Fish diet composition in floodplain lagoons of an Australian dryland river in relation to an extended dry period following flooding

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Abstract

Floodplain rivers worldwide are threatened by loss of connectivity to their floodplains and hence reduced benefits from floodplain energy subsidies. Dryland rivers with ‘boom and bust’ ecological responses to flooding and extended dry periods may be particularly vulnerable. This paper describes variations in dietary composition of three fish species of contrasting trophic position in dryland floodplain lagoons with variable flood inundation and drying histories. The study species were *Ambassis agassizii* - a microphagic carnivore, *Leiopotherapon unicolor* - a carnivore/omnivore, and *Nematalosa erebi* - an algivore/detritivor. Despite the range of food items recorded in fish guts, each species fed mostly on relatively few food categories and few food items within each category. Most of the spatial (i.e. among lagoons) and temporal dietary variation was associated with different proportional contributions of these food items. Given the absence or low magnitude of flooding during the study period, temporal changes in diets of the three species are probably the result of successional changes in composition of invertebrate prey as the dry season progressed. The focus of each fish species on relatively few food categories and a few reliable food items within each category may be the most profitable foraging strategy when food resources are limiting in progressively drying floodplain lagoons.

Additional keywords: Fish trophic position, dietary variability, invertebrate prey, foraging strategy

Introduction

The ecology of fish in floodplain river systems is of particular interest given that many rivers are losing their connections to the surrounding floodplain and hence may experience reduced benefits from floodplain energy subsidies (Welcomme et al. 2006; Tockner et al. 2008; 2010). In undisturbed floodplain rivers, fish that feed and grow on the floodplain may provide food for higher order consumers (e.g. waterbirds) using inundated floodplain areas (Balcombe et al. 2005; Kingsford et al. 2006), or their energy reserves may subsidize fish returning to river channels after floods recede (Winemiller 1996; Burford et al. 2008). In many floodplain landscapes, isolated waterbodies (lakes, lagoons, waterholes) left on the floodplain support fish throughout seasonal or extended dry periods (Rodriguez and Lewis 1997; Arthington et al. 2005). These remnant populations can provide important sources of individuals for recolonization of the river network when floods open up connectivity pathways and opportunities for movement (Welcomme 1985; Morton et al. 1995; Saint-Paul et al. 2000). In these contexts, it is of interest to understand how fish sustain themselves in drying waterbodies on the floodplain, especially in dryland rivers that typically experience extended dry periods between occasional large floods.

Dryland rivers can be characterized as ‘boom and bust’ ecological systems offering diverse but highly variable channel and floodplain habitats, food resources and opportunities for foraging (Bunn et al. 2003; 2006; Kingsford et al. 2006; Arthington and Balcombe 2011). Fish consumers in dryland floodplain rivers can use a range of trophic resources for nutrition (Balcombe et al. 2005; Medeiros and Arthington 2008a; Sternberg et al. 2008). These resources may be autochthonous, derived from within-waterhole primary production, or allochthonous, derived from terrestrial inputs (Bunn et al. 2003; Medeiros and Arthington 2011a). For species that do not feed directly on primary production (phytoplankton, aquatic plants, riparian leaves and flowers), zooplankton and invertebrates may be important energy resources for small species and the smaller size classes of large species that, in turn, provide energy to piscivorous fish and other consumers higher up the food web (Kingsford et al. 1999). In Australian floodplain

75 rivers, billabongs and floodplain lagoons (often termed ‘waterholes’) are regarded as
76 highly productive systems, supporting a large biomass and diverse array of
77 microorganisms and invertebrates (Bunn and Boon 1993; Butcher 1997; Hillman 1998)
78 that represent significant food resources for fish (Geddes and Puckridge 1989; Hillman
79 1995). It has been suggested that without intermittent connection to floodplains, dryland
80 river systems may not be sufficiently productive to support their local aquatic
81 communities (Sheldon et al. 2002; Jenkins and Boulton 2003).

82 During flooding, a rapid increase in production of food organisms, together with
83 wide dispersal of fish over inundated areas, favors intensive feeding (Balcombe et al.
84 2005; 2007). However, during long dry periods when the aquatic environment
85 progressively contracts, fish become concentrated in a few permanent waterbodies
86 disconnected from the main river, and food resources may become limiting. Pressure on
87 food resources is apparently greatest when water levels fall immediately after the wet
88 season and the number of fish species and individuals rises as they leave the receding
89 floodplain environment (Zaret and Rand 1971; Pusey et al. 1995; Burford et al. 2008).
90 Floodplain lagoons that do not experience flooding, and those that are flooded less
91 frequently than under natural conditions (e.g. due to flow regulation by dams), experience
92 increasing water drawdown over long dry periods (Hamilton et al. 2005; Medeiros and
93 Arthington 2011b). Under drying conditions, the aquatic habitats of floodplain lagoons
94 become increasingly distanced from any surrounding riparian vegetation and riparian
95 sources of food items. Fish confined to such lagoons must, therefore, depend largely on
96 autochthonous food resources.

97 This paper investigated the dietary composition and breadth of three species of
98 fish with contrasting feeding ecology and trophic position over an extended dry period in
99 an Australian dryland river. The species chosen were *Ambassis agassizii* Steindachner
100 1867, which has been described in the literature as a microphagic carnivore,
101 *Leiopotherapon unicolor* (Günther 1859), an omnivore, and *Nematalosa erebi* (Günther
102 1868), an algal/detritivorous species (Pusey et al. 2004). These species are relatively
103 common in coastal and inland drainages of Australia, being important consumers and also
104 sources of food for other species of fish and waterbirds (Pusey et al. 2004).

Our focus was patterns of variation in fish diet composition across floodplain lagoons with different connectivity to the parent river, and hence contrasting flood inundation patterns and drying histories. We also sought to understand the contribution of important food items to different size classes of fish, since it is a common observation that fish dietary composition and diversity change with ontogeny (Werner and Gilliam 1984; Winemiller 1989; Pusey et al. 2000). Since each lagoon presented a different pattern of flooding and subsequent drying, some being flooded and others not during our 2002-2003 study period (Medeiros and Arthington 2011b), seasonal and spatial variability were expected to influence the availability of various food items and hence fish diet composition. Accordingly, we tested two hypotheses: (1) fish consumers from each lagoon would segregate to a specific dietary composition depending on flooding and drying history, and (2) dietary composition would change as the dry season progressed.

Materials and Methods

Study area

This study was performed on the floodplain of the Macintyre River, a dryland river in the Border Rivers catchment, upper Murray-Darling Basin, Australia (Figure 1). The study area is characterized by a number of streams that diverge from the Macintyre River in the vicinity of the towns of Boggabilla and Goondiwindi where the river passes through a relatively well-defined floodplain containing numerous intermittently flooded and semi-permanent lagoons on dry river channels.

The study period spanned two years (from November 2001 to July 2003) and was characterized by relatively low flows in the main channel of the Macintyre River (Medeiros and Arthington 2011b). Discharges in the Macintyre River averaged 813.1 ± 1280.2 megaliters per day (ML/day) during the period 2001-2003 compared with an average of 3233.2 ± 12293.25 ML/day between 1995 and 2000 (data from the Boggabilla gauging station - 416002). Major to moderate summer floods occurred early and late in 2001 (the last flood inundating all study sites), whereas only minor to moderate floods were recorded in 2002 and 2003 (the study period), with peak discharges of 14487

ML/day on 31 March 2002 and 17412 ML/day on 26 February 2003 (Figure 2). Even though such floods may cause inundation of low lying areas adjacent to the main river channel, they were not sufficient to inundate all study sites (Medeiros and Arthington 2011b). Only two of the lagoons were flooded during the study period (South Callandoon East and Rainbow lagoons) and two dried up completely (South Callandoon West and Broomfield lagoons). The remaining sites (Maynes, Punbougul and Serpentine lagoons) decreased in water level and volume continuously throughout the study period but did not dry up completely (Table 1). Hence dietary comparisons across the study sites were expected to reflect progressive changes since each lagoon was last inundated (November 2001).

Study design and analyses

Seven lagoons and one site in the river channel were sampled between late 2002 and 2003 (Table 1, Figure 1). Fish sampling was performed at all sites in October 2002 (i.e. prior to February 2003 flooding of South Callandoon East, Rainbow lagoons and the Macintyre River site) and in March and July of 2003 following flooding of these sites. South Callandoon West and Broomfield lagoons were not flooded and dried out before these collections. Therefore, pre- and post-flooding comparisons of fish diets were only possible on flooded sites (South Callandoon East and Rainbow lagoons). The Macintyre River site was flooded but yielded too few species and individuals for dietary analysis. Three additional collections were performed in February, May and August 2002 at Rainbow and the South Callandoon sites to evaluate variations in diet composition over time elapsed since the flooding of November 2001.

Each lagoon was sampled along its margins using a seine net (25 m length x 2 m height, 1 cm mesh) from approximately 11:00 am to 2:00 pm (see Medeiros and Arthington 2008a). All individuals of the target species were euthanized in the field, upon collection, in an ice slurry (Blessing et al. 2010) and preserved whole in 4% buffered formalin. Later in the laboratory, fish were transferred to 70% ethanol and the necessary measurements and gut content analyses were performed. The proportional contribution of each category of food item to the diet of individual fish was estimated using Hyslop's

(1980) indirect volumetric method, where stomach items within each prey category are lumped together and squashed to a uniform depth of 1 mm and the area covered taken to represent the volumetric contribution of that food category to the total stomach contents in mm³ (cf. Arthington 1992; Pusey et al. 2000). Volumetric methods are preferable, since they take into account the size of the food item rather than just its occurrence, which may overestimate the contribution of smaller prey. For *Nematalosa erebi* both foregut and gizzard were considered in the estimation of stomach fullness and diet composition. Prey items were identified to the lowest possible level of taxonomic resolution and grouped into major categories.

The proportional volumetric dietary data for single individuals of each species from each sampling occasion were allocated into groups of 5 to 15 individuals based on the range of body sizes available (TL) and the number of individuals collected in each size class; the mean diet composition was calculated for each of these groups (Schafer et al. 2002). These data were also used to calculate the mean Shannon-Wiener diversity index of prey in the stomachs of each species, this index corresponding to dietary breadth (B) (Pusey et al. 1995; Marshall and Elliott 1997; Pusey et al. 2000). Unidentified material was excluded from the analysis since inclusion has the potential to bias diet composition results. For all statistical analysis, only stomachs with fullness equal to or greater than 20% were considered to prevent bias in the calculation of the proportional contribution of prey (Pusey et al. 1995).

Overall similarities in dietary composition within and between sampling occasions for each species were analyzed using Non-Metric Multidimensional Scaling (NMS) (McCune and Mefford 1999) based on the Relative Sorensen (Kulczynski) distance. Data was arcsine square root transformed (McCune and Grace 2002). The Multi-Response Permutation Procedure (MRPP) (Biondini et al. 1985; McCune and Mefford 1999) was used to test for differences in diet composition among sampling occasions. Where MRPP detected significant differences in composition of food items between sample groups, further analysis was performed to reveal which particular food items contributed significantly as the source of differences in diet composition using Indicator Species Analysis (ISA) (McCune and Mefford 1999). Statistical analyses were performed on PC-ORD version 4.20.

Results

Ambassis agassizii presented a generally lower dietary breadth per site ($B=0.4734-0.9877$) whereas *N. erebi* had a slightly wider and more variable dietary breadth ($B=0.2234-0.9860$) and *L. unicolor* presented the greatest range in food items consumed ($B=1.2605-1.8267$) (Table 2, Figures 3 to 5). Detritus, microcrustaceans and aquatic insects were the main food items consumed, making significant contributions to the diets of all species. Contributions of detritus were much greater for *N. erebi*, which also consumed small amounts of microcrustaceans, algae and vegetable matter. Microcrustaceans were the main food category in the diet of *A. agassizii*, mostly calanoids and moinid cladocerans. Even though *Leiopotherapon unicolor* also showed a relatively high consumption of microcrustaceans (moinid and daphniid cladocerans) this species fed mostly on aquatic insects (Corixidae, Notonectidae and larvae of Chironomidae). Shrimps and fish also contributed to the diet of *Leiopotherapon unicolor* (Table 2).

Ambassis agassizii diets

Diets of *Ambassis agassizii* showed considerable temporal variation and clear differentiation across lagoons (Figure 3). The Multi-Response Permutation Procedure showed significant differences in diets among sampling occasions (MRPP, $A=0.72$, $p<0.0001$) and across lagoons (MRPP, $A=0.37$, $p<0.0001$), except for the May 2002 and March 2003 samples from Rainbow Lagoon (MRPP, $A=0.08$, $p=0.0945$).

Indicator Species Analysis (ISA) showed that of the 11 identifiable food items consumed by *Ambassis agassizii* (see Table 2) Moinidae (IV=96.6%), Daphniidae (IV=76.6%), Calanoida (IV=58.9%) and, to a lesser degree, detritus (IV=24.1%), were significant contributors to the spatio-temporal patterns found ($p<0.03$) (Figure 3). Calanoids were consistently consumed by *A. agassizii* at Rainbow Lagoon, whereas both Callandoon lagoons presented relatively lower contributions of this copepod and increased consumption of Cladocera - Moinidae and Daphniidae. As a result of the high

dominance of calanoids in the diets of *A. agassizii* at Rainbow Lagoon, this site presented the narrowest diet breadth ($B=0.4734$), whereas South Callandoon West showed a higher breadth in dietary items consumed by *A. agassizii* ($B=0.9877$), mostly due to the lower dominance of a single food item in the diet of this species and the consumption of Cladocera and chironomid pupae. Samples from South Callandoon East also showed a relatively low average dietary breadth for *A. agassizii*. Differences in food items ingested between early and late post-flood diet samples were significant (MRPP, $A=0.06$, $p=0.0150$) and on average, *A. agassizii* presented a lower dietary breadth ($B=0.4231 \pm 0.20$) during early post-flood than during dry periods later after flooding ($B=0.8441 \pm 0.40$), such as August and October 2002. Fish diet breadth at South Callandoon West in May 2002 was an exception to this trend.

Leiopotherapon unicolor diets

Temporal differences in dietary composition of *Leiopotherapon unicolor* were significant (MRPP, $A=0.27$, $p<0.0001$) and dietary differences in fish from the two South Callandoon lagoons and Rainbow Lagoon were also significant (MRPP, $A=0.48$, $p<0.0001$) (Figure 4). These patterns were associated with fish size variations. For example, the seasonal differences in fish diets from South Callandoon West are likely to result from smaller fish caught in February 2002 (see Table 1). On the other hand, diets were temporally segregated across sites other than the South Callandoon lagoons, such as between Serpentine and Rainbow lagoons. Overall the results indicate a spatial/temporal pattern of dietary differentiation (Figure 4).

Indicator Species Analysis revealed that, of the 22 food items ingested by *Leiopotherapon unicolor*, Corixidae (IV=67.9%), shrimp (IV=53.8%), Notonectidae (IV=49.4%) and fish (IV=30.8%) were significant contributors to the spatial-temporal patterns across Serpentine, Rainbow and Broomfield lagoons ($p<0.03$). Chironomidae (Pupae IV=72.5% and larvae IV=68.5%), Cyclopoida (IV=97.6%), Daphniidae (IV=100%), Chydoridae (IV=62.6%), Ecnomidae (IV=62.4%), Conchostraca (IV=56.2%), Coenagrionidae (IV=60.6%), Leptophlebiidae (IV=46.1%) and Calanoida (IV=66%) were significant indicators of fish diet composition in May and July samples

($p \leq 0.02$). Detritus (IV=73%), Moinidae (IV=72.3%) and Ostracods (IV=69.7%) were significant indicators for the February dietary samples from South Callandoon West ($p=0.001$), whereas shrimp (IV=100%) and Notonectidae (IV=56.5%) were significant indicators for diets of fish from Rainbow Lagoon ($p<0.015$).

In both South Callandoon lagoons, *L. unicolor* showed greater consumption of zooplankton and smaller aquatic insects, such as Chironomidae and Coenagrionidae. Temporal segregation in zooplankton consumption was observed with differences in proportional contributions of Moinidae and Daphniidae (Figure 4). Rainbow, Serpentine and Broomfield samples showed little contribution by microcrustaceans to the diet of *L. unicolor*, whereas larger aquatic insects (Corixidae and Notonectidae), shrimps and fish were the most important food items in these sites. The range of food items ingested by *L. unicolor* from both South Callandoon lagoons was relatively wide, including microcrustaceans and a variety of aquatic insects ($B = 2.0477 \pm 0.29$). The diets of this species were more specialized in Rainbow, Serpentine and Broomfield lagoons, with lower diet breadth ($B = 1.2471 \pm 0.29$) (Figure 4).

Nematalosa erebi diets

Dietary analysis performed on smaller individuals of *N. erebi* (total length from 40-69 mm) shows segregation across sites and some variation in diet composition among sampling occasions (Figure 5). Differences were significant between the four sampling sites where small individuals occurred ($A=0.29$, $p=0.0002$) and between sampling occasions ($A=0.64$, $p<0.0001$) with more than one sample point. Pairwise comparisons for each site revealed that the dietary composition of *N. erebi* was significantly different across sampling occasions for Rainbow Lagoon ($A=0.58$, $p=0.0074$) and South Callandoon Lagoon East ($A=0.42$, $p=0.0221$). Temporal differences (October 2002-March 2003) for Maynes Lagoon were not significant ($A=0.17$, $p=0.0546$), whereas, despite the fact that both temporal samples from Punbougul Lagoon were closer together in the ordination plot (Figure 5), MRPP revealed that these differences were significant ($A=0.24$, $p=0.0265$). This result is a consequence of different proportional contributions

of vegetable matter to the diet of *N. erebi* at this site and the very low number of food items ingested (Figure 5).

Indicator Species Analysis revealed that only two sites were distinguished by significant indicator food items. Cyclopoida (IV =42.9%), Rotifera (IV=42.9%), Daphniidae (IV=42.9%) and Bosminidae (IV=42.9%) ($p<0.045$ in each case) were significant indicator food items for *N. erebi* diets in South Callandoon Lagoon East, whereas the indicator food items for Punbougall Lagoon were detritus (IV=44.3%) and vegetable matter (IV=59.7%) ($p<0.003$ in each case). ISA for each sampling occasion resulted in generally low or non-significant ($p>0.05$) IVs for the main food items consumed by smaller individuals of *N. erebi* (Moinidae IV=31.6%, $p=0.011$, Calanoida IV=26.5%, $p=0.011$ and detritus IV=20.4%, $p=0.1$), due to the fact that these items were consumed in relatively large quantities on most sampling occasions.

Even though microcrustaceans were preferred by smaller individuals of *N. erebi*, contributions of detritus to the diet of this size group were still large on most sampling occasions, reaching up to 99.4% by volume. Even so, microcrustaceans represented an important source of food, mostly in the form of Calanoida (up to 81.1%), Moinidae (up to 56.6%) and Daphniidae (up to 22.8%), with the remaining food items contributing less than 3.3% on any given occasion. As a consequence, dietary breadth was generally low, with lower average breadth for Rainbow ($B = 0.7760 \pm 0.42$) and Punbougall ($B = 0.2848 \pm 0.11$) lagoons, where detritus or calanoids dominated as food items. In South Callandoon and Maynes lagoons the average dietary breadth was wider ($B = 1.2896 \pm 0.13$ and $B = 1.0493 \pm 0.24$, respectively) due to a lower proportion of detritus associated with higher contributions from other food items, such as Moinidae and Calanoida. Temporal variation in dietary composition in Rainbow Lagoon was relatively high, with proportions of detritus and calanoids varying from 98.7 and 0% (respectively) in May 2002 to 18.9% of detritus and 81.1% of calanoids in July 2003.

Discussion

Dietary compositions of the three fish species generally conformed to those described in the literature (Merrick and Schmida 1984; McDowall 1996; Pusey et al.

2004; Medeiros and Arthington 2008a; Medeiros and Arthington 2008b). These results also corroborate the typical trophic positions of the study species, showing *A. agassizii* to be a microcarnivore and *L. unicolor* as a mostly insectivorous carnivore (Balcombe et al. 2005). Results presented show young and small *N. erebi* (total length between 40-69 mm) to be algivorous/detritivorous but tending towards microcarnivory, in accordance with other studies (Pusey et al. 2004; Balcombe et al. 2005). In Australian freshwaters, aquatic insects, microcrustaceans, algae and terrestrial material have been recognized as the most important food resources for fish (Pusey et al. 2004). Even though these food items were consumed by the three species studied here, the results presented indicate that microcrustaceans from the zooplankton were the most important food items consumed (Medeiros and Arthington 2008b), being part of the diet of all three species of fish collected from floodplain lagoons.

Diet breadth of the study species reflected their intrinsic morphological and behavioural characteristics. *Leiopotherapon unicolor* showed a generally higher range of food items consumed compared to the other species, based on microcrustaceans, aquatic insects, shrimp and fish, indicating opportunistic feeding habits and little morphological or behavioural specialisation to capture and process specific prey (Gehrke 1988). *Ambassis agassizii* presented a narrower breadth based mostly on microcrustaceans. This small microphagic species is limited in prey choice by constraints of body size, and consequently mouth gape and locomotory ability (Pusey et al. 2004). The presence of detrital matter, microcrustaceans and vegetable and algal material in the diet of *N. erebi* is reflected in a relatively higher and more spatially and temporally variable dietary breadth (in comparison with *A. agassizii*). The variety of body sizes of *N. erebi* individuals (Table 1) associated with ontogenetic morphological changes can explain the wide range of food items consumed by this species throughout the study. Pronounced size-related shifts in diet composition are a well-known feature of *N. erebi* dietary ecology (Bunn et al. 2003; Medeiros and Arthington 2008b, Figures 6 and 7). Variations in diet between juveniles and adults of *N. erebi* probably reflect increasing mouth size, and a change in mouth positioning, from dorso-terminal to terminal in fry and juveniles (related to planktivory), to ventro-terminal in adults (related to omnivory and detritivory), as well as enhanced foraging habitat (Atkins 1984).

Aquatic food webs, particularly those in floodplain rivers, can be significantly affected by spatial and temporal variability in patterns of waterbody connectivity, inundation levels and biotic processes. Thus fish assemblages and food webs in tropical rivers are characterized by high taxonomic diversity, diverse foraging modes, omnivory and an abundance of detritivores (Winemiller 1996; Jepsen and Winemiller 2002). However, in the present study, the dietary composition of the study species was generally narrow, based on relatively few food items within three major food categories (microcrustaceans, aquatic insects and detritus). On the whole, results suggest that during the study period, food resources available for fish in floodplain lagoons of the Macintyre River were relatively scarce since, despite the range of food items recorded in fish stomachs, individual species fed mostly on relatively few food categories and few food items within each category. Furthermore, most of the variation observed was associated with different proportional contributions of a few food items.

Tropical rivers have large spatial heterogeneity across a continuum of spatial scales that ranges from microhabitats to landscape scale (Winemiller and Jepsen 1998; Tockner et al. 2010). Habitats on the floodplain can be associated with very different hydrologies, soils, water quality and vegetation that ultimately affect the food resources available for fish (Wissmar et al. 1981; Day and Davies 1986). A similar variety of factors may have contributed to the observed variation in diet composition of fish in Macintyre floodplain lagoons. In the absence of large floods and significant floodplain inundation during the study period, local attributes of lagoons were likely to be increasingly important factors in determining fish food resources and dietary composition. Such attributes were the spatio-temporal variations in general physical conditions of floodplain lagoons (morphology, habitat characteristics and, possibly, influences of flow management in the Macintyre River) (Medeiros and Arthington 2011b).

It has been suggested that the connection and disconnection of floodplain waterbodies in dryland rivers can influence their invertebrate biota in a sequential fashion associated with fluctuations in hydrology and that, after disconnection each waterbody will behave as a separate unit with assemblage composition diverging in a manner that reflects those species present at the time of disconnection (Sheldon et al. 2003; Marshall

et al. 2006). Fish confined to isolated waterbodies might be expected to track these temporal patterns of divergence in the array of food items within each lagoon, depending on its flooding and drying history.

As expected, the diets of fish from each lagoon on the Macintyre floodplain tended to segregate into distinctive clusters and to vary in composition over time, according to the dominant food items consumed. These spatial-temporal patterns were most obvious for *A. agassizii* and *L. unicolor* which feed primarily on resources (i.e. zooplankton and other aquatic invertebrates) that are subject to seasonal and spatial changes (see Marchant 1982; Bass et al. 1997; Bishop et al. 2001). This seasonal segregation in dietary composition suggests that the composition of available prey items associated with flow history probably played an important role in the diet of *A. agassizii* and *L. unicolor* in the floodplain lagoons studied. Spatial and temporal variations in diets of *N. erebi* were not as clear as those observed for *A. agassizii* and *L. unicolor*, as larger *N. erebi* and, to a lesser extent, smaller individuals fed mostly on detritus material, a relatively abundant and widespread resource throughout most sites and sampling occasions.

Patterns of dietary composition present some interesting deviations from expectation in relation to flood history. For example, on average, *A. agassizii* presented a lower dietary breadth during early post-flood periods (i.e. May 2002 and March 2003) than during dry periods later after flooding, such as August and October 2002. This pattern goes against predictions that floodplain inundation would lead to higher diversity and abundance of prey available for fish (Junk et al. 1989). Furthermore, flooding of some of the study lagoons was not reflected in clear patterns of dietary change in comparison with sampling occasions prior to or long after flooding. Given the low magnitude or total absence of flooding events and, consequently, limited flood influences on lagoons during the study period, it is likely that the observed dietary variation was largely a consequence of successional changes in composition of the aquatic fauna as the dry season progressed (see Bishop et al. 2001; Sheldon et al. 2003; Balcombe et al. 2005).

On the whole, results suggest that during the study period, despite the range of food items recorded in fish stomachs, individual species fed mostly on relatively few

food categories and few food items within each category. Furthermore, most of the variation observed was associated with different proportional contributions of a few food items. The focus of each fish species on relatively few food categories and a few reliable food items within each category may be the most profitable foraging strategy when food resources are limiting in progressively drying floodplain lagoons.

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590 Tables

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Flooding	=	=	=	2000	2000	-
N	=	=	=	5	5	-
Mean TL (mm)	=	=	=	121(± 6.3)	137(± 14.8)	-
Mean fullness (%)	=	=	=	93(± 9.7)	82(± 8.4)	-
Broomfield (BFD)						
Flooding	Nov-01	=	=	-	d	d
N	8	=	=	-	d	d
Mean TL (mm)	64(± 5.1)	=	=	-	d	d
Mean fullness (%)	69(± 21.7)	=	=	-	d	d
<hr/> <i>N. erebi</i>						
Rainbow (RBW)						
Flooding	Nov-01	Nov-01	Nov-01	Nov-01	Feb-03	Feb-03
N	86	97	69	30	60	30
Mean TL (mm)	87(± 10.1)	72(± 5.8)	100(± 15.8)	92(± 7.6)	67(± 16.2)	66(± 6.7)
Mean fullness (%)	70(± 9.2)	64(± 3.0)	49(± 6.4)	83(± 8.7)	62(± 8.5)	55(± 1.6)
South Callandoon (SCE)						
Flooding	-	Nov-01	-	-	Feb-03	Feb-03
N	-	106	-	-	60	30
Mean TL (mm)	-	78(± 6.2)	-	-	73(± 13.2)	57(± 3.2)
Mean fullness (%)	-	60(± 3.9)	-	-	72(± 5.4)	49(± 1.2)
Maynes Lagoon						
Flooding	=	=	=	Nov-01	Nov-01	-
N	=	=	=	60	60	-
Mean TL (mm)	=	=	=	78(± 28.4)	82(± 22.7)	-
Mean fullness (%)	=	=	=	80(± 14.4)	68(± 7.6)	-
Punbougai (PBL)						
Flooding	=	=	=	Nov-01	Nov-01	-
N	=	=	=	90	60	-
Mean TL (mm)	=	=	=	88(± 27.2)	74(± 13.9)	-
Mean fullness (%)	=	=	=	67(± 11.1)	61(± 5.1)	-
Macintyre (RIV)						
Flooding	=	=	=	-	Feb-03	Feb-03
N	=	=	=	-	30	50
Mean TL (mm)	=	=	=	-	108(± 11.3)	99(± 10.8)
Mean fullness (%)	=	=	=	-	80(± 2.5)	79(± 3.7)
Serpentine (SPN)						
Flooding	=	=	=	-	2000	-
N	=	=	=	-	30	-
Mean TL (mm)	=	=	=	-	124(± 12.1)	-
Mean fullness (%)	=	=	=	-	70(± 3.5)	-

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Table 2 Contribution by volume (% Vol) and frequency of occurrence (% Freq) of different taxa and major dietary categories (in bold) to the diet of *A. agassizii*, *L. unicolor* and *N. erebi* collected from floodplain lagoons of the Macintyre River throughout the study. Dashes indicate zero values.

Major categories and dietary items	<i>A. agassizii</i>		<i>L. unicolor</i>		<i>N. erebi</i>	
	% Vol	% Freq	% Vol	% Freq	% Vol	% Freq
Detritus	0.28	1.93	1.98	14.05	93.73	85.86
Algae	-	-	-	-	0.36	31.22
<i>Volvox</i> colony	-	-	-	-	0.23	25.27
Filamentous algae	-	-	-	-	0.02	4.43
Algae matter	-	-	-	-	0.11	5.38
Vegetable matter	-	-	0.23	11.89	0.86	47.07
Microcrustaceans	97.77	99.42	24.60	80.27	4.93	35.23
Calanoida (Copepoda)	65.19	77.26	3.45	36.22	1.34	22.57
Cyclopoida (Copepoda)	0.55	7.90	0.26	15.41	0.04	2.64
Moinidae (Cladocera)	25.46	67.24	13.56	34.05	3.38	22.78
Daphniidae (Cladocera)	6.44	25.82	5.81	38.65	0.09	2.64
Bosminidae (Cladocera)	0.01	0.19	-	-	0.01	1.05
Chydoridae (Cladocera)	0.06	0.96	0.28	13.24	0.001	0.11
Sididae (Cladocera)	0.07	0.58	-	-	-	-
Ostracoda	-	-	0.97	14.05	0.06	6.43
Conchostraca	-	-	0.27	9.19	-	-
Aquatic insects	0.85	3.08	49.03	80.54	0.001	0.32
Leptophlebiidae (Ephemeroptera)	-	-	0.47	4.59	-	-
Coenagrionidae (Odonata)	-	-	4.00	7.57	-	-
Zigoptera (Odonata)	0.04	0.39	-	-	-	-
Notonectidae (Hemiptera)	-	-	15.78	6.22	-	-
Corixidae (Hemiptera)	-	-	17.73	26.76	-	-
Chironomidae (Larvae)	0.16	1.35	7.08	51.89	0.001	0.32
Chironomidae (Pupae)	0.66	1.35	3.13	25.95	-	-
Ecnomidae (Trichoptera)	-	-	0.76	8.38	-	-

Leptoceridae	-	-	0.07	0.81	-	-
(Trichoptera)						
Hydroptilidae	-	-	0.01	0.54	-	-
(Trichoptera)						
Molluscs	-	-	0.02	0.54	-	-
Planorbidae	-	-	0.02	0.54	-	-
Other invertebrates	-	-	15.94	6.76	0.002	1.58
Rotifera					0.001	0.95
Nematoda	-	-	0.001	0.27	0.001	0.63
Shrimp (<i>Macrobrachium</i>	-	-	15.94	6.49	-	-
spp)						
Fish	-	-	2.59	1.35	-	-
Unidentified	1.10	7.32	5.62	53.24	0.12	4.64
Insect fragment	-	-	0.54	9.19	0.02	2.64
Digested zooplankton	0.30	1.73	0.02	0.27	0.03	0.11
Digested matter	0.80	5.78	3.70	44.05	0.06	1.79
Unidentifiable matter	-	-	1.36	10.81	0.01	0.11
Total number of stomachs	519		370		948	

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Figures

Figure 1 Location of the study sites in the floodplain of the Macintyre River and the Border Rivers catchment within the Murray-Darling River system, Australia

Figure 2 Daily discharge (ML/day) and dates of peak discharge in the Macintyre River (recorded at the Boggabilla gauging station - 416002) between 2001 and 2003. Arrows indicate sampling occasions

Figure 3 Two-dimensional NMS ordination for averaged sequential sizes of *A. agassizii* and percentage contribution by volume of food items to the diet of *A. agassizii* in floodplain lagoons of the Macintyre River during the study period (2002-2003). Food items with low volumetric contribution, thus not identifiable in the bars, are not shown. (■) indicates the mean dietary breadth ($\pm$ SE); arrows indicate flooding up to two months before a sampling occasion; S indicates size class, TL in mm (S1=35-40, S2=41-45, S3=46-50, S4=51-55, S5=56-60). Insert box shows food items correlated ($r^2 > 0.2$) with diet sample points in ordination space (denoted by vectors). Dietary items are abbreviated from taxonomic identities given in Table 2

Figure 4 Two-dimensional NMS ordination for averaged sequential sizes of *L. unicolor* and percentage contribution by volume of food items to the diet of *L. unicolor* in floodplain lagoons of the Macintyre River during the study period (2002-2003). Food items with low volumetric contribution, thus not identifiable in the bars, are not shown. (■) indicates the mean dietary breadth ($\pm$ SE); arrows indicate flooding up to two months before a sampling occasion; S indicates size class, TL in mm (S1=35-40, S2=41-45, S3=46-50, S4=51-55, S5=56-60). Insert box shows food items correlated ($r^2 > 0.2$) with sample points in ordination space (denoted by vectors). Dietary items are abbreviated from taxonomic identities given in Table 2

Figure 5 Two-dimensional NMS ordination for averaged sequential sizes of *N. erebi* and percentage contribution by volume of food items to the diet of *N. erebi* during the study period (2002-2003) in floodplain lagoons of the Macintyre River during the study period (2002-2003). Food items with low volumetric contribution, thus not identifiable in the bars, are not shown. (■) indicates the mean dietary breadth ($\pm$ SE); arrows indicate

642 flooding up to two months before a sampling occasion; TL of all individuals range from
643 40-69 mm. Insert box shows food items correlated ($r^2 > 0.2$) with sample points in
644 ordination space (denoted by vectors). Dietary items are abbreviated from taxonomic
645 identities given in Table 2
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Figure 1

Figure 2

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