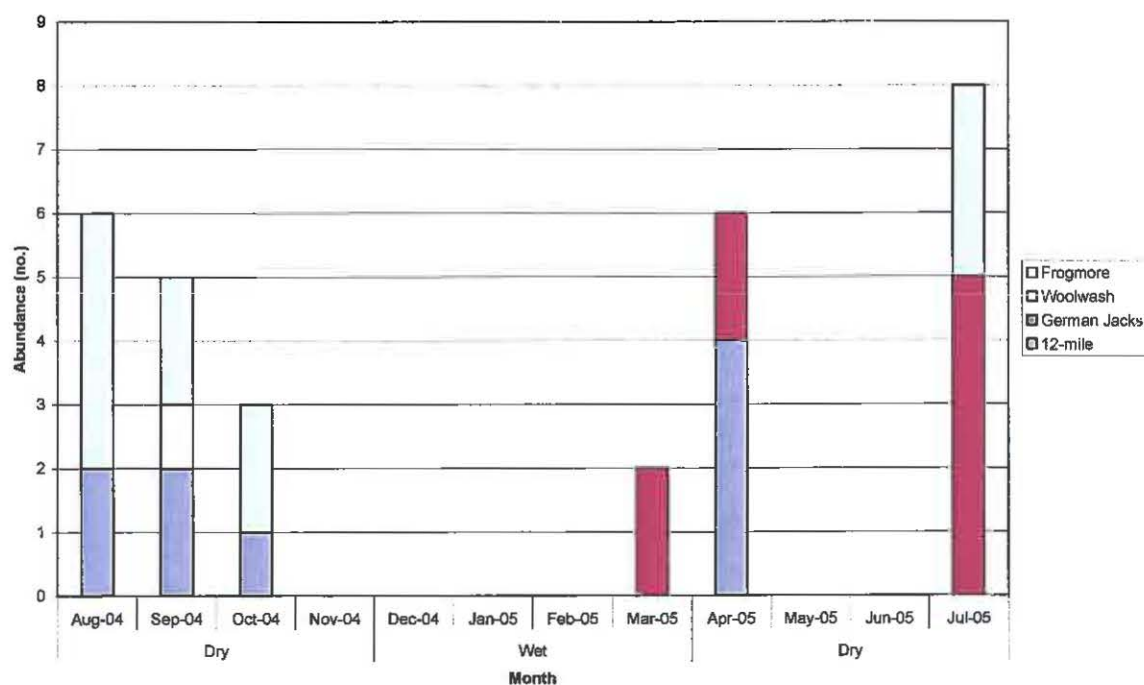
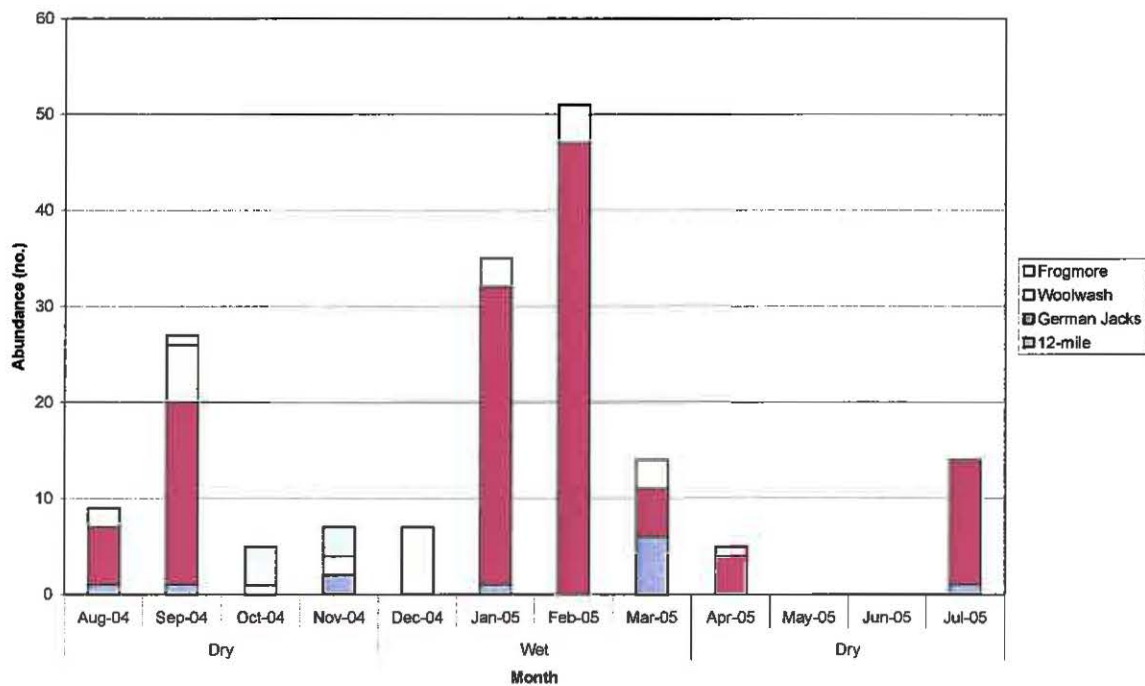
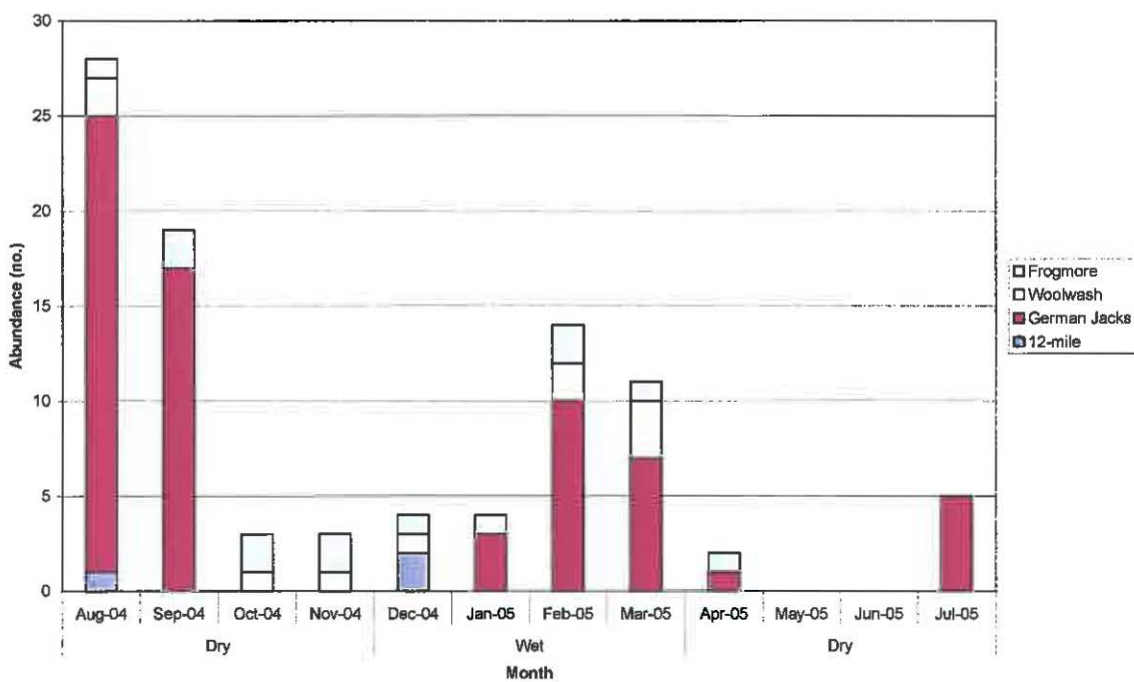


Figure 12.22. Monthly counts of Australasian grebes (divers) at each middle and lower site

Waders (Figures 12.23–12.25)**Figure 12.23. Monthly counts of great egrets (waders) at each middle and lower site****Figure 12.24. Monthly counts of little egrets (waders) at each middle and lower site**

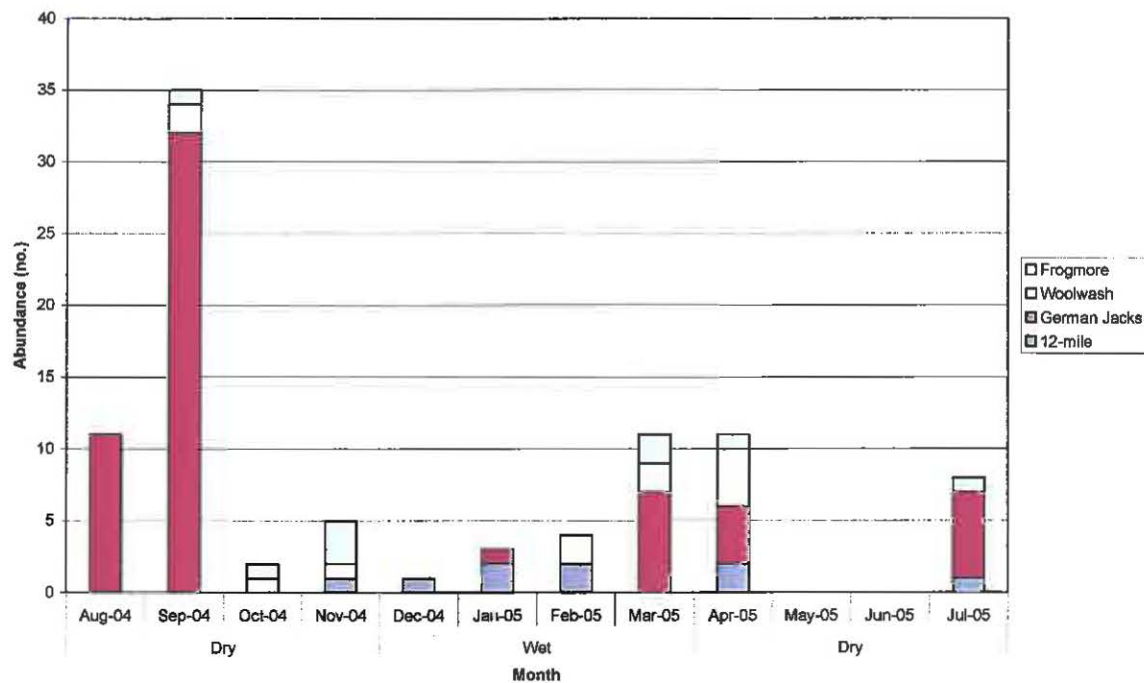


Figure 12.25. Monthly counts of white-faced herons (waders) at each middle and lower site

Plungers (Figures 12.26–12.29)

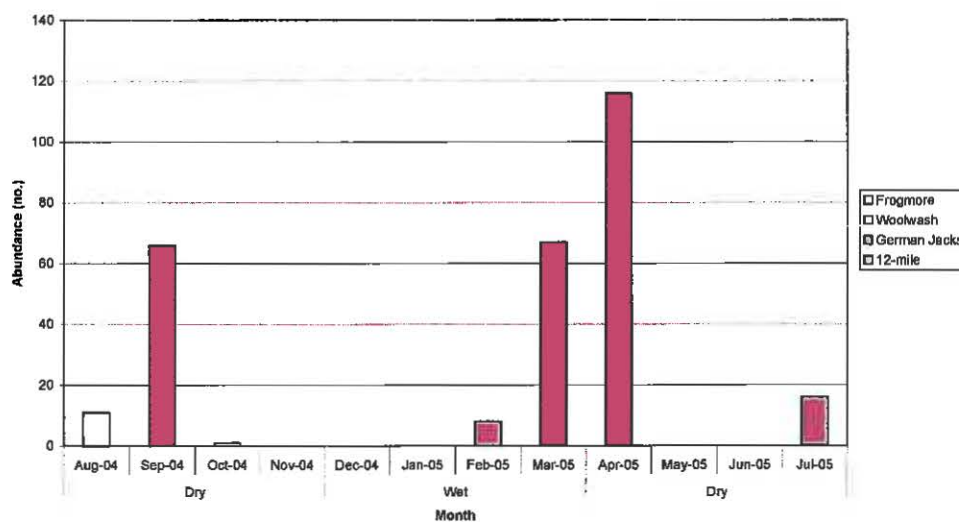


Figure 12.26. Monthly counts of gull-billed terns (plungers) at each middle and lower site

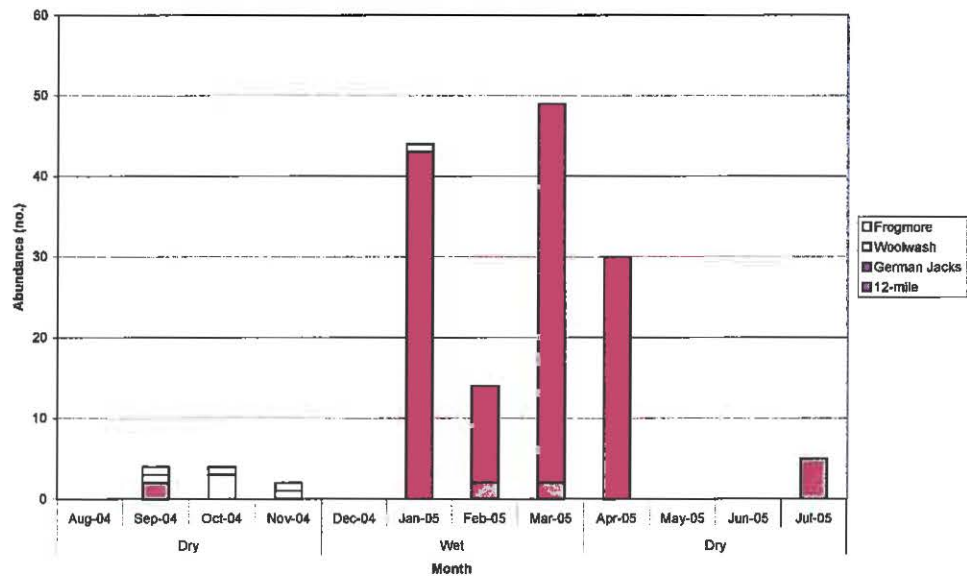


Figure 12.27. Monthly counts of Caspian terns (plungers) at each middle and lower site

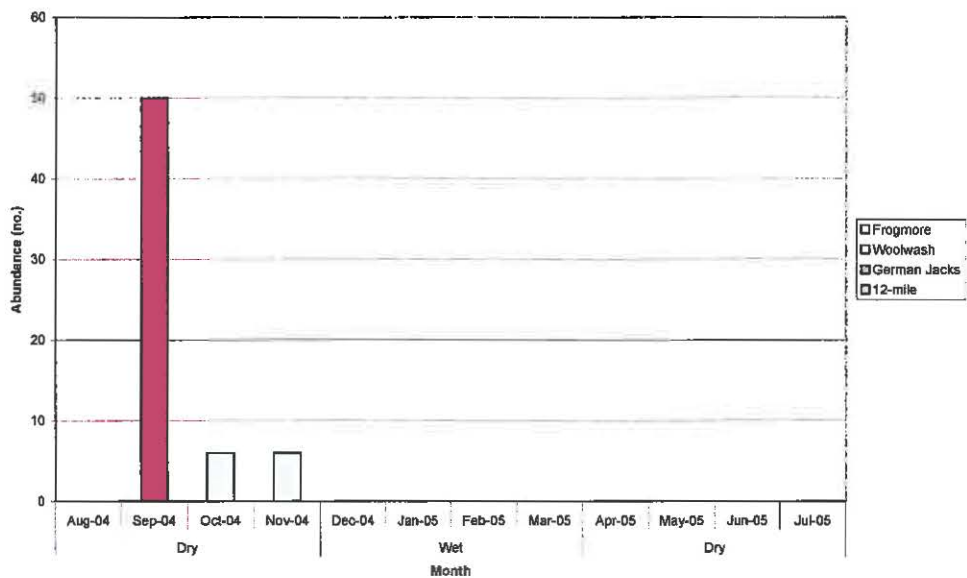


Figure 12.28. Monthly counts of whiskered terns (plungers) at each middle and lower site

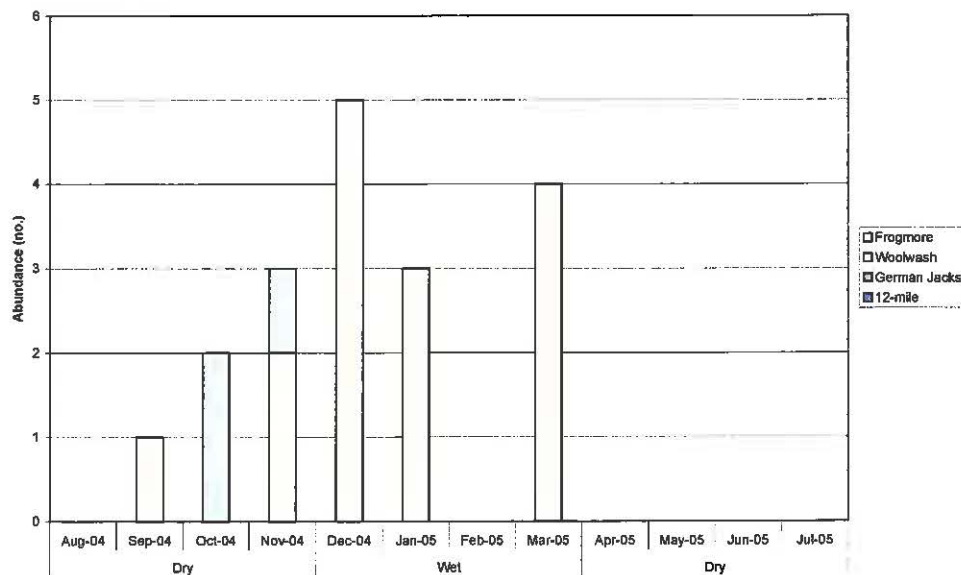


Figure 12.29. Monthly counts of sacred kingfishers (plungers) at each middle and lower site

Raptors (Figures 12.30–12.31)

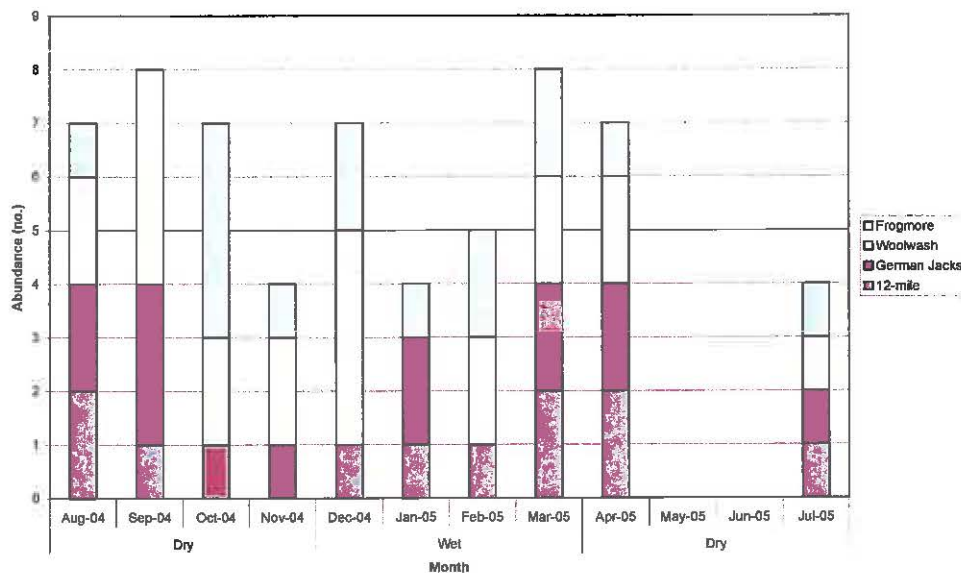


Figure 12.30. Monthly counts of whistling kites (raptors) at each middle and lower site

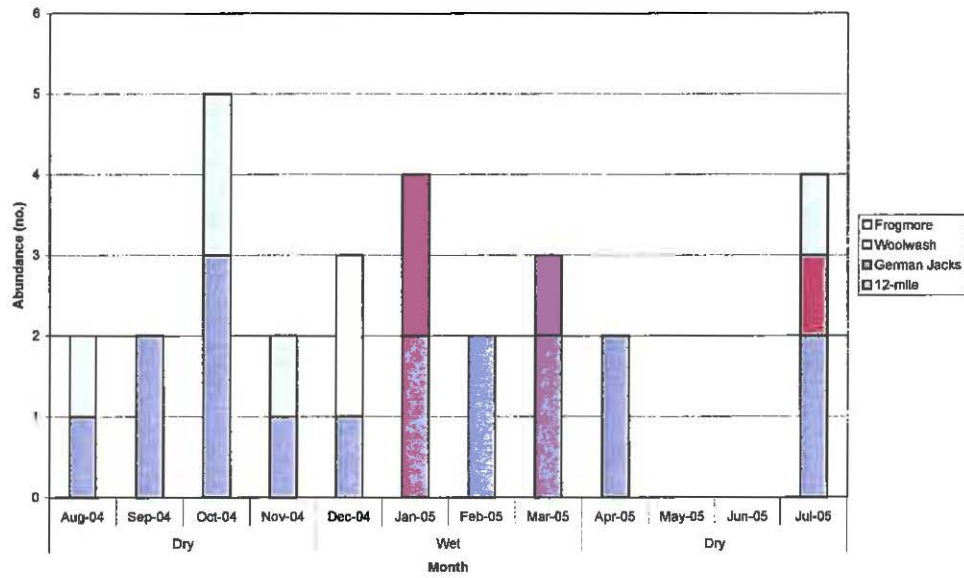


Figure 12.31. Monthly counts of white-bellied sea-eagles (raptors) at each middle and lower site

Community ecology

Univariate analyses

Rockhampton rainfall was lower than average during the 2004–05 wet season (Figure 12.32), with November 2004 and March 2005 much lower. The same pattern of a reduced wet season in 2004–05 was found elsewhere in the region although differences in timing of rainfall can be expected for sites >20 km from the weather station (e.g. German Jack's and Twelve Mile).

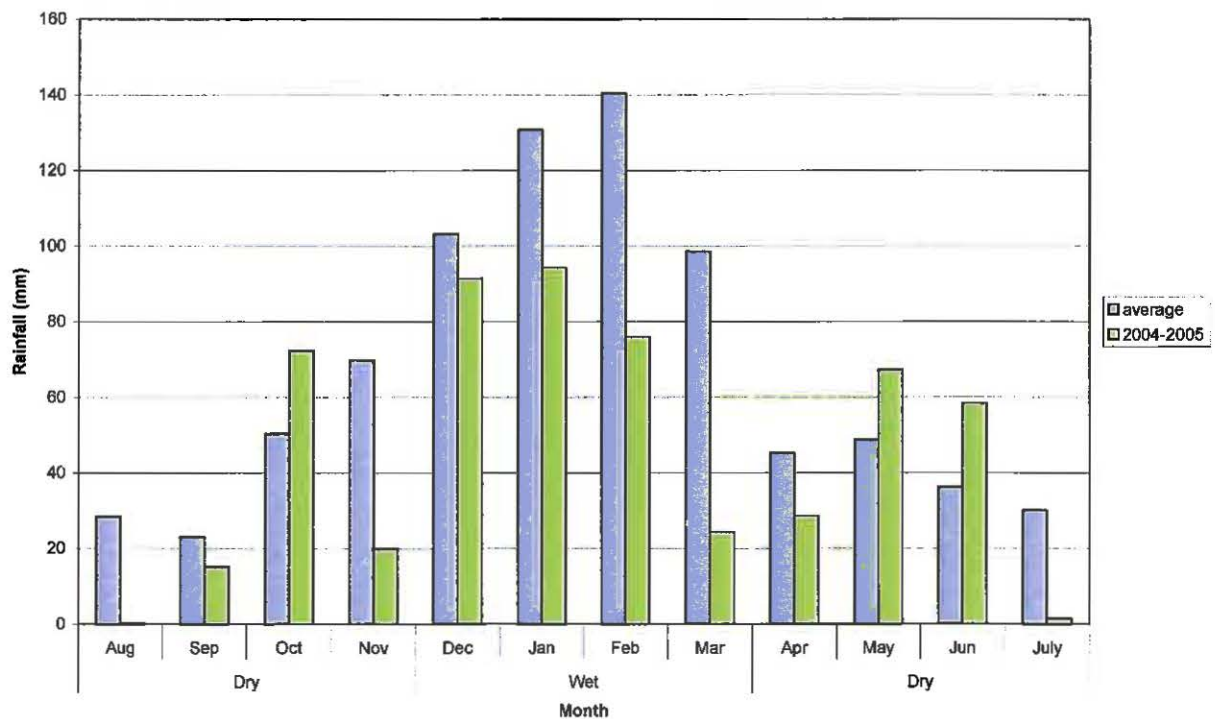


Figure 12.32. Rockhampton rainfall August 2004 to July 2005 with long-term average (65 years)

Twelve Mile Creek

A combination of rainfall in early December 2005 and tidal ingress, indicated by an increase in salinity, led to inundation of the downstream area of Twelve Mile Creek in December (Figure 12.33). This corresponded to an upsurge in piscivore abundance. Whether this was a response to inundation and fish breeding, recruitment of fish from the estuary or a combination of both is not known. Smaller peaks in piscivore abundance were observed in April and May as water levels fell in response to evaporative processes.

Australian pelicans were the dominant piscivore in most months including the December peak. Little black cormorants and darters were also relatively abundant from February 2005 as water levels fell.

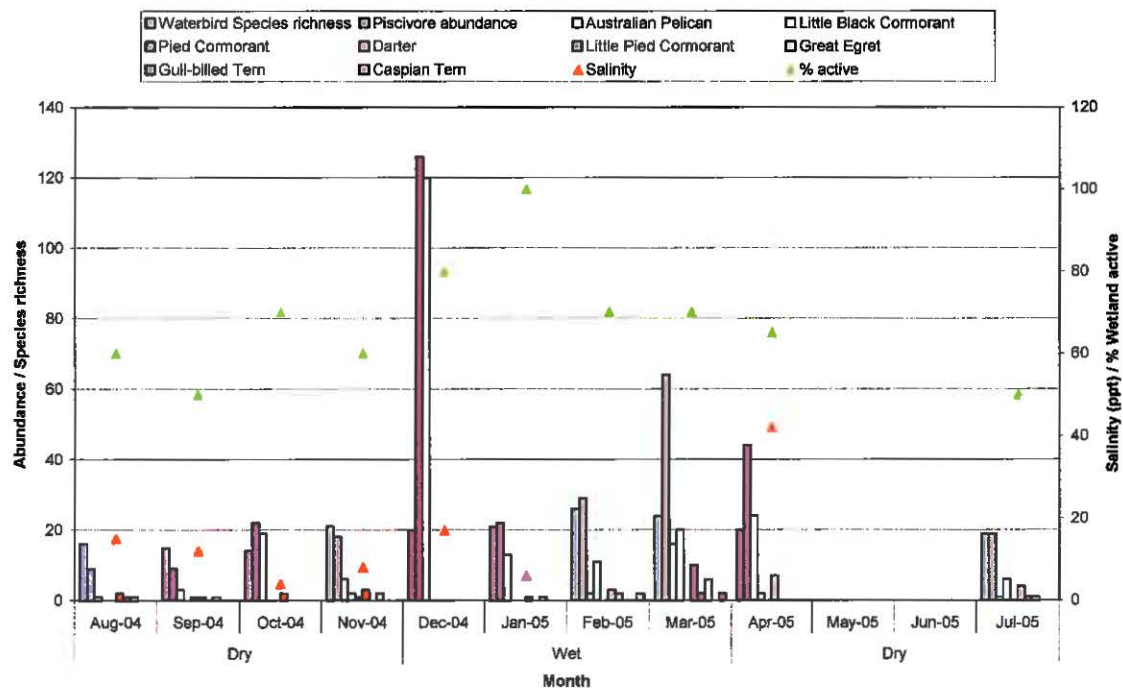


Figure 12.33. Monthly piscivore abundance (total and by dominant species) plus waterbird species richness at Twelve Mile Creek plus some salinity data and an index of inundation extent of the wetland (% wetland active)

As German Jack's dried rapidly in the late dry season it became extremely hypersaline (160 ppt in October 2004) and this corresponded to a loss of all piscivores in October and November prior to the wet season rains (Figure 12.34). Late December–January rainfall and a probable connection to the river in the same months led to an increase in the active area of the wetland and a fall in salinity from 160 ppt to 20 ppt in January 2005. This corresponded to a peak in piscivore abundance. Lesser peaks occurred in September 2004 and March–April 2005. The March–April peak corresponded to a gradual drying of the wetland following inundation in January.

The peak in January 2004 coincided with an influx of little black cormorants (300+). No single species dominated in other months and substantial contributions were made by Australian pelicans, great egrets, little pied cormorants and two species of tern (gull-billed and Caspian). The latter three species were relatively more abundant during the draw-down periods corresponding to minor peaks in September 2004 and March–April 2005. Australian pelicans also made substantial contributions to piscivore abundance in September and April 2005.

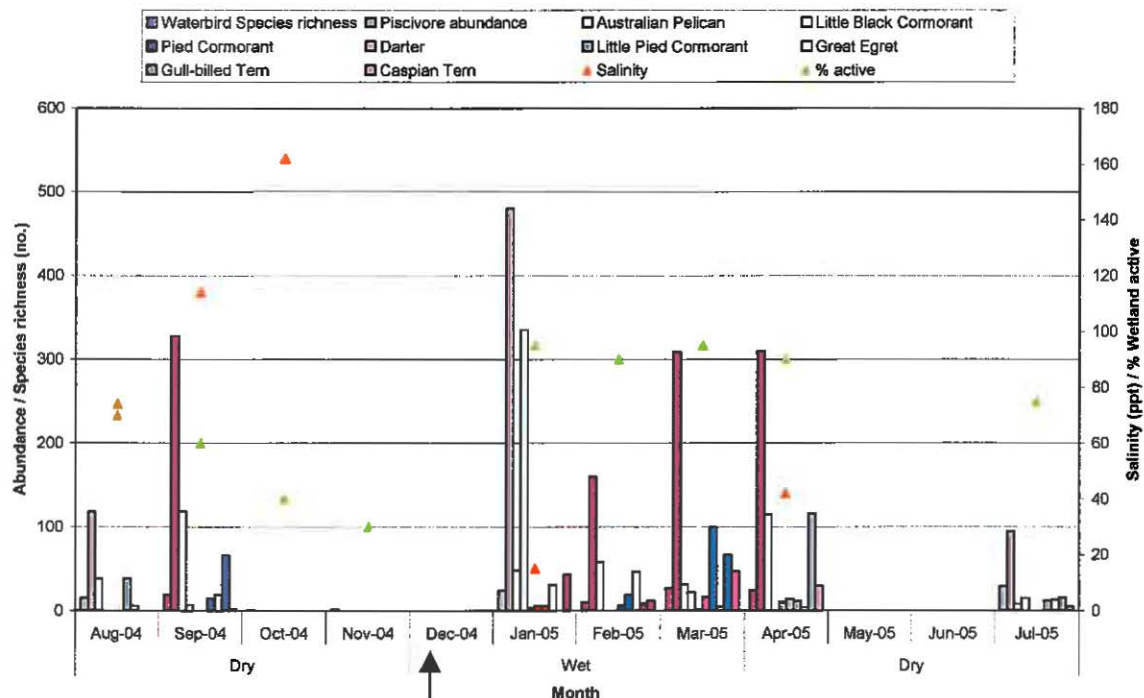


Figure 12.34. Monthly piscivore abundance (total and by dominant species), waterbird species richness at German Jack's plus some salinity data and an index of inundation extent of the wetland (% wetland active) (arrow indicates month not sampled)

Of all four regularly monitored sites, Woolwash lagoon had the lowest potential for an inundation event and during regular wet seasons would be dependent on input via overflows from Frogmore when it received surface flows from Gavial Creek or in extreme flood events. Some surface flow from its own small catchment was received in October 2004 resulting in a stabilised active area in October–November 2004. Subsequent local surface flows associated with wet season rainfall either did not occur or were overridden by high evaporation associated with high summer temperatures.

Piscivore abundance peaked in August 2004 (Figure 12.35) with a flock of 400+ little black cormorants observed feeding on bony bream. After this large peak, reflecting the lack of inundation events (indicated by stable or falling active wetland area), piscivore numbers remained at stable level until February 2005 followed by a rapid decline in March–April associated with very low water levels.

Australian pelicans were relatively abundant from August to November 2005, peaking in November but with few or none found after that. Pied cormorants seemed to follow an opposite trend and did not become important until December 2005, with a peak in February followed by a fall in numbers.

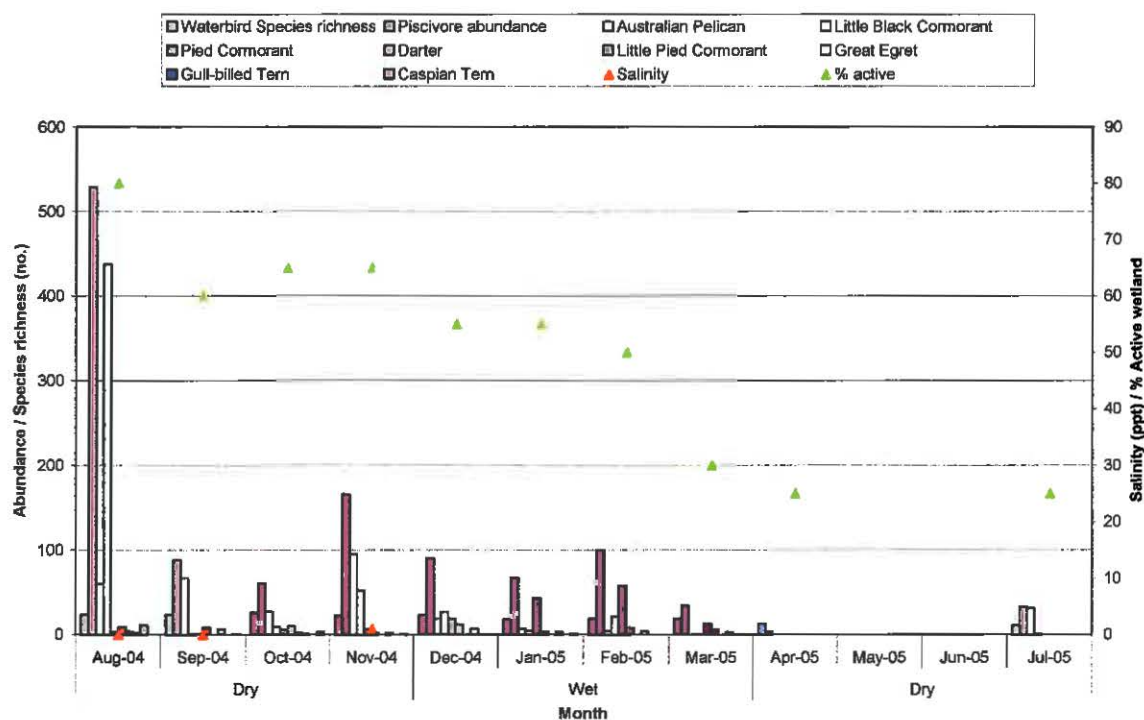


Figure 12.35. Monthly piscivore abundance (total and by dominant species), waterbird species richness at Woolwash lagoon plus some salinity data and an index of inundation extent of the wetland (% wetland active)

Frogmore is a much deeper system than Woolwash, providing greater deepwater refugia for fish. It also receives local catchment surface flows from Gavial Creek and at times connects to the river under extreme flood or tidal events. October rainfall produced an increase in the active area in November 2004 and water levels fell only marginally during the remainder of the study period reflecting either local inputs and/or relatively low evaporation rates due to a greater degree of shading and deepness providing a lower surface to volume ration than at the Woolwash.

Two peaks in piscivore abundance were observed (Figure 12.36), one in October–November 2004 and one in April–July 2005. These months corresponded to an inundation event following October rainfall (indicated by increase in % active wetland area) and draw-down following evaporative losses in April 2005.

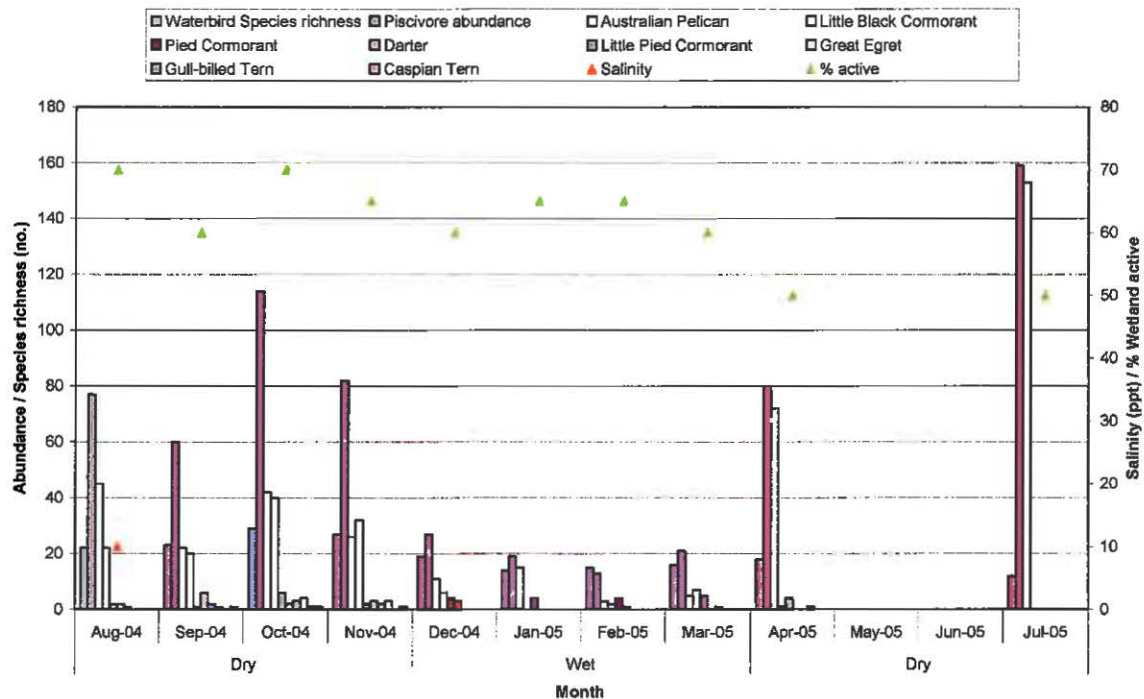


Figure 12.36. Monthly piscivore abundance (total and by dominant species), waterbird species richness at Frogmore lagoon plus some salinity data and an index of inundation extent of the wetland (% wetland active)

Australian pelicans were the dominant piscivore and maintained a relatively stable population of between 20 and 45 birds from August to November 2004 followed by a decline and then resurgence to a peak in April 2005 and July 2005 associated with draw-down. Another dominant species at this site was Little black cormorants, particularly from August to November 2004 (20–40 birds). Pied cormorants also made a contribution from October 2004 to April 2005 (mostly between 4 and 6 birds).

Overall the two upper floodplain sites, Woolwash and Frogmore, showed a similar successional sequence of piscivores:

1. Little black cormorant
2. Australian pelican.

Using limited water depth data (Marcus Sheaves unpublished data) from each upper floodplain site to estimate depth at each sampling event, little black cormorants peaked in abundance at approximately 3 m depth and Australian pelicans at approximately 2 m depth in both sites (Figure 12.37). This suggests that foraging success of these two species may be linked with water depth of these upper floodplain wetlands with their target prey becoming accessible to them at certain depths.

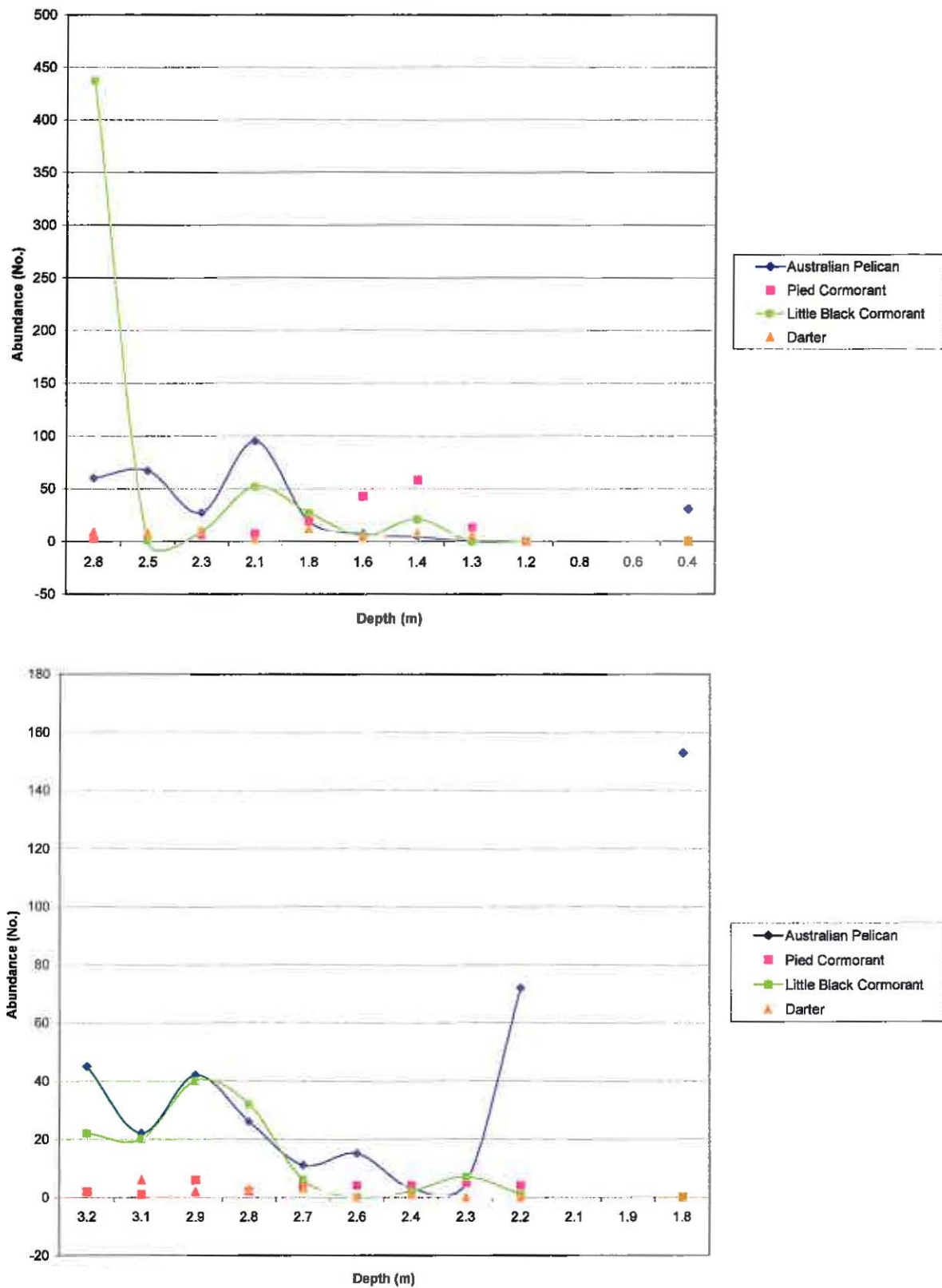


Figure 12.37. Abundance of dominant species of piscivores at upper floodplain sites (upper panel) Woolwash and (lower panel) Frogmore as a function of depth at each site over time

Multivariate analyses

Analysis of similarity showed that both wetland location in the floodplain (upper, middle or lower) and season (wet or dry) significantly influenced piscivore species composition and abundance of sites (ANOSIM, $R=0.502$, $P=0.001$, 999 random permutations and $R=0.135$, $P=0.023$, 999 random permutations respectively). These results are shown graphically for floodplain location (Figure 12.38) and there is a clear difference between lower sites that have good connectivity (lower floodplain sites Gonong and Munduran Creeks) compared with the others.

The cluster analysis (Figure 12.39) shows that both middle floodplain sites formed strong site groups (Twelve Mile and German Jack's) while upper floodplain sites formed a mixed grouping. There were exceptions and these were mainly those sites with <10 piscivore individuals in a survey [all Gonong and Munduran Creek samples plus two German Jack's (October and November 2004) and one Woolwash (April 2005)]. Removing these outliers helps to clarify the site relationships to highlight seasonal influences (Figure 12.40). Dry season sites had less scatter, indicating that they were more similar in their bird piscivore composition than the wet season piscivore composition of sites.

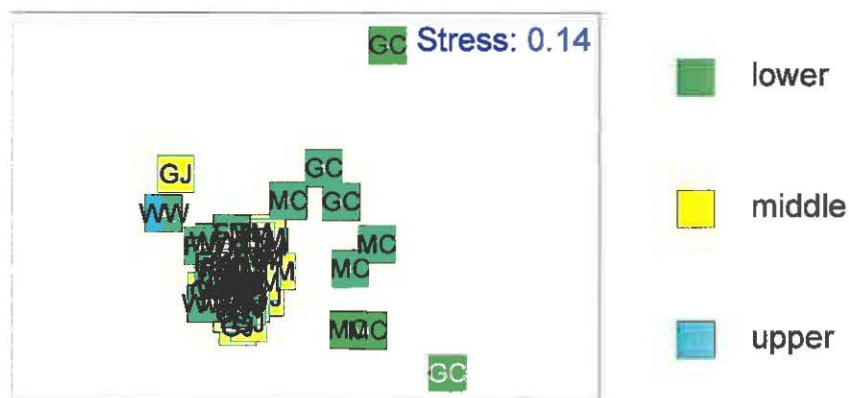


Figure 12.38. Scattergram of the NMDS ordination (Bray-Curtis similarity index on square root transformed data) to show site relationships and influence of the relative degree of connection of sites to the river

Lower=connects regularly, middle=connects on high spring tides; upper=connects rarely during flood events. GC=Gonong Creek, MC=Munduran Creek, TM=Twelve Mile Creek, GJ=German Jack's lagoon, WW=Woolwash lagoon, FM=Frogmore lagoon

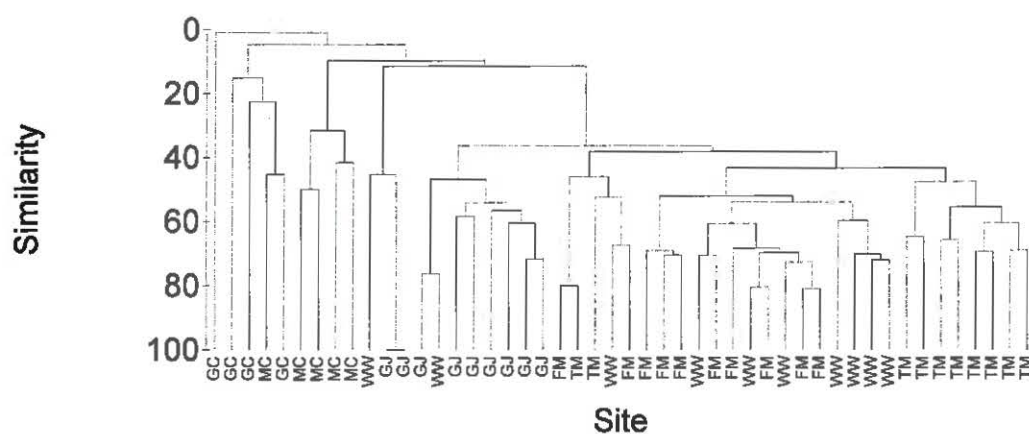


Figure 12.39. Cluster analysis (group average sorting) to show grouping of sites
 GC=Gonong Creek, MC=Munduran Creek, TM=Twelve Mile Creek,
 GJ=German Jack's lagoon, WW=Woolwash lagoon, FM=Frogmore lagoon



Figure 12.40. Scattergram of the NDMS ordination (excluding outliers = sites with piscivore abundance <10) to show influence of season (wet and dry)
 GC=Gonong Creek, MC=Munduran Creek, TM=Twelve Mile Creek,
 GJ=German Jack's lagoon, WW=Woolwash lagoon, FM=Frogmore lagoon

Fish consumption estimates

Based on estimates of percentage body weight consumed per day (<300 g: 30%; 300–3000 g: 20%; and >3000 g: 10%), the fish biomass consumed at each of the four main wetlands was estimated.

Guild overview

The scooper guild accounted for over 50% of the estimated fish biomass removed and was the most dominant guild at all middle and upper sites except Woolwash lagoon (Figure 12.41). This site was dominated by the diver guild and this guild was the second greatest contributor to the removal of fish biomass. The other three guilds were minor contributors.

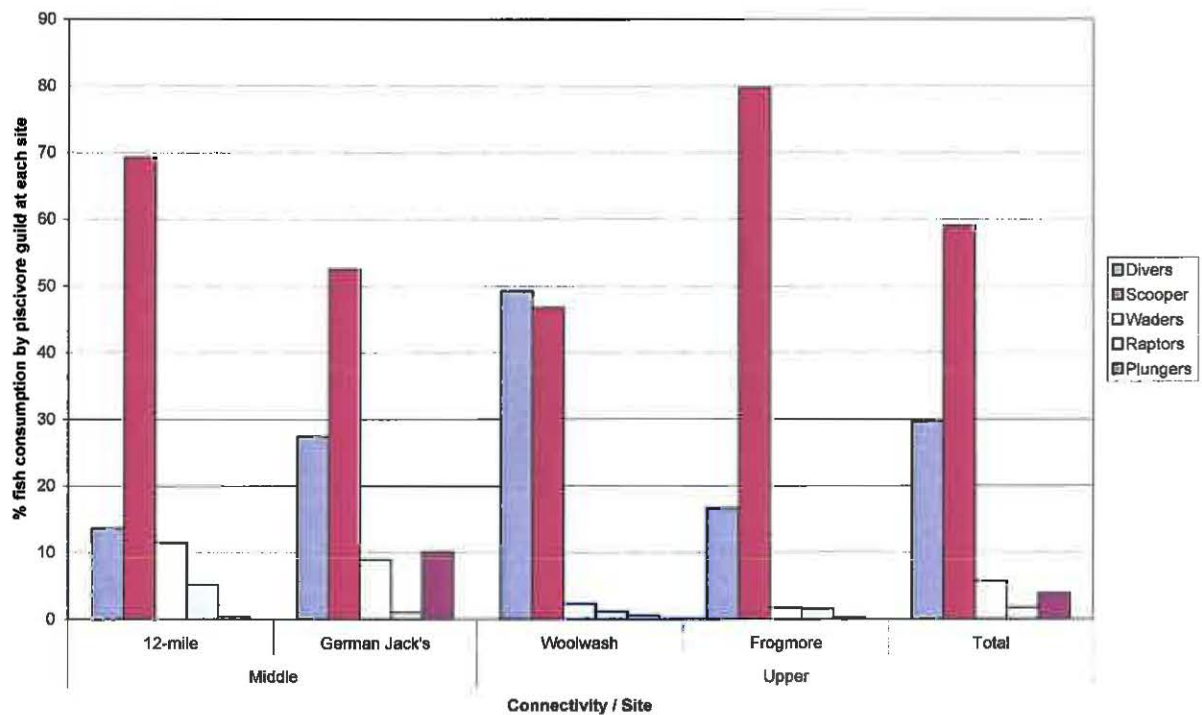


Figure 12.41. Estimated fish consumption by guild for each site

Overview by species

Australian pelicans comprising the scooper guild removed the greatest amount of fish biomass at all middle and upper sites (Figure 12.42). The remaining important species were all members of the diving guild and were little black cormorant, pied cormorant and darter. An additional four species made substantive contributions at German Jack's: little pied cormorant, great egret, gull-billed tern and Caspian tern.

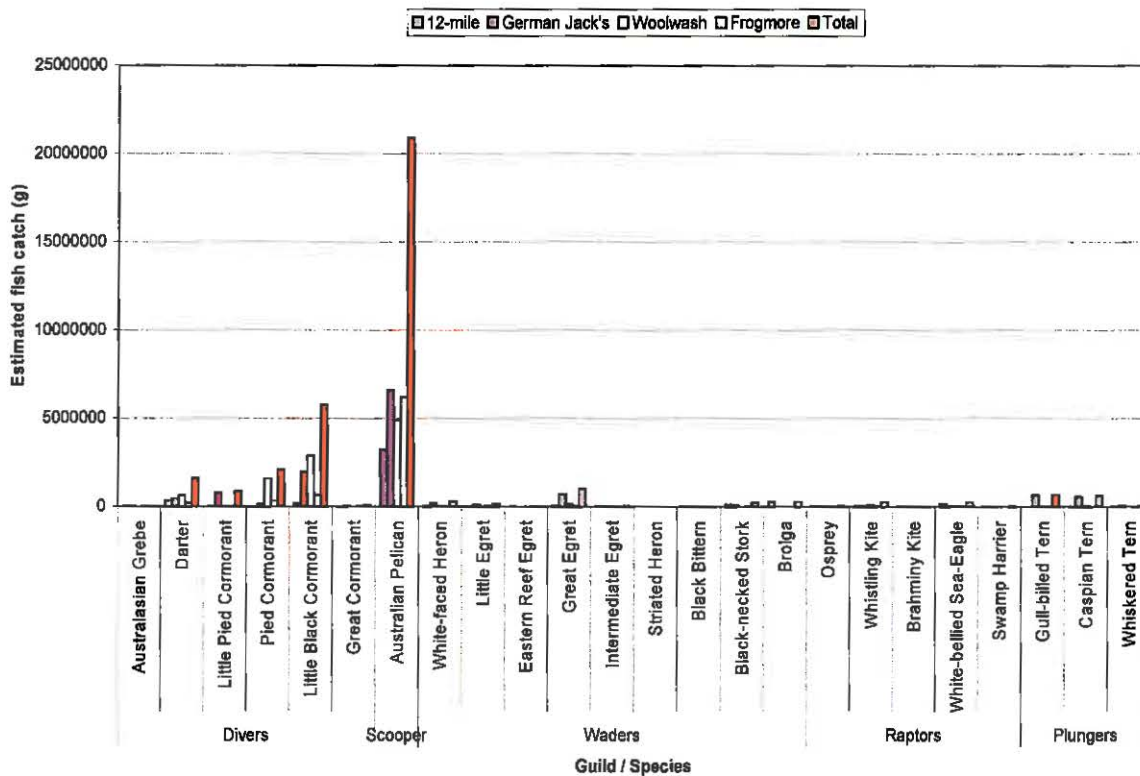


Figure 12.42. Estimated fish consumption by species

Seasonality

Only one site showed a seasonal pattern of fish consumption by piscivores—Frogmore, with greatest fish predation in the dry season (t-test, $P < 0.05$) (Figures 12.43–12.46). Peaks in Australian pelicans at both the Woolwash and Frogmore sites corresponded to draw-down to about 2 m water depth.

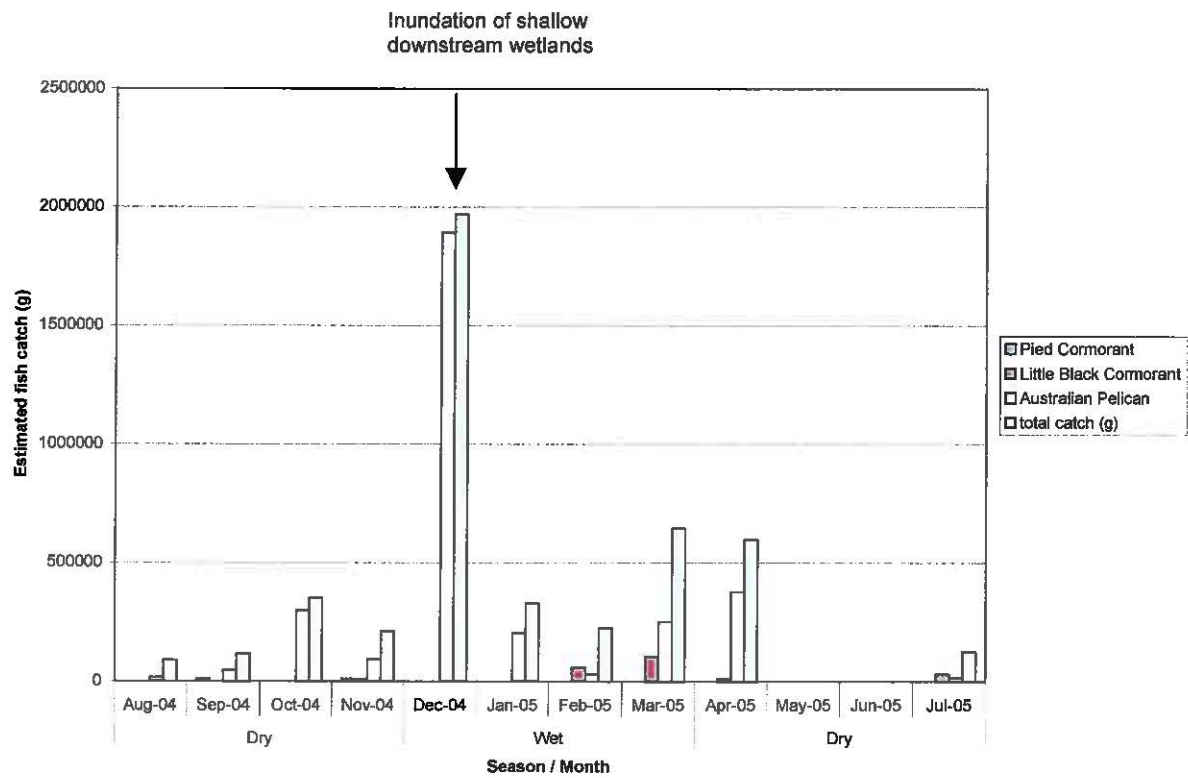


Figure 12.43. Estimated monthly fish consumption at Twelve Mile Creek and contribution by dominant piscivore species

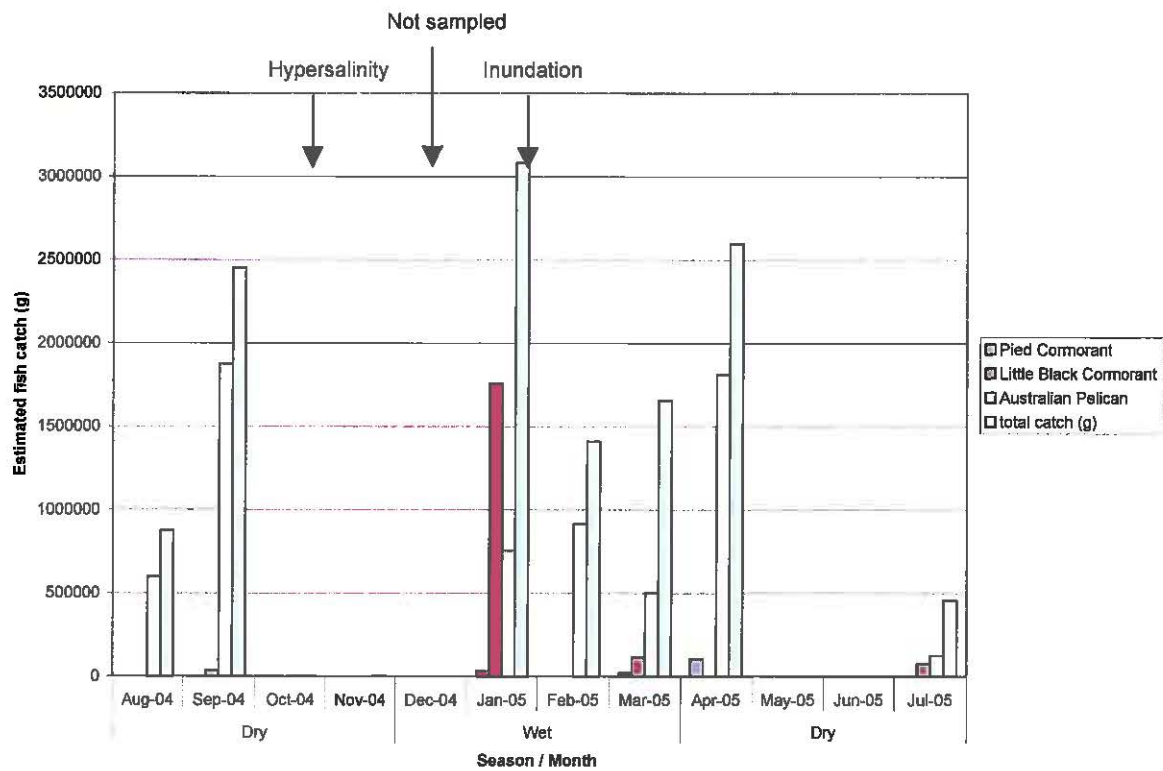


Figure 12.44. Estimated monthly fish consumption at German Jack's lagoon and contribution by dominant piscivore species

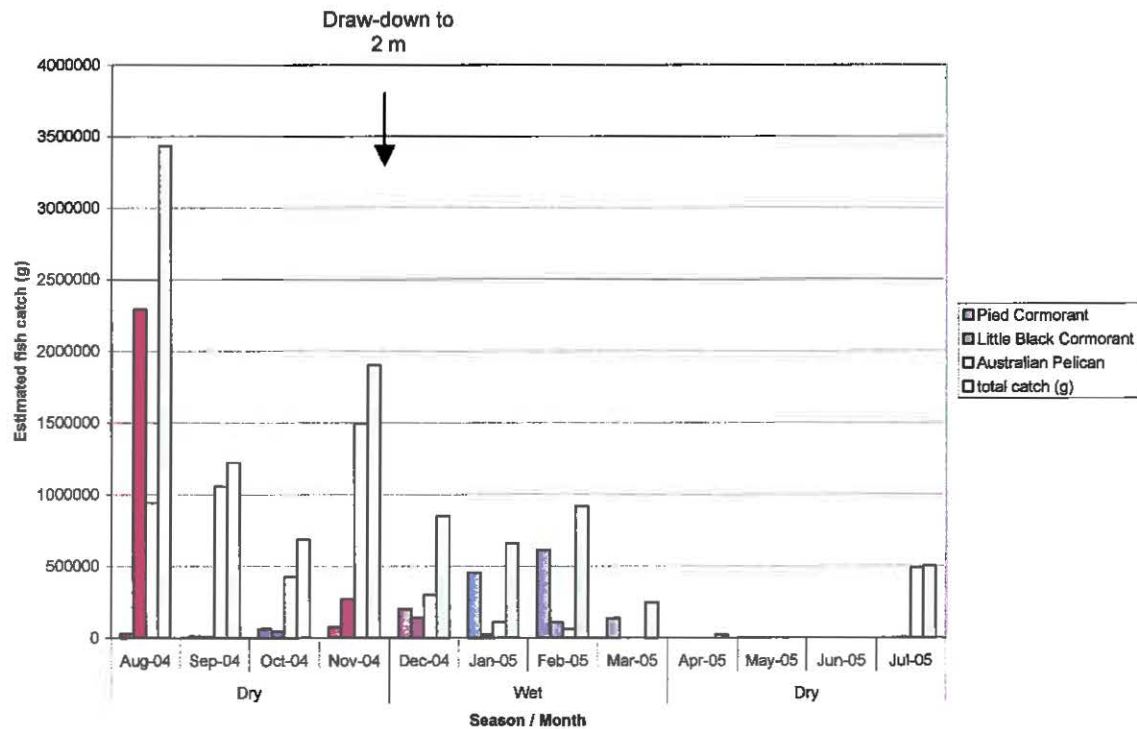


Figure 12.45. Estimated monthly fish consumption at Woolwash lagoon and contribution by dominant piscivore species

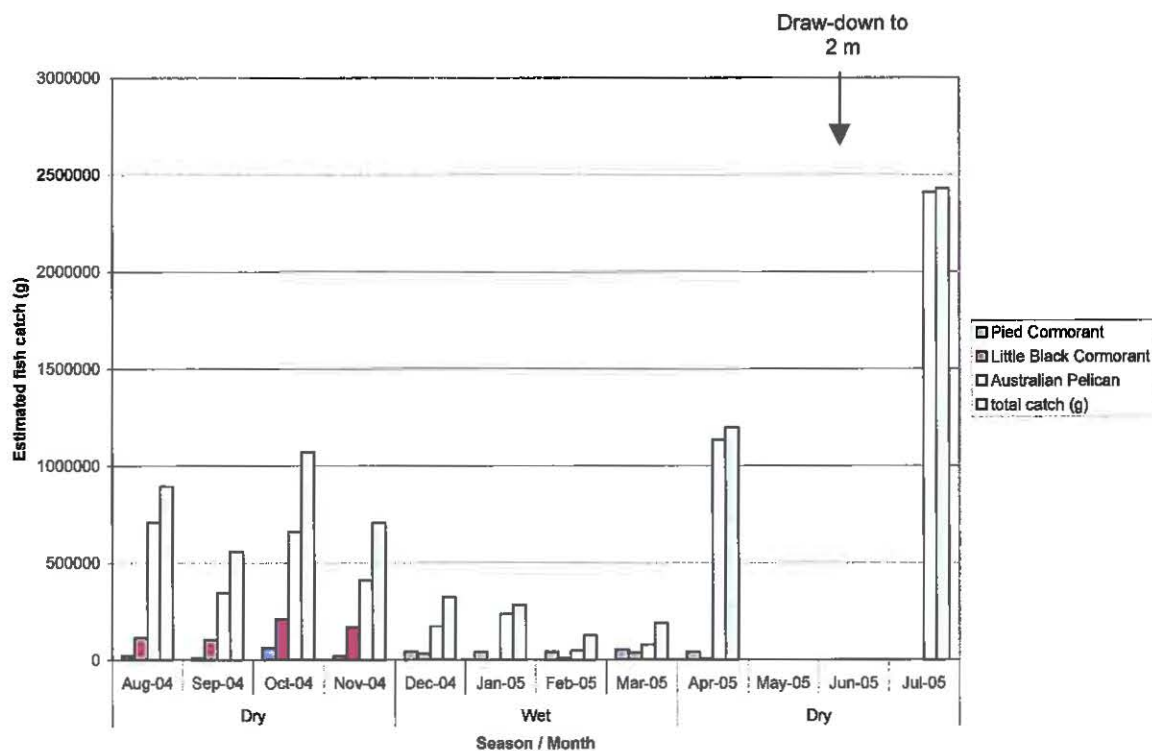


Figure 12.46. Estimated monthly fish consumption at Frogmore lagoon and contribution by dominant piscivore species

Discussion

General

Three bird piscivores have been identified as contributing most to fish predation in the middle and upper floodplain wetlands of the Fitzroy River Delta: Australian pelicans, little black cormorants and pied cormorants. The peak in pied cormorant abundance in January to March 2005 at the Woolwash coincided with loss of bony bream (*Nematalosa erebi*) from this system (Marcus Sheaves unpublished data). Decline in water quality may also have been a contributing factor to fish stock decline during this period of low water levels and high temperatures, particularly within Woolwash lagoon which was at very low levels in 2005.

These findings are suggestive of these species as important regulators of fish biomass. Removal of fish stocks in the late draw-down period may be beneficial for fish stocks. As fish stocks concentrate during the late draw-down period, oxygen depletion can lead to extensive fish-kills and loss of all fish stocks, as documented by Kushlan (1976).

Proximate drivers

Proximate drivers of bird piscivore predation within target wetlands are those that contribute directly to bird piscivore density within a wetland system, and several factors appear to be important in Fitzroy delta floodplain wetlands—hypersalinity, connection events to the river, inundation events and draw-down. These will be examined separately for both middle and upper wetland sites.

Hypersalinity was an important factor at one of the middle floodplain sites—German Jack's lagoon—and an increase in salinity from 118 ppt in September 2004 to >160 ppt in October 2004 resulted in loss of all piscivores from the system, most likely as a consequence of fish mortality. Situations favouring hypersalinity appear to develop where there are evaporative losses during a draw-down period combined with tidal intrusion, but may also be linked with relict salinity levels within soils that are estuarine in origin such as occur on estuarine margins along the lower Fitzroy River (Wright 1968).

Connection to the estuary appears to allow recruitment of fish populations and corresponded to peaks in bird piscivore numbers within both of the middle floodplain sites—Twelve Mile Creek (December 2004) and German Jack's (January 2005). The same pattern was also found in Florida saltmarsh wetlands (Stevens & Montague 2005).

Inundation by surface run-off associated with wet season rains may also have contributed to these peaks in production. However, the overlap of connection events and inundation by surface run-off events within these middle floodplain sites made it impossible to differentiate between the potential effects of these factors within wetlands in this part of the floodplain.

The effect of draw-down within middle sites appears to be important at German Jack's lagoon which is embedded in a estuarine plain of very low relief and it is likely that even at its greatest depth this site is <2 m deep. This was reflected in the relatively greater importance of the shallow-water-dependent wader guild at this site. The situation at Twelve Mile Creek was much more complex with a main brackish pool that remained >3 m deep at all times but with seasonally extensive shallow waters <1 m deep downstream of this main brackish pool. Bird piscivore populations were very low in the deep main brackish pool matching patterns found in lower floodplain sites such as Gonong and Munduran Creeks.

The brackish pool at Twelve Mile Creek differs from other wetlands in the region in that water levels in this pool are more stable. This probably reflects the coincidence of inputs of water from both inundation events and river connection events during the wet season, increasing the reliability of inflow events to this wetland compared with other wetlands depending mainly on one source of surface water. The relative deepness of the brackish pool and its steep sides also contribute by giving it a large volume to shallow edge ratio that reduces evaporative processes.

For upper floodplain wetlands, connection to the river is much rarer and other factors assume greater importance such as draw-down effects making certain groups of fish available to bird piscivores at species-dependent depths. Such was the case for wader piscivores in Florida, where wader densities increased when water depths fell below 0.7 m (Kushlan 1976). In the current study, peaks in little black cormorant and Australian pelican abundance coincided with draw-down in water levels at both the Woolwash and Frogmore lagoons to about 3 m and 2 m respectively. It is suspected that below this depth pelicans are able to access fish populations previously unavailable to them due to the availability of deeper waters providing fish refugia.

Although a small increase in bird piscivores was observed at Frogmore lagoon following the first substantial rains of the year in October 2004, the importance of inundation by surface run-off to promoting bird piscivore abundance was not possible to gauge because substantial inundation events did not occur at the upper floodplain sites during the survey period. If inundation was important it

would presumably be a result of an increase in nutrients and an upsurge in food-chain components supporting fish abundance and reproduction.

In summary, the most important proximate drivers of bird piscivore abundance in Fitzroy delta floodplain wetlands were:

- For middle floodplain sites: hypersalinity, connection to the river (plus possibly inundation by surface flows linked with rainfall) and drawdown events
- For upper floodplain sites: drawdown events and possibly inundation by surface flows linked with rainfall.

These factors interact with wetland depth and bathymetry to determine depth distribution, refugia for fish and accessibility of fish populations to various piscivore species depending on guild or feeding mode.

Indirect drivers

Indirect drivers of bird piscivore predation within target wetlands are those that contribute to the maintenance of a reservoir of piscivores in the region including:

- The extensive floodplain system with a large area of wetlands
- Variable hydroperiod and bathymetry of these wetlands as a consequence of landscape complexity and derivation of wetland types. The variable bathymetry within each wetland means there is always a wetland somewhere in the region of suitable depth for a range of bird piscivore guilds.

Together these factors help retain high numbers of piscivores in the region. As an example, while numbers of little black cormorants were low in several months compared to peaks of 400+ in two months, they were most likely retained within the region and counts of 100+ were observed at freshwater wetlands elsewhere in the lower Fitzroy River floodplain (Robert Black pers. comm.).

Conceptual models

Conceptual models are presented for middle floodplain sites (Figure 12.47) and upper floodplain sites (Figure 12.48).

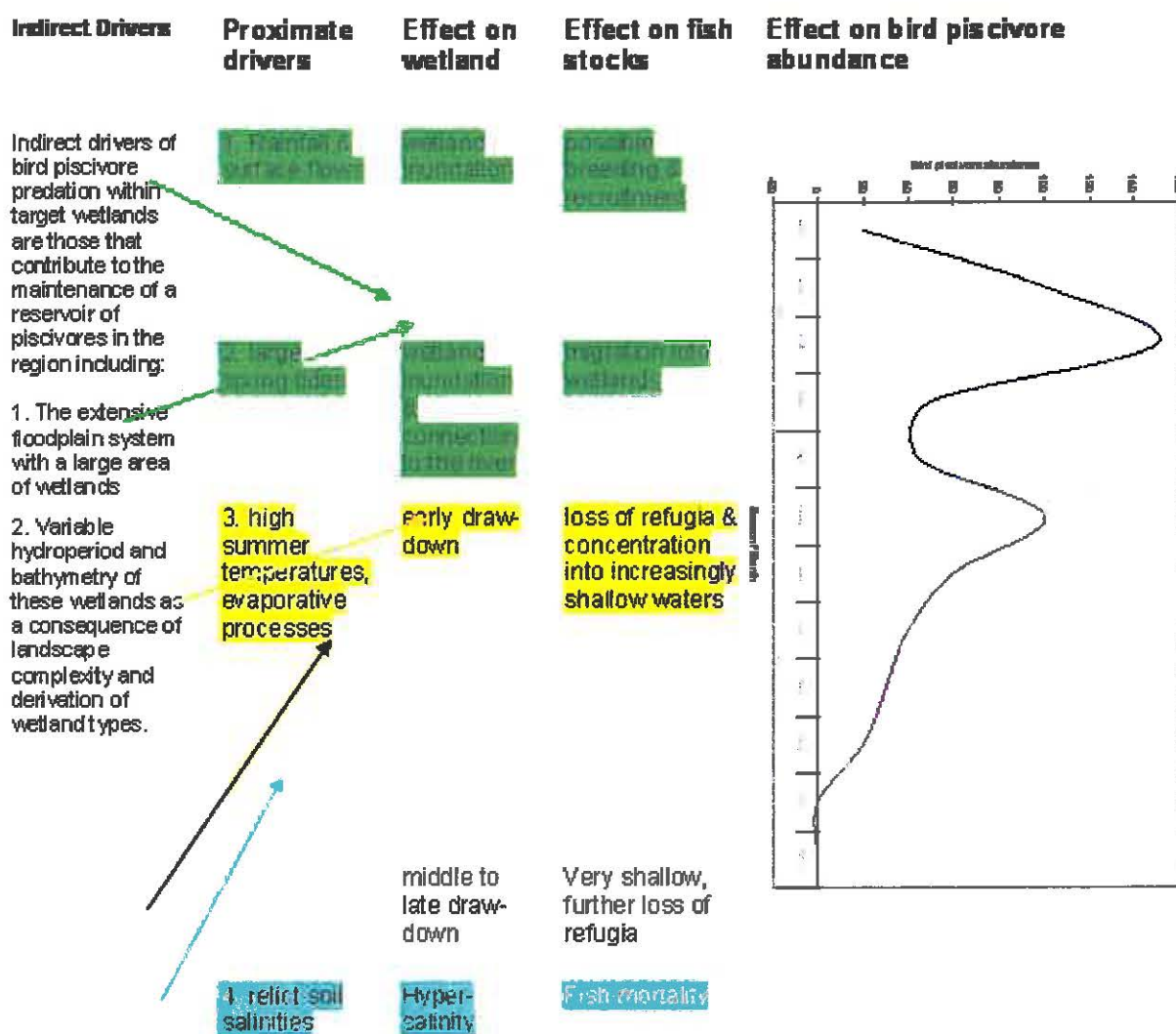


Figure 12.47. Conceptual model of drivers of fish predation by waterbird piscivores in middle floodplain sites of Fitzroy wetland pools

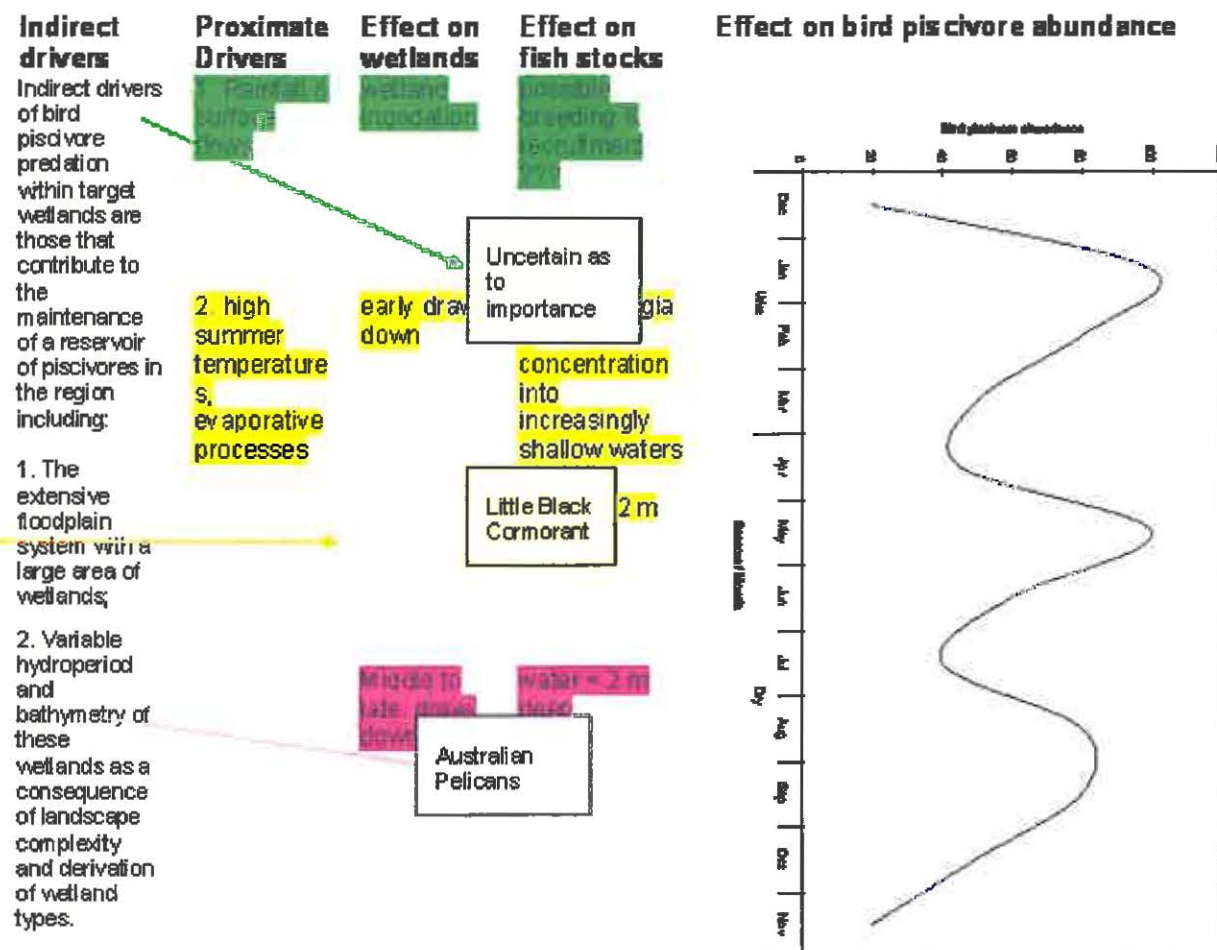


Figure 12.48. Conceptual model of drivers of fish predation by waterbird piscivores in upper floodplain sites of Fitzroy wetland pools

Chapter 13 General discussion

Marcus Sheaves

Important features of the Fitzroy wetland pools

The Fitzroy estuarine floodplain wetland pools have extensive aesthetic, cultural and recreational values to the people of the region. They also provide a variety of crucial ecological functions, ranging from the role as crucial links in the life cycles of animals using them as nursery grounds, to providing fertile feeding grounds for a variety of birds, including critically endangered species. The full spectrum of ecological processes operate in the pools at a variety of levels, and while in many cases these processes are typical of other systems and operate in similar ways, some processes are particular characteristics of wetland pool ecosystems that possess a variety of novel features not previously detailed.

Connectivity

Perhaps the most important and pervasive of these processes is connectivity—both the biological connectivity that connects the pools in the life-cycles of animals and the physical connectivity within which biological connectivity is set.

Physical connectivity is governed by rainfall and flooding regimes, the length and nature of the connecting channels, whether the pools have direct connections to the marine environment, and tidal anomalies that modify potential tidal connections. The degree of pool isolation interacts with their salinity regime to produce a diverse variety of environments for aquatic fauna (Figure 13.1). The particular nature of each pool determines the extent to which, and length of time the pool provides a useful habitat to its various inhabitants.

This in turn determines the extent to which the pools are valuable as nursery grounds. While the nursery ground role of wetland pools is now widely accepted by the public, this study underlines that nursery-ground provision is not an unchanging feature but is determined by the interplay of geomorphology and climate. Consequently, the central role of climate in regulating connectivity ensures that the nursery-ground value of wetland pools will be one of the ecological processes most directly impacted by the rapid advance of global climate change (Lough 2001).

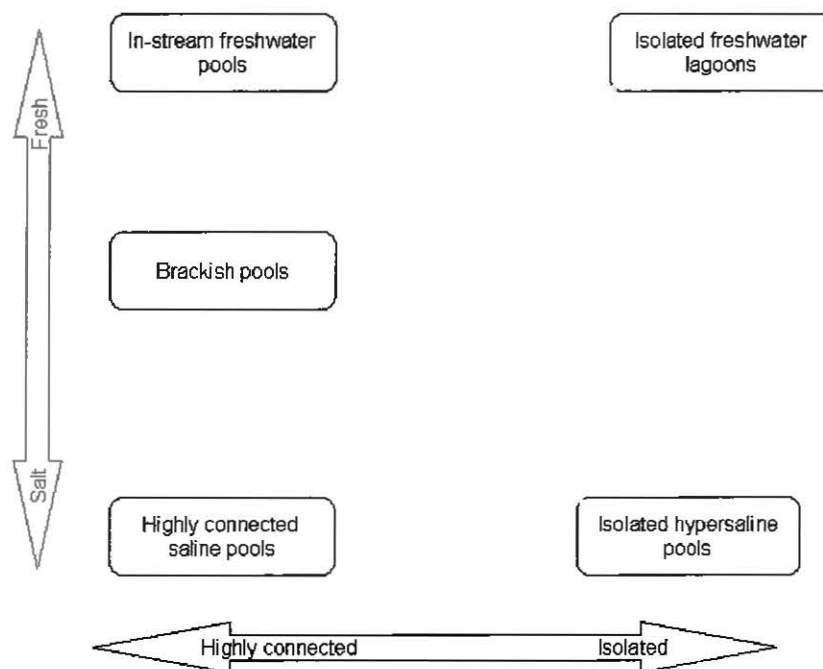


Figure 13.1. The interaction of connectivity and salinity regime in determining the nature of wetland pools

Beyond its role in nursery-ground function, connectivity is a conduit through which the productivity of wetland pools is exported to other ecosystems. Although yet to be demonstrated for Fitzroy wetland pools, the physical transport of nutrients from wetlands around the world donates considerable quantities of nutrients to other habitats, often providing a major component of their total nutrient budget. Over and above this, the migration of juveniles away from their wetland nurseries can export a substantial proportion of the nutrients generated in the wetlands (Deegan 1993). The importance of this biologically mediated export is increased by the efficient transport of nutrients through the short food chains that dominate the pools' trophic structures.

While fish rely on aquatic connections to facilitate their movements between pools and to and from the estuary, fish-eating waterbirds do not suffer this restriction. Waterbirds are able to fly between pools, producing biological connectivity independent of other physical connections. This action of birds connecting pools across the whole floodplain has far-reaching consequences for both the birds and the fish they feed on.

Predatory birds are particularly effective at feeding on fish when water depths become very shallow (around 1.5 m or less). Being able to fly between pools that

reach these shallow depths at different times means the birds are regularly able to find abundant supplies of fish that are easy to catch. In this way, as a connected unit, the wetland pools support large populations of waterbirds.

At the same time, the movement of birds to feed in pools at times when the fish become vulnerable has a considerable impact on patterns of mortality of fish in the pools. Small, open-water fish (like bony bream), that are the dominant species when pools are full, are more susceptible to attack by birds than larger, bottom-feeding fish (such as catfish). So when pools become shallow, preferential feeding on the smaller species can lead to profound changes in the fish community (i.e. change in dominance by detritus feeders [bony bream] to dominance by omnivores [catfish]). This results in a major change in pool foodweb structure, which represents ecosystem collapse. These changes in function cannot be redressed until the pools are reconnected to another pool from which the detritivore population can be replenished.

Trophic functions

The broad spectrum of pool environments provides the opportunity for a diversity of trophic function. Despite this the wetland pools have two striking features in common: a dominance of biomass by phyto-detritus-feeding fish, and the pervasive importance of wetland plants as the major contributors of primary productivity.

The dominance of phyto-detritivorous fish is particularly important for two reasons. Firstly, in systems where invertebrates are the major consumers of primary production, food chains tend to be long. The majority of invertebrate primary consumers are small and fed on by primary carnivores, which are in turn consumed by secondary consumers, perhaps leading to tertiary consumers—producing food webs with often as many as four trophic steps. In contrast, the phyto-detritivorous fish in the pools are mainly moderate-to-large individuals that are primarily consumed by apex predators. This results in short food chains (often with only two transfers) that lead to efficient transport of the energy produced in the pools to the top of the food web.

Secondly, phyto-detritivores can exist on organic matter from a variety of sources making pool food webs rather insensitive to changes in the type of organic matter available, thus conferring a high degree of resilience on the systems. This is likely to be an important factor given the likelihood of substantial changes wrought by ecosystem change and other human impacts.

The diets of both phyto-detritivorous fish and invertebrates in this study were based on algae, water plants, and littoral plants found around the pools. While this means that pool food webs are likely to be fairly independent of changes away from the immediate vicinity of the pools, it also means direct impact on water or wetland plants around the pools may have severe consequences.

Conclusions and implications

Fitzroy estuarine floodplain wetland pools provide a diversity of special and often unique habitats, with each class of pool harbouring a particular fauna reflecting its salinity and connectivity regimes. Pools vary in the duration that they provide hospitable habitats for fauna, and when isolated for too long develop adverse conditions and eventually dry out. Different classes of wetland pools are functionally different and each provides different outcomes for its fauna. Together these factors mean that different pool types are not ecologically interchangeable: the loss of any one pool is likely to be much more important than suggested by the fraction of the total number of pools or the total pool area it represents.

Wetland pool habitats are fragile; their unique characters are determined by small differences in height relative to tidal levels and by specific climatic patterns. But small changes in tidal levels or climate are likely to significantly change the nature of the pools and their quality as habitats. More extreme weather patterns will lead to more infrequent and unpredictable connectivities, resulting in a greater number and variety of pools moving to the point of ecosystem collapse. Consequently, global warming–induced climate change and sea-level rise are likely to profoundly influence the total area of pools available, the natures of individual pools and their quality as habitats. These changes will not just compromise species directly utilising the pools but will flow on to affect coastal and offshore ecosystems that are linked to the wetlands by the movement of organisms, nutrients and productivity.

There are many possible impacts of global climate change on wetland pools and the connectivity their biota depend on. One likely impact is alteration of the distribution of organisms, with communities moving to new areas as climatic conditions shift. To take one example, sea-level rise will increase the extent of marine connectivity by making connections deeper and more frequent, and eventually making marine connections to freshwater pools that currently have no direct connection to the marine environment. Consequently, brackish pools will become more saline; the likelihood of saltwater intruding into in-stream

freshwater streams will increase converting the more low-lying into brackish pools; isolated hypersaline pools will be more likely to resist drying out due to more regular connection; and isolated freshwater lagoons may be converted into saline or hypersaline lagoons if saltwater intrudes (Figure 13.2). Changes in rainfall patterns may either enhance or alleviate this effect depending on the details of the rainfall changes.

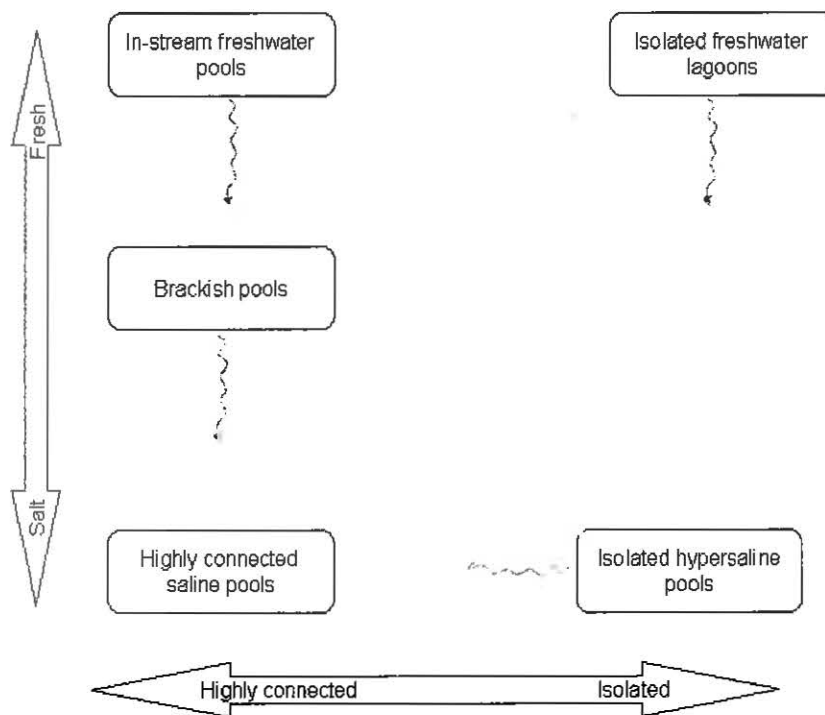


Figure 13.2. The interaction of connectivity and salinity regime in determining the nature of wetland pools: probable changes due to sea-level rise (zigzag lines)

These changes in pool character will obviously impact substantially on the fauna of particular pools, and therefore have far-reaching local impacts. Whether or not such changes in pool characteristics are important in a broader context will largely depend on the outcomes of these changes on the total area or number of the various pool types in a region.

Whatever happens, the greatest impacts of climate change are most likely to result in the interaction between change and human attempts to mitigate change. For instance, the most likely short-term local response to sea-level rise is to build levee banks and weirs to prevent the intrusion of sea water. The reduction in effective connectivity that results is likely to have much more pervasive and far-reaching impacts on pool communities than the sea-level induced changes

themselves. Thus the challenge for management is not to prevent climate change but to manage responses to climate change in a way that minimises the impacts of mitigation on ecosystems.

The complexities of biological connectivity need to be factored in to our understanding if we are to successfully manage the effects of future climate and sea-level changes. Careful management of habitat loss and rehabilitation of degraded pools is crucial to prevent further loss of ecological function in the face of climate change and adverse human intervention. Additionally, while clear shifts to different sources of organic carbon at different pools shows that the detritus-based food webs of the Fitzroy wetland pools are adaptable, labile and resilient to many changes in vegetation type, situations where pools become surrounded by monoculture of poor nutritional value should be avoided.

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